Digital restoration of the snout of *Khirtharia inflata* (Raoellidae, Artiodactyla) from the middle Eocene of northwest Himalaya

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Abstract
In this work, we digitally restore the snout of the raoellid *Khirtharia inflata* from the Kalakot area (Rajouri District, Jammu & Kashmir, India). Raoellids are small, semiaquatic ungulates closely related to cetaceans. The specimen is fairly complete and preserves left and right maxillae, left premaxilla, and part of the anterior and jugal dentition. The digital restoration of this quite complete but deformed specimen of *Khirtharia inflata* is a welcome addition to the data available for raoellids and will be used to further the understanding of the origins of cetaceans.

Keywords: Cetacea, incisor, India, raoellid

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Inv nr.	Description
M3#1454	deformed partial skull
M3#1455	half snout reconstruction
M3#1456	complete snout reconstruction

Table 1. List of models of the specimen GU/RJ/157 (*Khirtharia inflata*). Collection: HNB Garhwal University Paleontology Rajouri collection, Srinagar, Uttarakhand, India

INTRODUCTION

Raoellidae are Eocene small-size artiodactyls mostly retrieved from India and Pakistan. Several cladistic analyses place the family as sister taxon to the clade Cetacea (Geisler and Uhen, 2003, 2005; Thewissen et al., 2001, 2007; Orliac and Ducrocq, 2012; Gatesy et al., 2013), notably by the presence of an involucrum on the auditory bulla (Thewissen et al., 2007). The dental and cranial morphology of Raoellidae is widely understood based on the most well-known raoellid taxon, *Indohyus indirae* (Kumar and Sahni, 1985; Thewissen et al., 2020: Orliac and Thewissen, 2021; Patel et al., 2024). Cranial material of another raoellid genus, *Khirtharia*, has been retrieved from the Aiji-2 locality, Rajouri District, Jammu & Kashmir (Waqas and Rana, 2020). Among this material, the specimen GU/RJ/157 consists of a fairly complete snout preserving left and right maxillae, left premaxilla and part of the anterior and jugal dentition (Waqas et al. in press). The snout has undergone brittle deformation, i.e. fragmentation, and some plastic deformation; however, the specimen is amenable to restoration. In this work, we desassemble and digitally restore GU/RJ/157 (see Table 1) in order to better visualize the morphology of the snout of this Raoellidae.

METHODS

A first mechanical preparation of the specimen GU/RJ/157 was performed at the Garhwal University, Palaeontology laboratory and final preparation was performed at the Royal Belgian Institute of Natural Sciences (RBINS), Brussels. CT data was acquired at the RBINS CT scanner facility using an EasyTom 150 µ-CT scanner with a voxel size of 23.0 µm.

Preservation and completeness of GU/RJ/157

The specimen consists of a snout preserving the left premaxilla, left and right maxillae, fragments of the nasal and palatal bones, and part of the anterior and jugal dentition (Fig. 1). Despite of the completeness of the specimen, there is clear evidence of brittle deformation and some plastic deformation. The premaxilla is only preserved on the left side, broken off from the maxilla along the alveolus of the canine. The left maxilla bone is broken into three main fragments, with several bone splinters on the palatal side. The right maxilla is also fragmented and shows, in addition to breakages, strong plastic deformations (Fig. 1, 2D). The right side is offset anteriorly with respect to the left side judging from the relative position of the canine in ventral view (Fig. 2C). So dorsoventral compression and slight anterior shear of the right side are the main alterations to the specimens. If some parts of the bone remains are obviously missing, a first glance at the specimens indicate that most of the left and right nasal and palatal region are preserved, though broken into dozens of fragments. In many places, the breaks are clear and virtual restoration of the specimen appears a good option to access to important morphological features such as the morphology of the premaxilla, the shape and extension of the nasal and anterior palatine foramen, the width of the palate or the presence of diastemata. However, in addition to breakage,

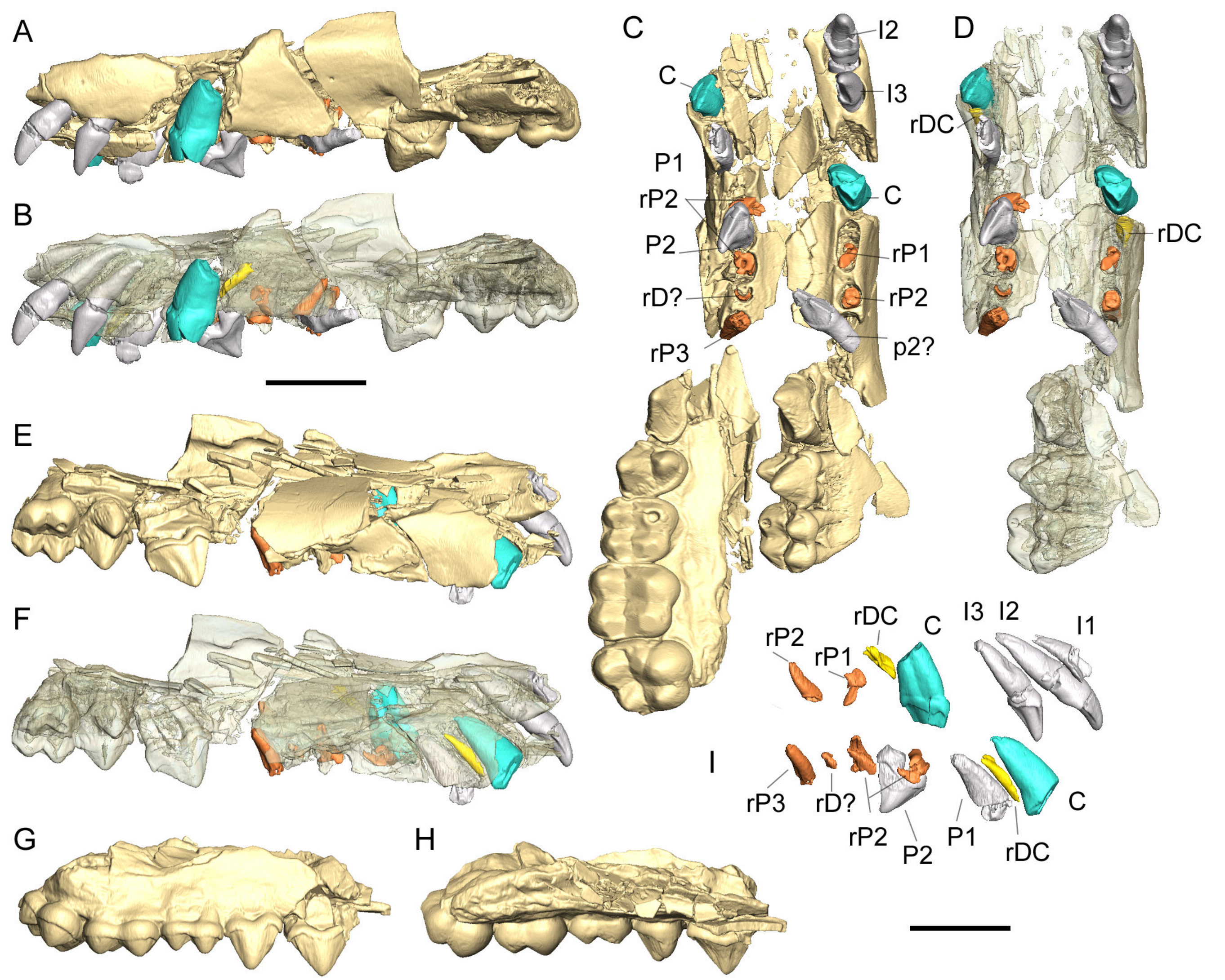

Figure 1. Illustration of the 3D model of GU/RJ/157 showing the preserved dentition in A-B) left lateral, C-D) ventral, E-F) right lateral, G-H) right and left lateral, I) right oblique (without bone) views; Abbreviations: r, root; D, decidual. Scale bar = 1cm.

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the specimen has also been deformed by tectonic phases of the Himalayan region, altering the original shape of the bones at different degree depending of the region. Our aim here is to digitally restore the specimen as much as possible by reassembling the fragments; we do not attempt to correct any plastic deformations for lack of proper referential. Regarding the dentition, GU/RJ/157 preserves on the left side, the root of I1 and the complete I2 and I3 in situ. It is worthy to note that the alveoli are wider than the actual diameter of the incisor roots. An isolated incisor is also present, apposed to the right anterior tip of the specimen. It is here tentatively interpreted as the left i3 based on the morphological difference with in situ upper incisors (i.e., lack of lingual cingulum, crown width, stylids and wide fossae). The left canine is also preserved in its alveolus, though cut in two by a wide breakage. A fragment of what is probably a lower p2 is apposed close to P2 alveolus; it probably belongs to the same individual (Fig. 1C). The P3-M1 are preserved in situ on the left side. The roots of P1 and P2 are partially preserved. On the right side, the premaxilla is missing; the canine and P1 are preserved in situ, but their crowns are broken off. The root of P1 indicates that it is a large tooth, almost as long as the canine. It is single rooted, but a groove underlining the distinction between anterior and posterior root is present, on the lingual aspect only. The right P2 is preserved but was set off its alveolus; its roots are badly deformed. A large fragment of right maxilla bearing P3-M3 is preserved, broken off from the rest of the specimen. It is worthy to note that some of the roots of the lacteal dentition are preserved and stayed in situ despite the eruption of the permanent dentition (Fig. 1B, D, F, I). It is the case for the deciduous canines and most probably for the DP2, leading to the presence of an additional root on the right side of the snout (Fig. 1C, I).

Restoration of the specimen GU/RJ/157

The restoration of the specimen involved the following two steps: 1) segmentation of the specimen both automatically and manually to generate distinct 3D meshes for the different bone fragments and teeth, 2) reassembling of the meshes to form a digitally restored snout. The segmentation process was performed using both the automatic threshold and the pencil tool of Avizo Lite 9.3.0 ® (Thermo Fisher Scientific-FEI). The bone fragments and the teeth were globally first selected using the automatic threshold. The result of segmentation was a 3D model of the entire specimen that included both contiguous and isolated fragments. Isolated fragments of this first 3D model were automatically separated into individual 3D models using the software MorphoDig (connectivity tool, Lebrun 2018; Fig. 3). Back in Avizo, the contiguous bone fragments and the teeth were separated manually using the pencil tool and then saved as separate 3D meshes. It was notably the case for most of the fragment of the nasal bone. The automatically and manually separated bone fragments and teeth where then all reassembled with MorphoDig (Lebrun 2018). The smallest isolated bone fragments were removed manually in order to clean the model

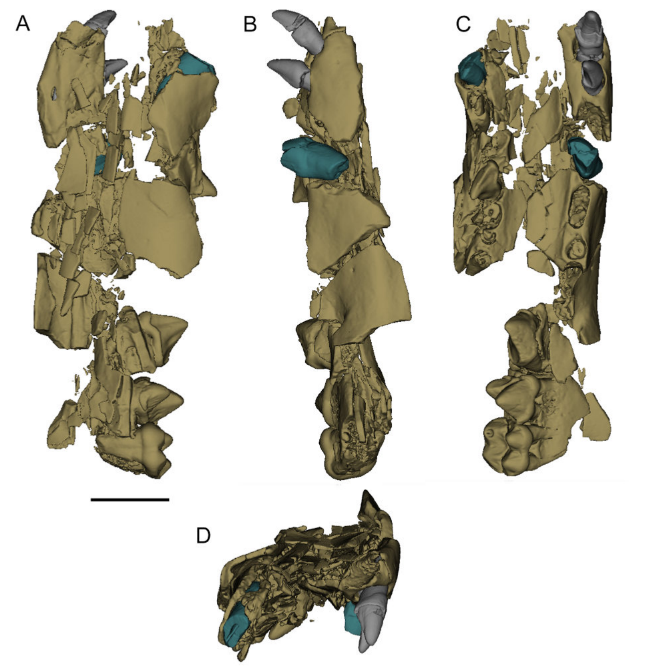

Figure 2. Illustration of the 3D model of GU/RJ/157 before restoration showing the breakage and main deformations, especially the shearing between right and left sides taking the canine as a hallmark (in blue) in A) dorsal, B) lateral, C) ventral, D) anterior views; the canines are highlighted in blue, incisors in grey. Scale bar = 1cm.

and reduce its weight. The main goal of the restoration was to reassemble the bone fragments of the left side of the snout into their original in vivo positions i.e., brittle retrodeformation (Fig. 4). The right side of the snout exhibited more deformation than the left and was therefore not included in the restoration, except for the crown of right p2 and the large posterior fragment of the right maxilla. If this restoration process allows to get back together the broken pieces, some parts are still deformed: the shape of the maxilla for example is slightly compressed dorsoventrally, concurrently, the nasal is not in its perfect original position so that the suture between right and left nasals is not on the sagittal plane. We decided not to retro-deform the specimen because each bone responded to deformation differently, and the task would have been very complicated, and maybe not satisfactory. Yet, the reassembled model gives a satisfactory overview of what the specimen must have been like before breakage. Putting back together the anterior-most part of the snout was pretty straightforward and the bones surrounding the anterior palatine foramen could be repositioned without difficulty (Fig. 4C-D). Reassembly of the different parts of the left maxilla bone and assessing the relative disposition of the maxilla and premaxilla was also rather simple given the good correspondence of the broken edges (Fig. 4E, F). The restoration of the nasal was made separately, after reassembling the various elements. Both the left and right nasal bones were restored in order to provide additional support to the choices made for the whole restoration (Fig. 5). Indeed, most of the fragments were displaced and there was no closely related taxon to guide the restoration; gathering the information on both sides allows for

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relying on symmetry and strengthen anatomical plausibility. The right nasal was put back in its putative original position using the correspondence between its external surface and the internal surface of the maxilla bone. The good correspondence between the restorations of the left and right nasals indicate that they are complete and satisfactorily located in the final restoration (Fig. 5B). A more complete restoration of the specimen (Fig. 6) was achieved by applying a mirror modifier to the restored left half snout. The duplicated mirrored right mesh was then assembled to the left part along the sagittal suture of the maxilla bone. The large posterior fragment of right maxilla was also added to the model in order to get the complete tooth row, with the exception of P1 which is lacking. This model is an initial attempt to reconstruct the raoellid snout, but there is still plenty of room for improvement. It is a compromise between restoring the integrity of the ventral surface and limiting the inconsistency of the dorsal aspect due to deformation and remaining breakage of the bones. Indeed, notably due to the deformation of the anterior part of the maxilla and to the collapse of the floor of the palate (depriving access to the palate width), it is impossible to get a clean reconstruction of the dorsal surface of the snout, which is too large, and obviously not in the original shape. Despite this, we can still glean key morphological characteristics from the digital restoration of GU/RJ/157.

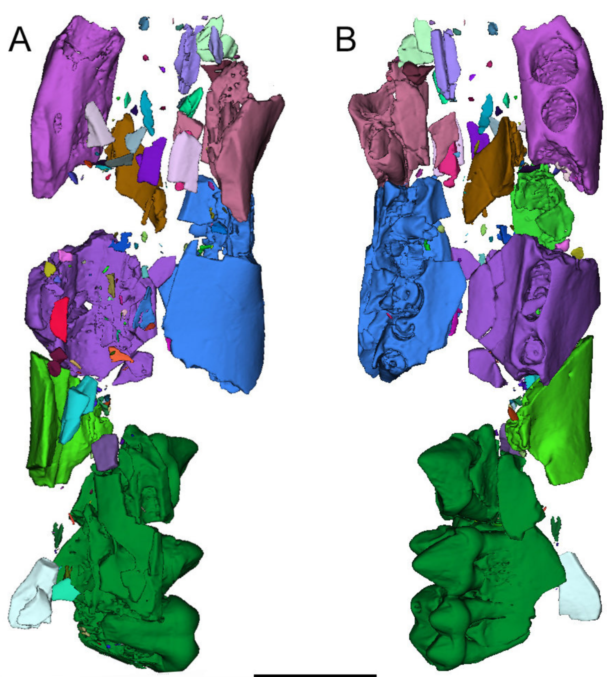

Figure 3. Illustration of the initial model in A) dorsal and B) ventral views showing the various non-contiguous parts that could be automatically separated as individual 3D objects using MorphoDig (Lebrun 2018, connectivity tool, decomposition, random colors); the anterior dentition and contiguous bone fragments were removed manually through segmentation process with the software Avizo Lite 9.3.0 ® (Thermo Fisher Scientific). Scale bar = 1cm.

Morphological observations resulting from the restoration of the specimen GU/RJ/157

The process described here only consists in a restoration of the specimen, the parts that were broken apart are set back in connection, but the specimen still presents some deformations that most probably have slightly affected its height even on the left side. Similarly, the inclination of the anterior part of the snout, the premaxilla, relative to the maxilla is presented here as the most plausible; however, it does not rely on a direct morphological continuity because of breakage anterior to P3 on both sides of the specimen. The restoration nevertheless provides good insight into the snout morphology of *Khirtharia inflata* and is sufficient for taking measurements. Based on the virtually reconstructed model, the width of the palate equals 11 mm at the level of the canine, 11 mm at P2 and 15 mm at M1. It is also possible to have a quite good idea of the dimensions of the nasal bone, even if they are also most obviously slightly underestimated. It was dorsally around 6 mm in width at the level of the canine. The dorsal edge of the maxilla slightly overlaps the dorsal aspect of the nasal. The restoration of the nasal indicates that it extended anteriorly to the level of I3 (Fig. 4B). The posterior edge of the nasal opening reaches at least the level of the anterior margin of the canine. Yet its exact shape is impossible to assess with certainty, as part of its anterior tip is probably missing. On the ventral aspect of the specimen, the shape and dimensions of the incisive foramen is here reconstructed with confidence. It appears as a large aperture bordered by the palate posteromedially and by the premaxilla anterolaterally. The suture between the premaxilla and the maxilla is discernable and extends medio-anteriorly to the lateral margin of the incisive foramen. The specimen also brings information regarding the implantation of the anterior dentition. The elongated premaxilla of GU/RJ/157 preserves I1-3 in situ on the left side, yet the crown of I1 is broken. The incisors are curved and pointed (i.e., "caniniform") and distribute on a widely opened arch with I3-2 aligned with the canine. The I1 alveolus indicates that both I1 most probably did not contact each other. The disposition, orientation, and morphology of the incisors is raptorial and most probably adapted for seizing preys. The lateral wall of the maxilla is high and a large infraorbital foramen is located over P3 (Fig. 4F). The reconstruction of the teeth and of the maxilla fragments highlighted the presence of some of the roots of the decidual teeth, at the level of the canines and of the right P2. If this is not an isolated case among raoellid specimens, it might suggest that the replacement of the lacteal dentition was a quite brutal and rapid process in raoellids.

DISCUSSION

The virtual restoration of the specimen GU/RJ/157 provides a good estimate for the snout morphology of the raoellid *Khirtharia*. The snout morphology closely resembles that of *Indohyus indirae*, the other raoellid genus for which the snout is partially documented, illustrated by Thewissen et al. (2020). This later specimen was quite deformed and restoration of GU/RJ/157

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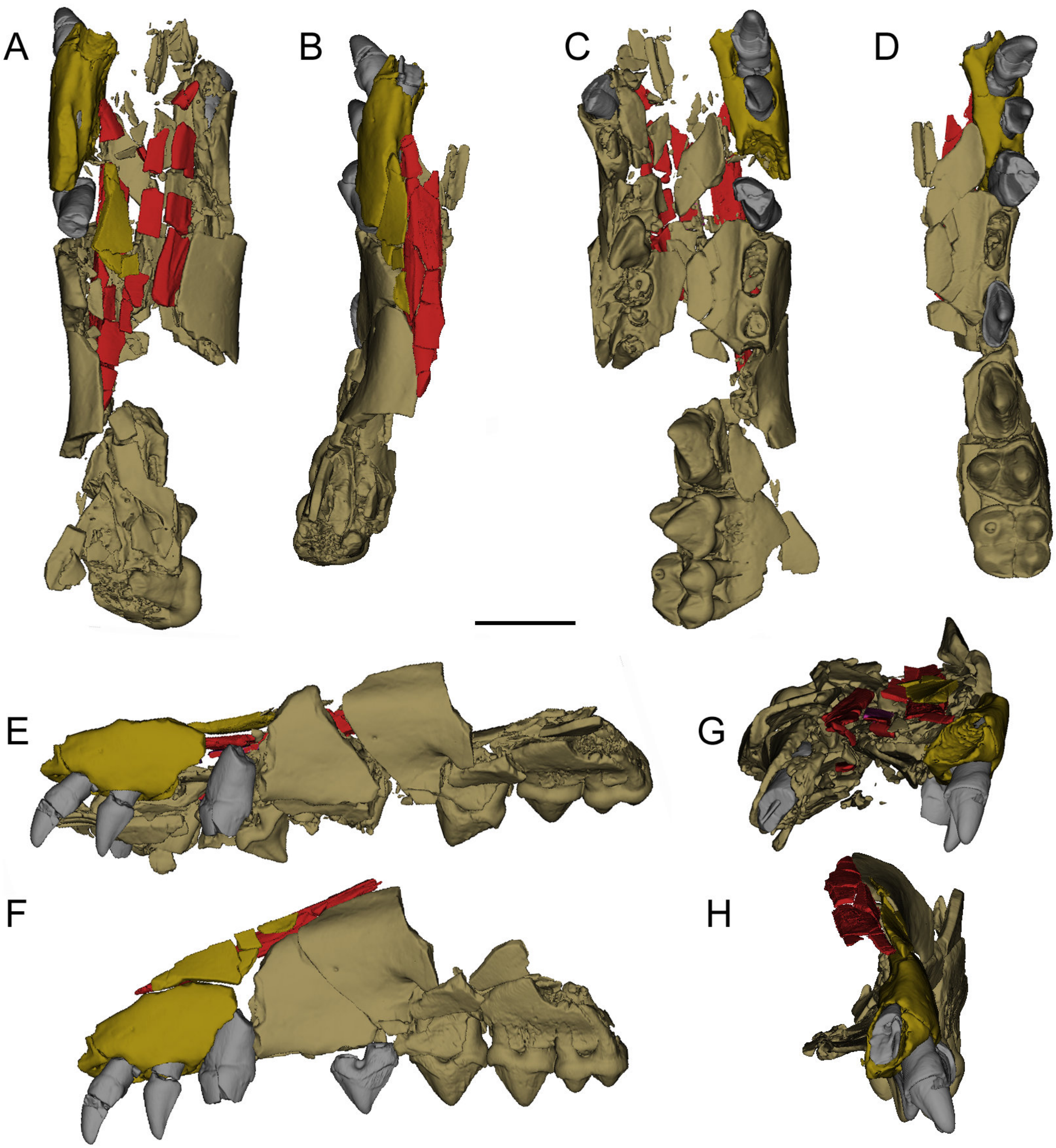

Figure 4. Restoration of the left side of the specimen GU/RJ/157; A, C, E, G, dorsal, ventral, left lateral and anterior views respectively showing the broken specimen; B, D, F, H, dorsal, ventral, left lateral and anterior views respectively showing the restored specimen. Premaxilla fragment appear in yellow, nasal fragments in red. The P2 was mirrored from the right side of the specimen where it is preserved. Scale bar = 1cm.

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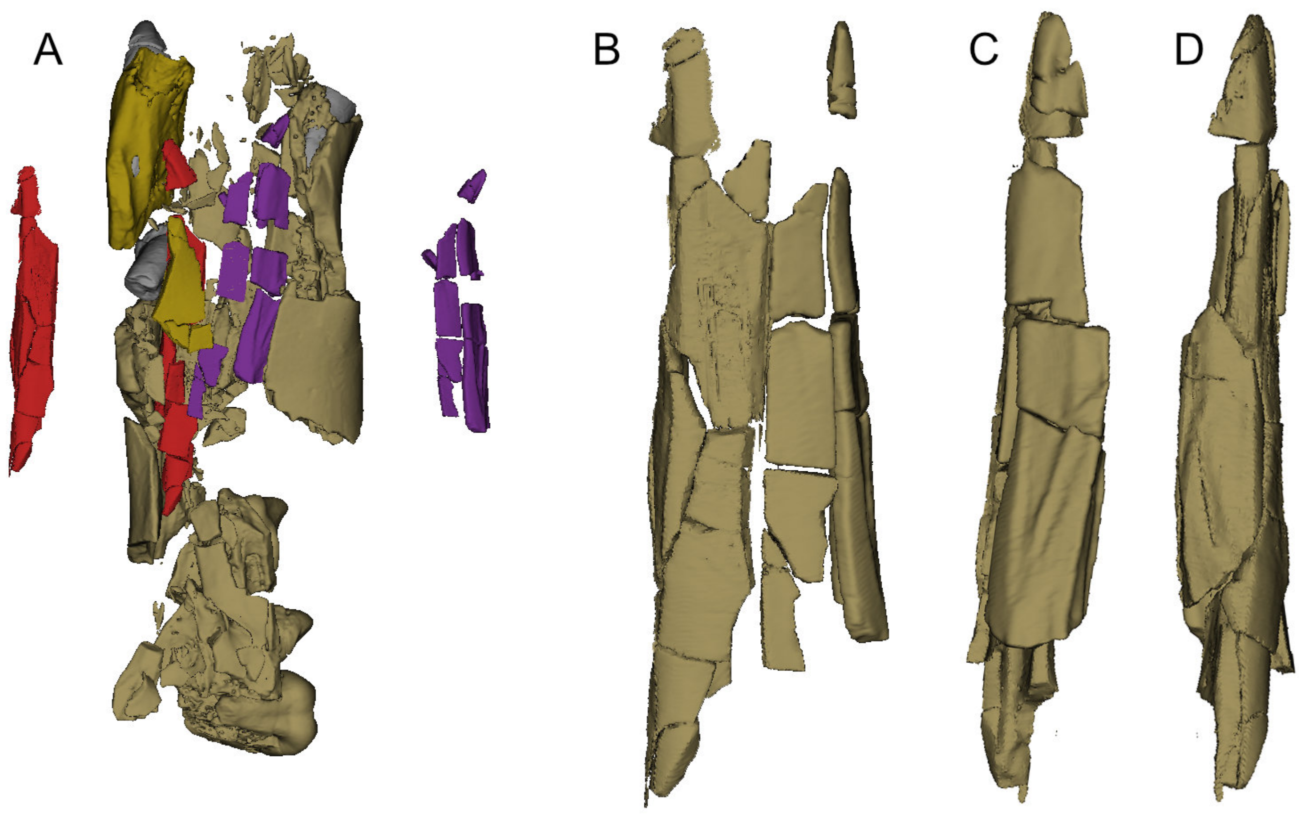

Figure 5. Restoration process for the nasal bone. A) Original specimen showing the in situ fragments of the left (in red) and right (in purple) nasal bones and the reconstruction of both on each side; B) virtual restoration of the joined left and right nasals; C-D) lateral views of the right and left nasals respectively. Scale bars = 1 cm.

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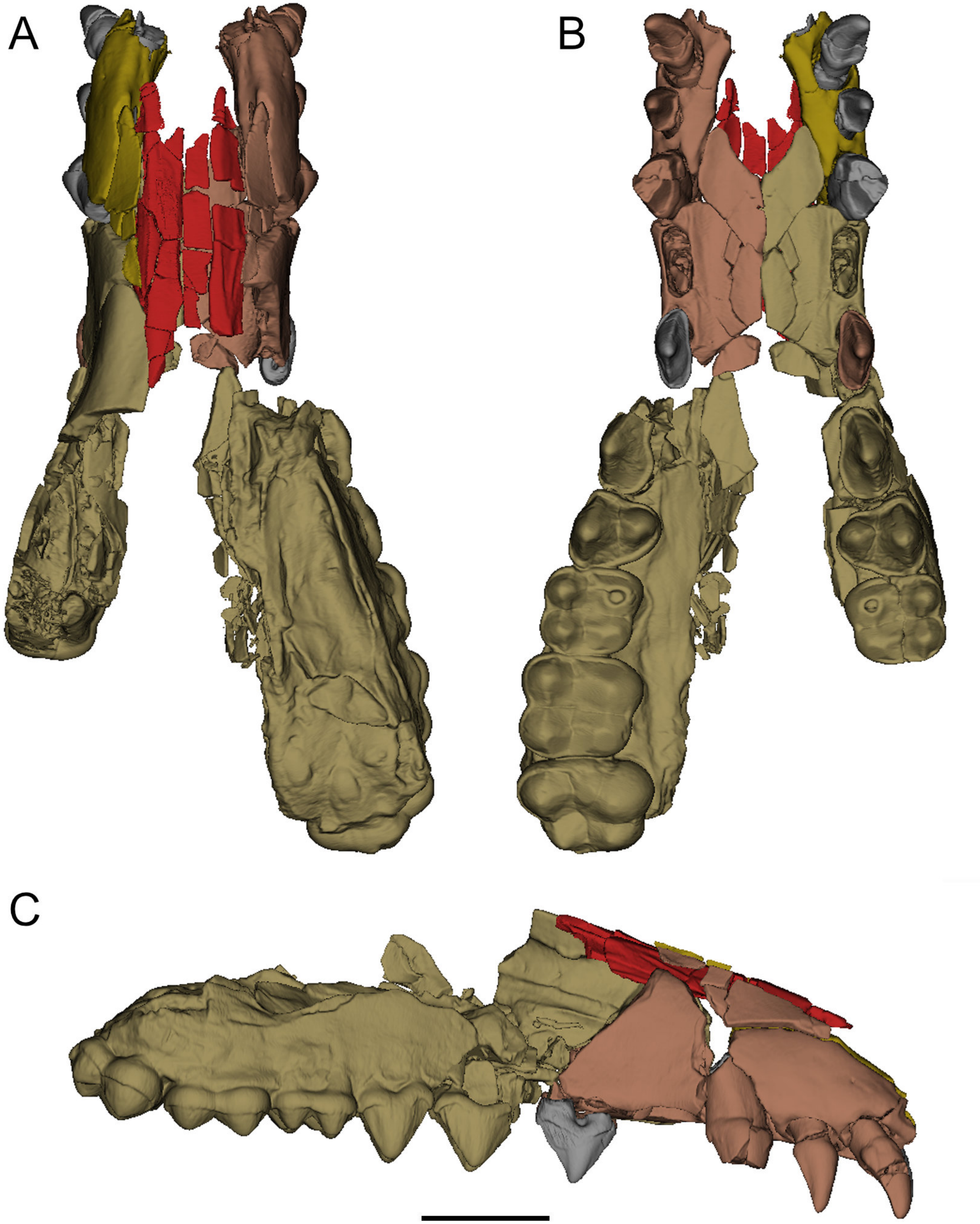

Figure 6. Tentative restoration of a “complete snout” using mirror meshes of the left part (in pink) and the large fragment of right maxilla bone. Scale bar = 1 cm.

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gives access to a better idea of the raoellid snout profile. Reconstruction of the nasal bone indicates that the nares opening was probably similar to small Eocene terrestrial artiodactyls like *Diacodexis* (Russell et al., 1983:figs.2, 5), and located at the level of I3. The elongation of the premaxilla anterior to the canine is limited and there is no clear increase of the distance between the anterior margin of the nasal and the anterior extremity of the snout, setting back the nares opening. The most striking feature of the *Khirtharia* snout is the raptorial character of the anterior dentition, foreshadowing the early cetacean condition and questioning further the diet of this peculiar taxon. The presence of the roots of the deciduous dentition in *Khirtharia* along with already-erupted permanent dentition has potentially widespread implications for a violent and rapid tooth replacement process in raoellids and should be studied further.

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