Unexpected Convergent Evolution of Nasal Domes between Pleistocene Bovids and Cretaceous Hadrosaur Dinosaurs

Highlights

- Pleistocene Rusingoryx atopocranion are first known mammals with hollow nasal crests
- Rusingoryx ontogeny and evolution are broadly similar to lambeosaurine hadrosaurs
- The best-supported nasal crest function is phonic modification
- Combination of convergent ontogeny, evolution, and function may explain crest rarity

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In Brief

O’Brien et al. analyze first known mammalian osseous nasal crests from a new Rusingoryx assemblage. Analogous to those of lambeosaurine hadrosaurs, these crests may facilitate vocalization. This morphology is an outstanding example of convergent evolution between dinosaurs and bovids, driven by ontogenetic, evolutionary, and environmental pressures.
Unexpected Convergent Evolution of Nasal Domes between Pleistocene Bovids and Cretaceous Hadrosaur Dinosaurs

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SUMMARY

The fossil record provides tangible, historical evidence for the mode and operation of evolution across deep time. Striking patterns of convergence are some of the strongest examples of these operations, whereby, over time, similar environmental and/or behavioral pressures precipitate similarity in form and function between disparately related taxa. Here we present fossil evidence for an unexpected convergence between gregarious plant-eating mammals and dinosaurs. Recent excavations of Late Pleistocene deposits on Rusinga Island, Kenya, have uncovered a catastrophic assemblage of the wildebeest-like bovid Rusingoryx atopocranion. Previously known from fragmentary material, these new specimens reveal large, hollow, osseous nasal crests: a craniofacial novelty for mammoths and hadrosaur dinosaurs. Using adult and juvenile material from this assemblage, as well as computed tomographic imaging, we investigate this convergence from morphological, developmental, functional, and paleoenvironmental perspectives. Our detailed analyses reveal broad parallels between R. atopocranion and basal Lambeosaurinae, suggesting that osseous nasal crests may require a highly specific combination of ontogeny, evolution, and environmental pressures in order to develop.

RESULTS AND DISCUSSION

Abbreviated Description

Rusingoryx atopocranion was first described from a partial skull (National Museum of Kenya [KNM]-RU-10553A) collected from the Wasiriya Beds at the Wakondo locality of Rusinga Island, Kenya (Figure 1; [1]). The holotype consists of basicranial, occipital, and frontal regions, as well as a right horncore [1]; however, the facial region is not preserved. Due to 3 cm of upwardly angled nasal bones, it was initially postulated that Rusingoryx may have had a proboscis or an enlarged, domed nasal region [1]. Due in part to the incompleteness of the type specimen, this reconstruction was dismissed and the taxonomic validity of Rusingoryx was questioned [2] until a more recent reexamination and expanded sample of horn cores and dental material [3]. Here we present six new Rusingoryx cranial specimens excavated en masse from a channel deposit within the type locality [4]. These new specimens reveal the presence of an extreme, osseous nasal dome and associated anatomical features unparalleled among extant vertebrates. Because there are numerous specimens across a spectrum of ages, from old to young, this dataset facilitates ontogenetic, evolutionary, and functional analyses of this bizarre Late Pleistocene bovid morphology. Our analyses focus on KNM-RU-52572, a complete adult skull that includes all craniofacial bones, maxillary dentition, and the right horncore. For within-species comparison, we refer to skulls of an ~12- to 16-month-old juvenile (KNM-RU-59434) from the Wakondo assemblage and a putative female referable to the genus Rusingoryx (KNM-HA-54933) with a diminutive nasal crest collected from the nearby Pleistocene (~285,000–40,000 years ago) Luanda West locality on the Homa Peninsula. Interspecific comparisons were also made across extinct and extant Alcelaphinae, with intracranial morphology also studied for Megalotragus isaaci (paratype: KNM-ER-2000).

KNM-RU-52572 is post-depositionally compressed in the sagittal plane. The caudal portion of the cranium matches the holotype, and the dentition follows recent descriptions of fragmentary material [3]. In mature individuals, the frontal, nasal, and premaxillary elements form a prominent, osseous nasal dome. Palatal morphology, best exemplified in comparative material from the Homa Peninsula (KNM-HA-54933;
Figures 1A–1D and S1), is likewise exaggerated. The hard palate projects deeply caudal to the lateral palatal indentations and bears deep grooves corresponding to attachment sites for palatal and supralaryngeal musculature (Figure S1). The horizontal palatine bone is completely closed and does not allow for the passage of the internal nares. Instead, the airway passes over inflated maxillopalatine paranasal sinuses, resulting in a nasal passage that enters the pharynx from the dorsal aspect (Figure 1; Movie S1). For a detailed description of R. atopocranion cranial morphology, see Supplemental Experimental Procedures.

Internal morphology reveals further peculiarities. The floor of the nasal tract significantly departs from the hard palate, ascending parallel to the outer surface of the nasal dome and serving as a roof to the extraordinarily voluminous maxillopalatine paranasal sinuses. These sinuses comprise the largest proportion of cranial volume and extend to the midline, where they are separated by a median septum (Figures 1C and 1G). Based on careful examination of computed tomography (CT) scans, the paranasal sinuses and the airway are not connected by ostia larger than 2 mm, rendering them dead airspace (Movie S1). The nasal tract is straight through the rostral portion of the cranium but deviates ventrally in the frontal region, forming an “S”-shaped curve. This morphology has not been observed previously in mammalian taxa. The closest analog is, instead, the nasal tract of basal lambeosaurine hadrosaur dinosaurs [4–10].

Figures 1A–1D and S1).

(A–D) KNM-HA-54933, putative Rusingoryx female from Homa Peninsula. (A) Skull, right lateral view. (B) Digital rendering, with reconstruction of the supralaryngeal vocal tract (SVT) in yellow. (C and D) Coronal and sagittal CT sections demonstrating enlarged maxillary sinuses and the course of the nasal tract. (E–H) KNM-RU-52571, adult R. atopocranion from Wakondo. (E) Skull, right lateral view. (F) The SVT ascends parallel to the outer contour of the skull, departing from the hard palate near the caudal border of the premaxilla. After reaching its apex, the SVT descends toward the internal nares in an “S”-shaped curve. (G and H) Coronal and sagittal CT sections. (I–L) KNM-RU-59434, juvenile R. atopocranion excavated from Wakondo. (I) Skull and mandible in right lateral view. (J–L) Digital reconstruction, coronal, and sagittal CT sections (respectively) of the SVT demonstrate ontogenetic differences between adult (KNM-RU-52571) and juvenile R. atopocranion. The nasal portion of the SVT is deeper in the juvenile, and the caudal portion is relatively more voluminous. Scale bars, 4 cm. Abbreviations: aPSep, anterior palatine sinus septum; ms, maxillary sinus; MSep, maxillary sinus septum; NFL, nasal floor; NSep, nasal septum; pPSep, posterior palatine sinus septum (anterior wall of airway); ps, palatine sinus. See also Figures S1 and S2.
In addition to gross morphology, the following investigations of ontogeny, evolution, and function of the *Rusingoryx* nasal dome also reveal broad-scale similarities between Alcelaphinae and Lambeosaurinae.

**Juvenile Morphology**

In addition to mature individuals, the assemblage contains the complete skull of a juvenile (KNM-RU-59434), ontogenetic age approximately 12–16 months (Supplemental Experimental Procedures). This skull bears an incipient crest with a slight degree of angulation rostral to the frontonasal suture. The nasal bones are slightly elevated, and the premaxilla contacts the maxilla and nasals on its caudal border. This suggests that the crest shifts caudally throughout maturation, such that in adults it initiates posterior to the caudal margin of the orbit (Figure 2). The maxilla heightens throughout development, ultimately forming the lateral wall of the crest. Internally, the angle between the floor of the nasal cavity and hard palate becomes more obtuse, and the portion of the chamber enclosing maxilloturbinates in the juvenile is relatively larger than that of adults. In these respects, the suite of apparent ontogenetic changes in *Rusingoryx* show remarkable similarities to lambeosaurine hadrosaur crest development (Figure 2). In both groups, the crest enlarges by (1) increased angulation of the analogous prefrontal and frontal bones (hadrosaur and bovid, respectively; herein abbreviated as the (pre)frontal elements) (2), simultaneous elongation and caudal migration of the rostral facial bones, and (3) distension of lateral facial elements.

**Evolution**

To evaluate the evolutionary trajectory of nasal dome acquisition, we incorporated new *Rusingoryx* and referred Homa Peninsula specimens into a phylogenetic analysis of extinct and extant alcelaphines (Figure S2; Supplemental Experimental Procedures). Subsequent character-mapping nasal morphology illuminates the stepwise morphological acquisition of the nasal dome. The most primitive nasal-domed alcelaphine in our phylogeny, *Megalotragus isaaci*, possesses a diminutive nasal dome with internal nares that enter the cranium anteriorly (Figure 3). Next in succession, *M. kattwinkeli* demonstrates that crest elevation is preceded by a dorsal migration of the nasal passages (Figures 2 and 3). Subsequent elaboration of crest morphology is predominately accomplished by inflation of lateral facial bones and sinuses. As with ontogeny, these morphological changes mirror the evolutionary transition from primitive to derived lambeosaurine hadrosaurs, wherein dorsal translation of the internal nares occurs prior to the heightening and elongation of the rostral and lateral facial bones (Figure 3).

**Function**

Because the nasal dome and tortuous nasal tract are novel structures within Mammalia, direct functional comparisons with living taxa cannot be made. Plausible functional interpretations were therefore based on morphological inferences and mathematical models. As *Rusingoryx* is an open-grassland species, we prioritized thermoregulation, visual display, and vocalization as functions particularly relevant to...
increased fitness in climatologically arid and behaviorally gregarious contexts. These functions have also been hypothesized for the nasal domes of lambeosaurine hadrosaurs [9, 10, 12], enabling another means of comparison between these groups.

We first looked for evidence that the *Rusingoryx* nasal dome houses exceptional variants of osseous structures related to thermoregulation. In mammals, cranial thermoregulation is achieved via evaporative cooling across the mucosae of the maxilloturbinates [13]. Elaboration of the maxilloturbinates is positively correlated with an increased demand to conserve respiratory water [13, 14], such that filling its enlarged nasal chamber with a higher surface area of maxilloturbinates could be beneficial for the thermal and hydrological budgets of *Rusingoryx*. However, because the elevated nasal cavity floor restricts the volume of the dome available for turbinates (Figure 1; Movie S1), the intracranial morphology of *Rusingoryx* is not consistent with a hypothesis of enhanced turbinate function. In addition to turbinates, circulating air through the large maxillary sinuses may also dissipate heat; however, there is little evidence for the requisite airflow between the sinuses and nasal passages that would facilitate evaporative cooling [15]. Like all mammals, the maxilloturbinates of *R. atopocranion* would have assisted with thermoregulation, but there is little conclusive evidence that the elaborate nasal dome enhanced these capacities beyond those of other bovids.

We next evaluated the potential for visual display, which among bovids is often realized in the form of male-male honest or combative signaling ornaments, like horns. Given the propensity for head-striking behavior among artiodactyls [16, 17], the dome could be used for combative display. Nasal dome morphology, however, is less congruent with such a hypothesis: the narrow depth of the skull bones and voluminous, non-buttressed cranial cavities (Figure 1; Figures 1 and S1), it is unreasonable to implicate the nasal dome as having an effective role in aggressive male-male combat.

Competition among males, as well as intra- and interspecific signaling, can also be accomplished vocally, and there are numerous morphological details that substantiate the hypothesis that the nasal dome may play a role in long-distance vocalization and/or sonic display. Externally, the hard palate possesses deep, bilateral grooves for attachment of the muscles that shorten the pharynx and elevate the soft palate and larynx.

**Figure 3. Comparative Evolution of Nasal Crests between Lambeosaurinae and Alcelaphinae**

Lambeosaurinae are in black text and Alcelaphinae in purple text. Trait acquisition of the nasal dome in both groups follows grossly similar patterns. In the earliest members of both groups, the nasal passages enter the cranium horizontally, and the (pre)frontal elements reflect the primitive condition. Frontal elements then begin to telescope as the nasal passages migrate to enter the pharynx dorsally. This sequence initiates crest formation. Lateral facial elements, including the premaxilla of hadrosaurs and the maxilla of alcelaphines, are then recruited to form the lateral walls of the nasal vestibule. Crest elaboration is at its most derived when the caudal margin of the crest rotates, forming an acute angle with the skull roof. Internally, the nasal airway must contour to follow the roof of the nasal passage. Black elements represent structures that are not preserved. Parasaurolophini presented for consistency with source; redrawn from [8]. See also Figure S3.
calculated for lambeosaurine hadrosaurs Rusingoryx Perhaps most surprising is the almost complete overlap between low and potentially below the range detectable by predators. Furthermore, the large maxillary and palatal sinuses may have amplified vocal output by acting as resonating chambers.

Table 1. Reconstructed Resonant Frequencies

<table>
<thead>
<tr>
<th>Taxon Specimen</th>
<th>SVT Length</th>
<th>n = 1</th>
<th>n = 2</th>
<th>n = 3</th>
<th>Note Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rusingoryx atopocranion KNM-RU-52572 0.74026 m</td>
<td>248.872 Hz</td>
<td>497.744 Hz</td>
<td>746.616 Hz</td>
<td>B3–F4</td>
<td></td>
</tr>
<tr>
<td>cf. Rusingoryx female KNM-HA-54933 0.42371 m</td>
<td>390.597 Hz</td>
<td>781.194 Hz</td>
<td>1,171.791 Hz</td>
<td>G4–D5</td>
<td></td>
</tr>
<tr>
<td>Megalotragus isaaci KNM-ER-2000 0.64147 m</td>
<td>258.001 Hz</td>
<td>516.002 Hz</td>
<td>774.003 Hz</td>
<td>C3–G5</td>
<td></td>
</tr>
</tbody>
</table>

Values are based on the length of the osseous supralaryngeal vocal tract (SVT) and were calculated using equations described in Supplemental Experimental Procedures.

Digital renderings of the osseous supralaryngeal vocal tract (SVT; Figure 1) enabled quantitative assessment of the potential for phonic modification using simple bioacoustic models [9, 10, 20, 23]. In mammals, the pharynx and nasal passages, together with the SVT, modify the sound waves produced in the larynx by vibrating preferentially at certain resonant frequencies that are inversely proportional to vocal tract length [18–25]. Acoustic models for harmonic wave production [9, 10, 24] suggest that the Rusingoryx nasal dome could be capable of propagating low-pitched sounds, between 248 and 746 Hz (Table 1; Supplemental Experimental Procedures). Because the soft-tissue vocal tract length cannot be reconstructed, these estimated frequencies are conservatively high. An addition of only 20 cm to the vocal tract length would result in vocalizations below 200 Hz, closer to the range of infrasound. Comparatively, the vocal ranges of many other mammals initiate around ~1,100 Hz [23], suggesting that Rusingoryx vocalizations are low and potentially below the range detectable by predators. Perhaps most surprising is the almost complete overlap between Rusingoryx resonant frequency reconstructions and those calculated for lambeosaurine hadrosaurs [9, 10].

Environmentally, vocalization is a practical function for the crest of Rusingoryx. In animals that form large or diffuse aggregations, efficient communication over long distances, particularly through infrasonic vocalizations, may aid in predator avoidance and inaspecific signaling [26]. Within contemporary Alcelaphinæ, wildebeests (Connochaetes spp.) and hartebeest (Alcelaphus buselaphus) are found in large herds across semi-arid, short-grass savannas of Sub-Saharan Africa. Social behavior is integral in alcelaphines to the extent that elaborate horns, loud vocalizations, and conspicuous coloration in adults suggest that selection may favor species-specific social signals over predator selection against conspicuousness [27]. Nasal vocalizations of Rusingoryx may similarly fall under this evolutionary pretext. Paleoenvironmental evidence from the Wasiriya Beds [3, 11, 28, 29] indicates widespread semi-arid grasslands, and a markedly high degree of hypsodonty in Rusingoryx molars implies a preference for such habitats [3]. Dry environments are ideal for low-frequency vocalizations, as these sound waves can travel over 10 km in such environments [26]. Potential selective pressures may also involve mitigation of the trade-offs between intraspecific communication and predator avoidance because very low-frequency vocalizations may be outside of the potential hearing range of many East African carnivores. It has been hypothesized that similar habitat pressures may have influenced vocal potential in lambeosaurine hadrosaurs [9], with low-frequency vocalizations allowing these gregarious animals to communicate intraspecifically in open and closed habitats. Prior to this discovery, completely ossified nasal crests have only been observed in Archosauria. The large nasal dome of Rusingoryx presents a new, mammalian context for studying these elaborate structures and sheds light on the gross morphological and developmental changes that predicate elevation of the nasal skeleton. In two distantly related vertebrate groups, lambeosaurine hadrosaurs and alcelaphine bovids, crest formation follows homoplastic increases in maxillary height and dorsal migration of the internal nares during both ontogeny and evolution. In both groups, the crest is interpreted to produce vocalizations across the analogous life history contexts of herd forming and herbivory. Although similar behaviors are prevalent throughout modern vertebrates, they are accomplished largely through soft tissue structures. Just as telescoping of the nasal bones and reducing the anterior facial skeleton is common to vertebrates that have developed fleshy trunks, the comparable sequences of evolutionary and ontogenetic changes observed for hollow dome formation (in conjunction with similar selective pressures) suggests that there are potentially few sequences of stepwise transformations that result in the formation of large, hollow, osseous nasal crests. Expanding comparative studies to additional taxa may begin to explain the rarity of such skull morphology in other vertebrates.

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures, one table, Supplemental Data, Supplemental Experimental Procedures, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.12.050.

AUTHOR CONTRIBUTIONS


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