Linking form to function: a scoping review of the evolution of paranasal sinuses in mammals

Landon E. Ebbert[1], Nitish Kumar[2], Mary K. Ebbert[3], Tyson Pace[1], Pedro Lança Gomes[2], Lisa A. Marks[4], Devyani Lal[2]

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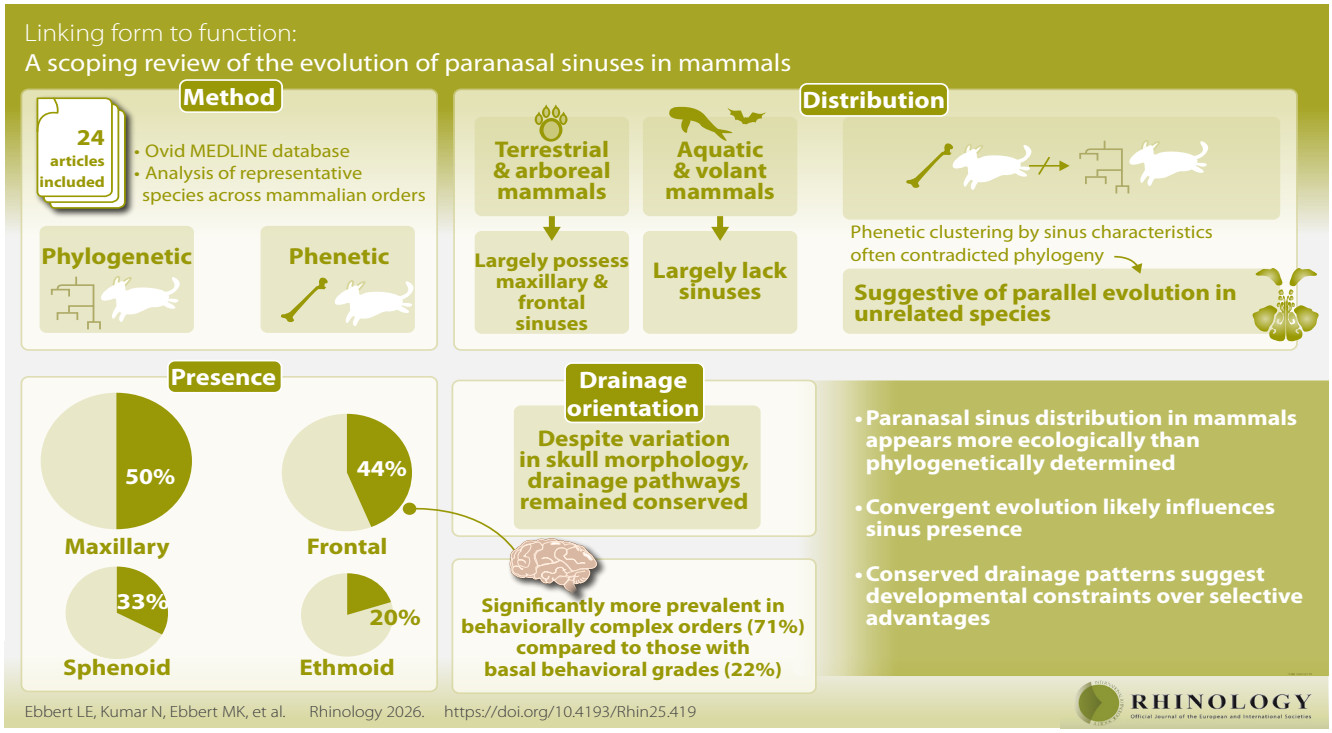

Abstract

Background: The evolutionary origin and function of paranasal sinuses remain unclear. We investigated their presence, distribution, and drainage orientation across mammalian orders, to better understand their evolutionary development and roles.

Methodology: A scoping review of anatomical, radiological, and descriptive literature was conducted in Ovid MEDLINE database (1946-2024). Data on sinus presence, type, and drainage pathways were extracted from representative species across mammalian orders. Phylogenetic (grouping by evolutionary ancestry) and phenetic (grouping by anatomical similarity) analyses were used to identify evolutionary patterns.

Results: Final review included 24 articles. Sinus prevalence in mammalian orders was maxillary (50%), frontal (44%), sphenoid (33%) and ethmoid (20%). Frontal sinuses were more common in behaviorally complex orders (71% vs. 22%). Frontal and maxillary sinuses predominated in terrestrial and arboreal mammals, while aquatic and volant mammals largely lacked sinuses. Phenetic clustering by sinus characteristics often contradicted phylogeny, suggesting parallel evolution driven by environment over ancestry. Despite variation in morphology, drainage pathways remained conserved.

Conclusions: Paranasal sinus distribution in mammals appears more ecologically than phylogenetically determined, with convergent evolution likely influencing their presence. Conserved drainage patterns suggest developmental constraints over selective advantages. Further studies incorporating underrepresented mammalian orders and sinus size quantification are needed to refine our understanding of paranasal sinus function and evolution.

Key words: drainage pathway, evolution, mammal, ostia, paranasal sinuses

Introduction

Paranasal sinuses are pneumatized spaces lined with respiratory mucosa within the skull that drain into the nasal cavity. While absent in Testudines (turtles) and Lepidosauria (lizards and snakes), these sinuses are present in many mammalian species, as well as in some birds and reptiles. Their structural characteristics vary widely across taxa: in mammals, paranasal sinuses are typically enclosed dead-gas spaces within bone, whereas in reptiles and birds, they are often partially surrounded by soft tissue and possess a more active ventilation mechanism [1].

Despite their widespread occurrence, the functional significance of paranasal sinuses remains controversial. Numerous hypotheses have been proposed, including their role in protecting against facial trauma, warming and humidifying inspired air, producing and storing nitric oxide to defend against pathogens, cooling the brain, and reducing skull weight [2-7]. Recent studies emphasize a respiratory role, proposing that the paranasal sinuses act as nitric oxide reservoirs, with release into the nasal cavity actively regulated by the ostial sphincter [8]. Another theory suggests that sinus pneumatization may have evolved to aid buoyancy in mammals adapting to aquatic environments [9]. Additionally, sinuses have been implicated in modulating vocal resonance, with alterations in voice quality reported after sinus surgery [5,10-13].

Part of this functional ambiguity may stem from the remarkable diversity in sinus morphology and distribution across species. While *Homo sapiens* have maxillary, frontal, ethmoidal, and sphenoid sinuses, a subset of other mammalian species are characterized by additional accessory sinuses such as the sphenopalatine, lacrimal, palatine, dorsal conchal, ventral conchal, and middle conchal. Unlike the primary paranasal sinuses (maxillary, frontal, ethmoid, sphenoid), which are named after the major cranial bones that they occupy, accessory sinuses are named after the pneumatization of smaller internal nasal structures. For example, conchal sinuses occupy the nasal conchae. Furthermore, the orientation of mucociliary drainage varies, with both gravitational and antigravitational patterns observed. These anatomical and functional differences may hold key insights into the evolutionary pressures that shaped sinus development, as well as the etiology of various sinonasal diseases.

To our knowledge, no prior study has comprehensively examined both the presence and drainage pathways of paranasal sinuses across mammalian orders. To address this gap, we conducted a scoping review of the literature, synthesizing radiological, anatomical, and descriptive data to assess sinus distribution and drainage orientation. Through both phylogenetic (grouping by evolutionary ancestry) and phenetic (grouping by anatomical similarity) frameworks, we aim to infer functional significance and trace the evolutionary trajectory of paranasal sinuses in mammals.

Materials and methods

Literature search

A comprehensive literature search was conducted in the Ovid MEDLINE database by a medical librarian, covering the period from 1946 to June 2024. The search strategy employed a combination of Medical Subject Headings (MeSH) and keywords. MeSH terms related to paranasal sinuses included: "ethmoid sinus," "frontal sinus," "maxillary sinus," "paranasal sinuses," "sphenoid sinus," "nasal cavity," and "skull." These terms were further refined using subheadings relevant to anatomy and histology as well as growth and development. 41 MeSH terms representing various mammalian species were used, along with an additional 30 species-related keywords not covered by MeSH, yielding a total of 71 mammalian species. Other MeSH terms included: "biological evolution," "drainage," and "bodily secretions."

The search terms were combined using the Boolean operator "AND", first linking sinus-related terms with mammalian species, then incorporating "biological evolution", "drainage", and "bodily secretions". The search was limited to English-language publications and returned 1,582 references for screening against inclusion and exclusion criteria.

To ensure a comprehensive assessment of available evidence, a supplementary search was conducted using PubMed, MEDLINE, Scopus, and Google Scholar. The keywords included: "paranasal", "ostia", "mammal", "cranial", "anatomy", "sinus", and "cavity". This search identified 55 additional sources. A complete list of search terms is provided in the Supplemental Materials.

Duplicate studies were removed. Studies were excluded if they did not focus on modern mammals, lacked relevance to paranasal sinuses or their ostia, were redundant with other included studies, contained low-quality or insufficient anatomical data, or failed to describe sinus presence, location, ostia, or drainage pathways. For this review, modern mammals were defined as extant species. Extinct mammalian species were excluded to ensure the analysis focused on anatomical phenotypes that have been retained through evolutionary selection. Furthermore, restricting the dataset to extant species minimized potential inaccuracies in determining drainage orientation, as fossilized specimens may lack the structural integrity required to definitively localize the ostium relative to the sinus floor. To maintain a taxonomically balanced dataset and prevent the overrepresentation of commonly studied orders (e.g., Rodentia, Carnivora), a maximum of three species per order were included. These representatives were selected sequentially based on the order of study identification during the screening process. Additionally, conference abstracts, posters, commentaries, press releases, and inaccessible full texts were excluded. The literature search process is outlined as a PRISMA (Preferred Reporting Items for Systematic Review and Meta-Analysis statement) diagram in Figure 1, as constructed using an online PRISMA flow diagram generator [14]. This scoping review was conducted and reported

Table 1. The 24 studies that qualified for final analysis with their associated publication years and studied mammal(s).

Study	Year	Species Studied
Rossie [20]	2006	*Platyrrhini*
Cave et al. [21]	1940	*Hoolock hoolock*
Alsafy et al. [9]	2022	*Equus asinus, Equus ferus caballus, Canis lupus familiaris*
Alsafy et al. [22]	2014	*Camelus bactrianus*
Alsafy et al. [23]	2013	*Bubalus bubalis*
Jacob et al. [24]	2006	*Mus musculus*
Ferreira et al. [25]	2022	*Hydrochoerus hydrochaeris*
Núñez-Cook et al. [26]	2024	*Hippocamelus bisulcus*
Reidenberg et al. [27]	2008	*Cetacea, Sirenia*
Negus [28]	1957	*Ornithorhynchidae*
Losonsky et al. [29]	1997	*Felis catus*
Wheelhouse et al. [30]	2021	*Zaglossus bartoni, Tachyglossus aculeatus*
Billet et al. [31]	2017	*Dasypus novemcinctus*
Farha et al. [32]	2021	*Myrmecophaga tridactyla*
Kelemen [33]	1955	*Oryctolagus cuniculus*
Hemsley et al. [34]	2013	*Phascolarctos cinereus*
Nelson et al. [35]	2017	*Osphranter rufus*
Curtis et al. [36]	2014	*Hydrurga leptonyx*
Smith et al. [37]	2021	*Rousettus leschenaultii*
Bhatnagar et al. [38]	1974	*Artibeus jamaicensis, Myotis lucifugus*
Rowe et al. [39]	2005	*Monodelphis domestica*
Henson et al. [2]	2018	*Homo sapiens*
Daniels et al. [40]	2003	*Homo sapiens*
Hanken et al. [41]	1993	Dasyuromorphia, Insectivora

in accordance with the PRISMA extension for Scoping Reviews (PRISMA-ScR) guidelines.

Data collection and interpretation

Gross and radiological images were acquired from the selected manuscripts and were entered into a spreadsheet. These images were independently reviewed by three blinded evaluators, who classified each sinus's drainage as either gravitational or antigravitational. If the ostium was located on the floor of the sinus cavity, drainage would be considered gravitational; otherwise, it was deemed antigravitational. In cases of disagreement among reviewers, the majority opinion was recorded. Simple bony recesses lacking distinct pneumatization and a discrete ostium were not categorized as sinuses.

For analysis, we classified mammalian orders into two groups based on evolutionary grades of behavioral complexity. The following were categorized as mammals of complex behavioral grade (CBG): Artiodactyla (even-toed hoofed mammals, e.g. cattle), Carnivora (carnivores), Cetacea (whales and dolphins), Perissodactyla (odd-toed hoofed mammals, e.g. horses), Pilosa (sloths and anteaters), Primate (primates), and Sirenia (sea cows). Mammals with a basal behavioral grade (BBG) included: Chiroptera (bats), Dasyuromorphia (carnivorous marsupials), Didelphimorphia (opossums), Eulipotyphla (hedgehogs and moles), Lagomorpha (rabbits and hares), Diprotodontia (marsupials), Monotremata (egg-laying mammals, e.g. platypuses and echidnas), Rodentia (rodents), and Cingulata (armadillos).

Phenetic and phylogenetic tree generation

A phylogenetic tree was created based on the current NCBI taxonomic hierarchy using the phyloT web tool and visualized via the Interactive Tree of Life (iTOL) program [15]. Taxonomic identifiers (NCBI taxonomy IDs) for each species, family, or suborder were compiled and inputted into phyloT to generate the tree in Figure 2A.

Next, we grouped those species/families/suborders based on the presence of the following sinuses using hierarchical clustering: maxillary, frontal, ethmoid, sphenopalatine, lacrimal, sphenoid, ventral conchal, dorsal conchal, and middle conchal sinuses. Clustering was performed using Python and the SciPy library (v1.12.0), specifically the scipy.spatial.distance and scipy.cluster.hierarchy modules. Jaccard distance was used to quantify dissimilarity, as it emphasizes shared presence rather than shared absence of traits, ideal for anatomical feature comparison [16-18]. Hierarchical agglomerative clustering was conducted using the unweighted pair group method with arithmetic mean (UPGMA) to generate a dendrogram [19]. The neighbor-joining method was also attempted but did not produce sufficiently distinct clusters and was thus not selected for the final analysis.

Results

The complete literature review and study selection process has been illustrated in the PRISMA diagram, in Figure 1. After careful review, 24 articles were included in this scoping review which are listed in Table 1, and the species and mammalian orders are provided in Table 2.

There was variation in the distribution of paranasal sinuses across mammalian species, as is summarized in Table 3. Of the mammalian orders studies, 56% had maxillary sinuses and 44% had frontal sinuses. Sphenoidal and ethmoidal sinuses were present to a lesser extent, appearing at 33% and 20% respectively. Accessory sinuses, namely dorsal conchal (18.8%), ventral conchal (12.5%), middle conchal (12.5%), lacrimal (6.3%), palatine (6.3%), and sphenopalatine (6.3%), were present to a smaller degree.

Intra-order variations in sinus morphology

Across mammalian orders, the median number of distinct paranasal types was 1. Artiodactyla had the greatest variety of

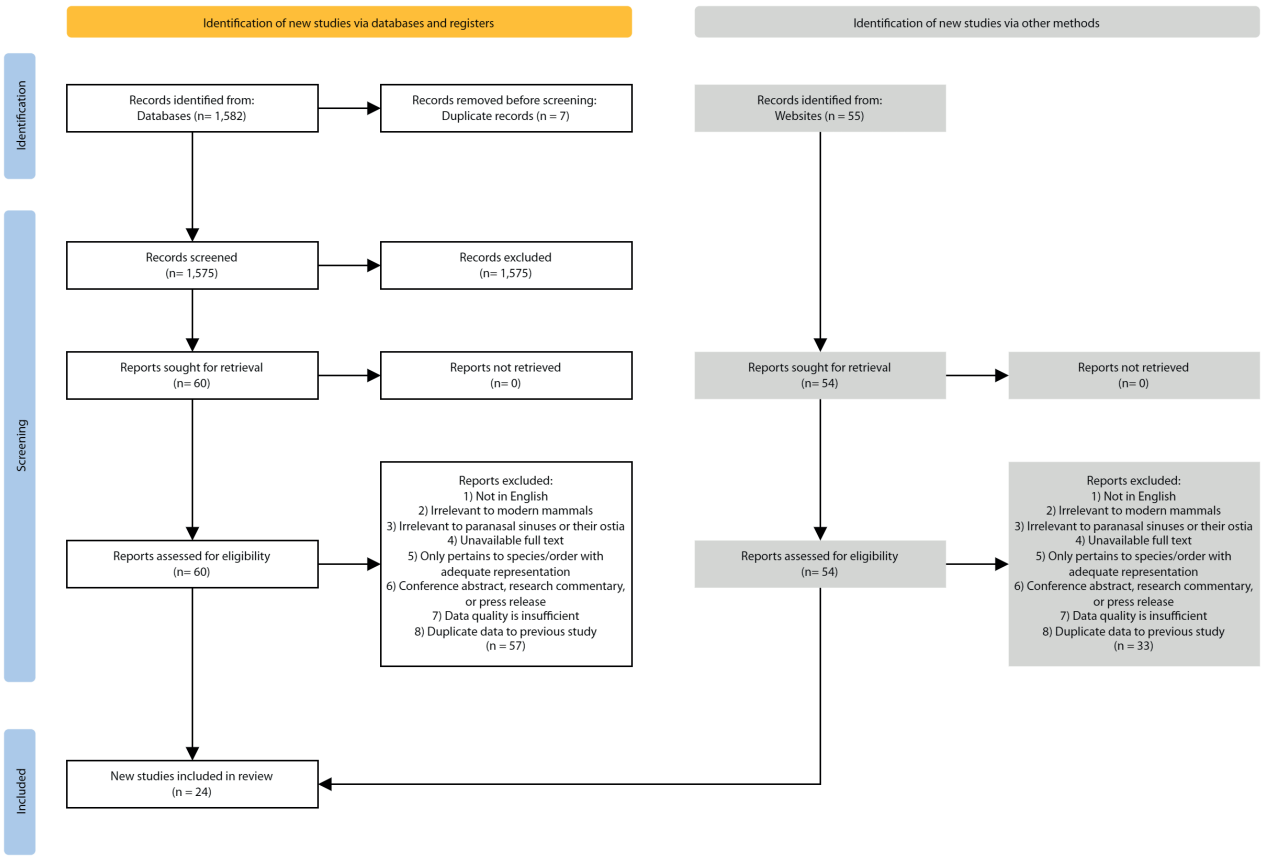

Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram.

paranasal sinuses, with eight unique types (maxillary, frontal, ethmoidal, sphenoidal, lacrimal, palatine, dorsal conchal and middle conchal). Perissodactyla had the second most with 6 (maxillary, frontal, sphenopalatine, dorsal conchal, ventral conchal, and middle conchal). Mammalian orders that lacked paranasal sinuses entirely include the following: Cetacea, Chiroptera (exception: *Artibeus jamaicensis* [Jamaican fruit bat]), Dasyuromorphia, Monotremata, Sirenia, and a subset of Carnivora (*Hydrurga leptonyx* [leopard seal]).

The presence of sinuses also greatly varied within the orders. In order Chiroptera, *Artibeus jamaicensis* had a frontal sinus whereas the other two species did not. Similarly, in order Carnivora, *Felis catus* (domestic cat) and *Canis lupus familiaris* (domestic dog) had frontal sinuses, only *Felis catus* had sphenoidal sinuses, while *Hydrurga leptonyx* lacked paranasal sinuses entirely. In order Diprotodontia, *Osphranter rufus* (red kangaroo) had only accessory ventral conchal sinuses, while the other species, *Phascolarctos cinereus* (koala), had maxillary, frontal, and sphenoidal sinuses in addition to ventral conchal. In order Rodentia, *Mus musculus* (house mouse) had maxillary, ethmoidal and sphenoidal sinuses, but *Hydrochoerus hydrochaeris* (capybara) only had a maxillary sinus. In order Artiodactyla, all three of the species studied had different combinations of sinus types. In contrast, some orders demonstrated high conservation of sinus morphology. The three subgroups of the Primate order: Platyrrhini (New World monkeys), *Hoolock hoolock* (Hoolock gibbon), and *Homo sapiens* (human), all had maxillary, frontal, ethmoidal, and sphenoidal sinuses, with similar drainage pathways. In order Monotremata, all studies species lacked paranasal sinuses. Perissodactyla further showed consistency in paranasal sinus morphology, with both species studied: *Equus asinus* (donkey) and *Equus ferus caballus* (horse), possessing maxillary, frontal, sphenopalatine, dorsal conchal, ventral conchal, and middle conchal sinuses.

Functional and environmental correlation with sinus morphology

Most terrestrial and arboreal mammals were characterized by possession of paranasal sinuses, with the exception of Dasyuromorphia and Monotremata. Aquatic mammals: *Hydruga leptonyx*, Cetacea, Sirenia, and Ornithorhynchidae (platypus) lacked paranasal sinuses completely. Chiroptera, the only mammalian order that engages in flight, also had no paranasal sinuses, except for *Artibeus jamaicensis*.

Drainage orientation of paranasal sinuses across orders

The frontal and ethmoidal sinuses always drained gravitationally, whenever present. Sphenoidal sinuses drained gravitationally

Table 2. The species are grouped into their respective clusters, as determined by the hierarchical clustering analysis.

C	Order	Taxon	Common Name	Locomotor Mode	Posture	Behavioral Grade	Max	Front	Eth	Sphen	Acc
1	Chiroptera	*Rousettus leschenaultii*	Fruit bat	Aerial	Biped	Basal	—	—	—	—	—
	Carnivora	*Hydrurga leptonyx*	Leopard seal	Aquatic	Quadruped	Complex	—	—	—	—	—
	Monotremata	*Zaglossus bartoni*	Long-beaked echidna	Terrestrial	Quadruped	Basal	—	—	—	—	—
	Sirenia	Sirenia	Sea cows	Aquatic	Quadruped	Complex	—	—	—	—	—
	Monotremata	Ornithorhynchidae	Platypus	Aquatic/ Terrestrial	Quadruped	Basal	—	—	—	—	—
	Monotremata	*Tachyglossus aculeatus*	Short-beaked echidna	Terrestrial	Quadruped	Basal	—	—	—	—	—
	Dasyuromorphia	Dasyuromorphia	Carnivorous marsupials	Terrestrial	Quadruped	Basal	—	—	—	—	—
	Cetacea	Cetacea	Whales, dolphins, porpoises	Aquatic	Quadruped	Complex	—	—	—	—	—
	Chiroptera	*Myotis lucifugus*	Little brown bat	Aerial	Biped	Basal	—	—	—	—	—
2	Diprotodontia	*Osphranter rufus*	Red kangaroo	Terrestrial	Quadruped	Basal	—	—	—	—	Y
3	Carnivora	*Felis catus*	Domestic cat	Terrestrial	Quadruped	Complex	—	G	—	Y	—
	Pilosa	*Myrmecophaga tridactyla*	Giant anteater	Terrestrial	Quadruped	Complex	—	Y	—	—	—
	Carnivora	*Canis lupus familiaris*	Domestic dog	Terrestrial	Quadruped	Complex	—	Y	—	—	—
	Cingulata	*Dasypus novemcinctus*	Nine-banded armadillo	Terrestrial	Quadruped	Basal	—	Y	—	—	—
4	Lagomorpha	*Oryctolagus cuniculus*	European rabbit	Terrestrial	Quadruped	Basal	A	—	—	—	Y
	Rodentia	*Hydrochoerus hydrochaeris*	Capybara	Terrestrial	Quadruped	Basal	Y	—	—	—	—
	Eulipotyphla	Insectivora	Hedgehogs, shrews, moles	Terrestrial	Quadruped	Basal	Y	—	—	—	—
	Chiroptera	*Artibeus jamaicensis*	Jamaican fruit bat	Aerial	Biped	Basal	A	—	—	—	—
	Didelphimorphia	*Monodelphis domestica*	Gray short-tailed opossum	Terrestrial	Quadruped	Basal	Y	—	—	—	—
5	Diprotodontia	*Phascolarctos cinereus*	Koala	Terrestrial	Quadruped	Basal	Y	G	—	Y	Y
	Rodentia	*Mus musculus*	House mouse	Terrestrial	Quadruped	Basal	G	—	G	G	—
	Primate	*Homo sapiens*	Human	Terrestrial	Biped	Complex	A	G	G	A	—
	Primate	Platyrrhini	New World monkeys	Terrestrial	Biped	Complex	A	G	G	A	—
	Primate	*Hoolock hoolock*	Western Hoolock gibbon	Terrestrial	Biped	Complex	A	G	G	A	—
6	Perissodactyla	*Equus asinus*	Donkey	Terrestrial	Quadruped	Complex	A	G	—	—	Y
	Perissodactyla	*Equus ferus caballus*	Domestic horse	Terrestrial	Quadruped	Complex	Y	Y	—	—	Y
	Artiodactyla	*Hippocamelus bisulcus*	South Andean deer	Terrestrial	Quadruped	Complex	Y	Y	—	Y	Y
	Artiodactyla	*Camelus bactrianus*	Bactrian camel	Terrestrial	Quadruped	Complex	A	G	G	G	Y
	Artiowdactyla	*Bubalus bubalis*	Domestic water buffalo	Terrestrial	Quadruped	Complex	A	G	G	G	Y

Sinus Abbreviations: Max: Maxillary; Front: Frontal; Eth: Ethmoidal; Sphen: Sphenoidal; Acc: Accessory Sinus(es) (including palatine, lacrimal, and conchal variants). Symbols: —: Absent; Y: Sinus present (drainage not specified); G: Gravitationally draining sinus; A: Antigravitationally draining sinus.

in 67% of mammalian orders, but maxillary sinuses drained gravitationally in only 20% of the assessed mammals in which they were present. The only mammalian species with gravitationally cleared maxillary sinuses was *Mus musculus* (Rodentia order).

Paranasal sinus morphology in CBG versus BBG mammals

When grouped by evolutionary complexity, CBG mammals were associated with a higher prevalence of frontal (71% vs. 22% in BBG mammals), ethmoidal (29% vs. 13%) and sphenoidal (43% vs. 25%) sinuses. BBG mammals had a greater prevalence of maxillary sinuses (56% vs. 43% in CBG mammals). Sphenoidal sinuses in CBG mammals showed both gravitational and antigravitational drainage, whereas in BBG mammals, they were exclusively gravitational.

Phenetic versus phylogenetic analysis

Hierarchical clustering analysis yielded six distinct groups: cluster one with no sinuses; cluster two with only ventral sinuses; cluster three with only frontal sinuses; cluster four with only maxillary sinuses; cluster five with maxillary, frontal, ethmoidal, sphenoidal, but no accessory sinuses; cluster six with both primary and accessory sinuses. There was moderate conservation of taxonomy within clusters, where Diprotodontia, Chiroptera, Carnivora, and Rodentia had species spread across multiple clusters, but Monotremata, Primates, Artiodactyla, and Perissodactyla maintained cluster consistency.

A comparison of the hierarchical cluster analysis (phenetic) tree and the NCBI phylogenetic tree can be visualized through Figure 2. None of the clusters were preserved completely in the phylogenetic tree except cluster two, which had only one member. There was some preservation of clusters, with clusters three and six showing preserved subgroups. Clusters one, four, and five displayed substantial dispersal of constituent members in the phylogenetic tree.

Discussion

We conducted a scoping review to investigate the diversity of paranasal sinuses and drainage pathways across various mammalian orders, aiming to derive insight into their function and evolutionary progression. The frontal and maxillary sinuses were most commonly present across the species studied. Our findings suggest that paranasal sinuses may have evolved independently in unrelated species occupying similar ecological niches, an example of parallel evolution. Thus, relying solely on phenotypic classification of sinuses is insufficient to infer evolutionary relationships among mammals. Comparing the phenetic and phylogenetic trees revealed notable discrepancies. Species clustered together based on sinus presence were dispersed in the phylogenetic tree, highlighting that similar sinus patterns likely arose due to analogous evolutionary pressures rather than shared ancestry. This phenomenon has been observed in previous studies, where single phenotypic traits failed to accurately reflect evolutionary relationships due to parallel or convergent evolution [42]. Our results indicate that classifying mammals based solely on paranasal sinus presence is an unreliable method for establishing evolutionary relatedness. Nevertheless, phenetic clustering can still offer insights into functional or environmental factors driving similar anatomical adaptations in unrelated species.

Functional hypotheses and ecological drivers

Larger quadrupeds such as *Equus asinus*, *Equus ferus caballus*, and *Camelus bactrianus* (Bactrian camel) had a greater number of sinus types compared to smaller mammals like *Oryctolagus cuniculus* (European rabbit) or *Monodelphis domestica* (gray short-tailed opossum), which possessed only maxillary sinuses. This may reflect skull size differences: larger skulls may require additional pneumatization to reduce weight for postural reasons. Moreover, species in arid environments, such as *Camelus bactrianus*, exhibited extensive pneumatization. This finding lends support to the hypothesis that paranasal sinuses facilitate thermoregulation, air humidification, and water conservation in dry climates. Conversely, such complex pneumatization appears less essential for smaller, burrow-dwelling species like *Mus musculus*, which possesses fewer sinuses and inhabits more stable microclimates.

When the mammals were categorized by their locomotor classifications, the majority exhibited terrestrial locomotion. Chiropterans, the primary volant (flying) group, generally lacked sinuses, except for one species possessing only maxillary sinuses. This absence is intriguing, as pneumatization might be expected to benefit flight by reducing cranial weight. However, Chiroptera typically have small skulls, potentially reducing the need for weight-reducing adaptations such as sinuses. Thus, this suggests that the skull lightening function of pneumatization may be scale-dependent; while unnecessary for the lightweight skulls of small volant mammals, it appears increasingly critical for maintaining structural integrity without excessive mass in larger terrestrial quadrupeds. Furthermore, our data supports the hypothesis that sinus size roughly correlates with skull size, although this correlation is imperfect [41].

Among aquatic mammals, including members of Cetacea, Ornithorhynchidae, Sirenia, and *Hydrurga leptonyx*, none possessed true paranasal sinuses or salient homologous structures. Interestingly, Cetaceans do contain paranasal air sacs that may serve analogous functions, but these structures differ structurally, with flexible walls rather than rigid bony cavities [27]. Prior studies have noted that animals that spend significant time in water likely do not have sinuses, as they may interfere with diving by increasing buoyancy or collapsing under pressure [27,43]. The absence of any paranasal pneumatization in fish species further indicates that paranasal sinuses likely do not present an aquatic

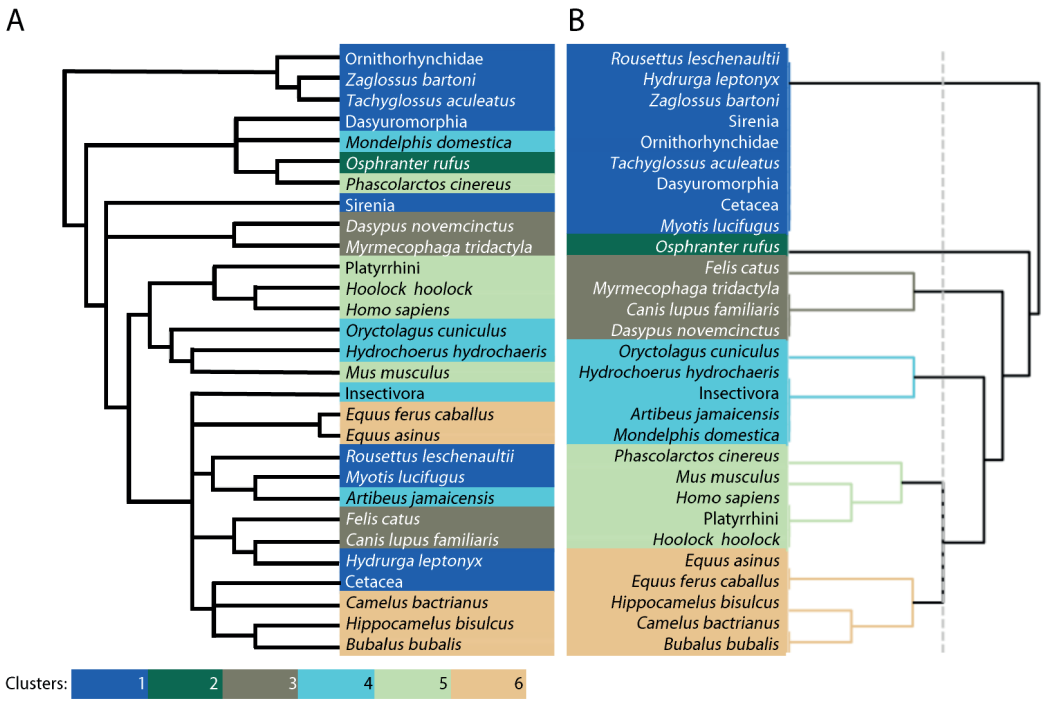

Figure 2. (A) PhyloT phylogenetic tree. (B) Phenetic sinus hierarchical clustering dendrogram; the dashed line indicates the point at which clusters were identified; colors in both parts indicate the groups to which the species belonged as determined through the hierarchical clustering analysis.

advantage [1]. Although some theories propose a buoyancy role for sinuses in humans [9], this advantage remains speculative and likely secondary, as our data suggests the contrary.

In contrast, 86% of terrestrial and arboreal mammals possessed sinuses. This supports the theory that sinuses may confer an evolutionary benefit in land-dwelling species, potentially by lightening the skull to facilitate upright posture and efficient ambulation. Previous studies showing that burrowing mammals also tend to have smaller or absent sinuses further support this theory [44].

Anatomical distribution and prevalence

Among all sinuses, the maxillary was the most prevalent, followed by the frontal sinus, consistent with prior literature [44]. Ethmoidal, sphenoidal, and the accessory sinuses were present to a lesser extent. Interestingly, species lacking frontal sinuses were highly unlikely to possess ethmoidal or sphenoidal sinuses, *Mus musculus* being the sole exception. This suggests that the maxillary and frontal sinuses may play increasingly essential roles in mammalian survival. The frontal sinus, for instance, may serve as a protective function for the central nervous system by dissipating impact forces away from the intracranial cavity. Our observation of the frequent presence of frontal sinuses in behaviorally advanced species with larger brains supports this theory.

The maxillary sinus, nearly ubiquitous among Eutherians (placental mammals) and absent in most marsupials and all monotremes, may represent a derived trait of placental mammals [1]. While its specific functional role remains unclear, it consistently drained against gravity (antigravitational drainage), suggesting a dependence on mucociliary clearance. Ethmoidal, sphenoidal, and accessory sinuses, given their lower prevalence, likely serve less critical roles and may arise more sporadically under weaker evolutionary pressures.

Another explanation for the ubiquity of frontal and maxillary sinuses is that they were the first to evolve, possibly in a common Eutherian ancestor after divergence from Metatherian (marsupial) and Prototherian (monotreme) lineages. This hypothesis is supported by the widespread persistence of maxillary sinuses among Eutherians despite their diverse ecosystems and environmental pressures. Yet this theory is weakened by the well-determined phenomenon that pneumatizations in the skull are very sensitive to evolutionary pressures and thus, they may appear or disappear in species quickly [1]. For example, the loss of maxillary sinuses in some cercopithecoid monkeys illustrates the fluidity of sinus development [45].

Drainage pathways and evo-devo theory

Drainage pathways were well conserved across all mammalian orders. Despite the anatomical diversity of sinuses, there was little variation in mucociliary drainage mechanisms. This suggests that sinus drainage pathways may not have evolved as adaptations per se but rather emerged as structural byproducts, or "spandrels", of cranial anatomy [46].

Table 3. Percentages relate to mammalian orders and not individual species of each order; percentages referring to drainage of a particular sinus relate to the number of orders with a particular draining pathway divided by the total number of mammalian orders characterized by that sinus.

	All Mammals	Complex Behavioral Grade	Basal Behavioral Grade	Bipeds	Quadrupeds
% Bipeds	13%	14%	11%	100%	0%
% Quadrupeds	87%	86%	89%	0%	100%
% w/ Maxillary Sinus	50%	43%	56%	50%	56%
% w/ Frontal Sinus	44%	71%	22%	50%	44%
% w/ Ethmoidal Sinus	20%	29%	13%	50%	20%
% w/ Sphenoidal Sinus	33%	43%	25%	50%	33%
% w/ Sphenopalatine Sinus	6%	14%	0%	0%	7%
% w/ Lacrimal Sinus	6%	14%	0%	0%	7%
% w/ Palatine Sinus	6%	14%	0%	0%	7%
% w/ Dorsal Conchal Sinus	19%	29%	11%	0%	21%
% w/ Ventral Conchal Sinus	13%	14%	11%	0%	14%
% w/ Middle Conchal Sinus	13%	29%	0%	0%	14%
% w/AG Maxillary	80%	10%	50%	100%	83%
% w/AG Frontal	0%	0%	0%	0%	0%
% w/AG Ethmoidal	0%	0%	0%	0%	0%
% w/AG Sphenoidal	33%	50%	0%	100%	33%

AG: Antigravitationally draining sinus.

Our findings of conserved drainage pathways and their evolution as potential "spandrels" aligns with the evo-devo theory as outlined by Jankowski and Márquez [47,48]. The evo-devo theory suggests that the paranasal sinuses, particularly the ethmoid complex, represent the developmental remnants of the olfactory capsule. Through this perspective, the persistence of specific ostia across sundry mammalian orders may indeed reflect developmental constraints from the ancestral olfactory organ rather than active selection for other functions.

Knowledge gaps and future directions

The functional purpose of paranasal sinuses remains incompletely understood, and several knowledge gaps persist. Specifically, many mammalian orders, such as Scandentia (tree shrews), Macroscelidea (elephant shrews), Microbiotheria (monito del monte), Notoryctemorphia (marsupial moles), and others, remain poorly characterized in the literature. Future studies should aim to fill these gaps to better validate the trends observed here. While this review focused on the presence or absence of sinuses, future investigations could examine sinus size variation, allowing for more quantitative and statistically robust analyses. Cross-sectional imaging studies in humans correlating sinus size with clinical outcomes could also enhance understanding of the physiological relevance of sinus anatomy in health and disease.

Limitations

This study has several limitations. While there were 31 mammalian orders, we were unable to obtain adequate data for all due to limited published studies. Indeed, while data scarcity limits generalization across all mammalian orders, the consistency of observed anatomical patterns among the represented species provides a robust preliminary framework. These findings serve as a baseline synthesis that highlights current knowledge gaps. To mitigate availability bias, we limited inclusion to a maximum of three representatives per order. However, given the significant intra-order and intra-family variation, our conclusions may not be broadly generalizable beyond the specific species studied. Additionally, some subjectivity exists in distinguishing between sinuses and recesses, and source materials were occasionally inconsistent in terminology. This study does not analyze sinus volume, surface area, or other quantitative variables, which could add an objective metric to comparative evaluations and may influence interpretations of function. Our categorization of CBG and BBG mammals based on behavioral complexity may also oversimplify the phylogenetic continuum and introduce bias from anthropocentric perspectives. Also, species that are more commonly used in research (e.g., mice, rabbits, dogs) are li-

kely overrepresented in the literature, which may skew generalizability of sinus trends across broader wild mammalian diversity.

Conclusion

This scoping review highlights the diversity and distribution of paranasal sinuses across mammalian orders, revealing that frontal and maxillary sinuses are most prevalent among terrestrial mammals, while aquatic and volant species largely lack them. These findings suggest that sinus presence may be shaped more by ecological pressures than by phylogenetic lineage. The observed mismatch between phenetic and phylogenetic groupings supports the influence of convergent evolution. Despite morphological diversity, drainage pathways remain conserved, possibly reflecting anatomical constraints rather than adaptive selection. Significant gaps remain due to limited data across certain mammalian orders. Further research integrating anatomical, ecological, and evolutionary perspectives is needed to clarify the function and evolutionary significance of paranasal sinuses in mammals.

Author contributions

Conceptualization: LEE, PLG, DL. Data curation: LEE, PLG, TP, DL. Formal analysis: LEE, TP, MKE, NK. Investigation: LEE, PLG, TP, MKE, DL. Methodology: LEE, PLG, TP, MKE, LAM, DL. Project administration: DL. Resources: MKE, LAM. Supervision: PLG, NK, DL. Writing – original draft: LEE, NK. Writing – review & editing: LEE, PLG, TP, MKE, NK, DL.

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Conflict of interest

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Devyani Lal, M.D., F.A.R.S.
Professor & Consultant
Otolaryngology
Head & Neck Surgery
Chair, Division of Rhinology
Mayo Clinic in Arizona
Dean, Education
Mayo Clinic School of Continuous Professional Development
Mayo Clinic in Arizona
5777 East Mayo Blvd.
Phoenix
AZ 85054
USA

Tel: +1-480-342-2374
Fax: +1-480-342-2626
E-mail: lal.devyani@mayo.edu

Landon E. Ebbert[1], Nitish Kumar[2], Mary K. Ebbert[3], Tyson Pace[1], Pedro Lança Gomes[2], Lisa A. Marks[4], Devyani Lal[2]

[1] Mayo Clinic Alix School of Medicine, Scottsdale, AZ, USA

[2] Department of Otorhinolaryngology - Head and Neck Surgery, Mayo Clinic, Phoenix, AZ, USA

[3] Independent scholar

[4] Division of Education, Department of Library Services, Mayo Clinic, Scottsdale, AZ, USA

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