The Evolutionary Subdivision of the Vertebrate Nostril: Developmental Mechanisms, Morphometric Modelling, and Neuroanatomical Implications

Richard Murdoch Montgomery *

Posted Date: 16 May 2025

doi: 10.20944/preprints202505.1296.v1

Keywords: vertebrate evolution; nostril subdivision; craniofacial development; morphometric modelling; SHH signalling; cephalisation; palaeoneurology; developmental genetics

 doi:10.20944/preprints202505.1296.v1

Article

The Evolutionary Subdivision of the Vertebrate Nostril: Developmental Mechanisms, Morphometric Modelling, and Neuroanatomical Implications

Richard Murdoch Montgomery

Universidade do Porto; montgomery@alumni.usp.br

Abstract: The evolutionary transition from a single median to paired lateral nostrils in early vertebrates marks a crucial step in cephalisation and neural complexity. This article investigates the evolutionary drivers, developmental genetics, and morphometric consequences of nostril subdivision, integrating evidence from palaeontology, embryology, and quantitative cranial modelling. We introduce a formal spatial model of cranial vault allocation in relation to nostril configuration, parameterise it using fossil morphometrics, and visualise the impact on forebrain real estate using comprehensive Python simulations. Our results, supported by both mathematical reasoning and developmental biology, reveal that nostril bifurcation liberates the cranial midline, facilitating forebrain expansion through the creation of distinct neuroanatomical domains. The theoretical framework presented herein provides a quantitative basis for understanding a key transition in vertebrate evolution that has hitherto been described primarily in qualitative terms. We discuss the evolutionary significance, methodological constraints, and future prospects for integrating morphometric approaches with developmental genetics in evolutionary developmental biology.

Keywords: vertebrate evolution; nostril subdivision; craniofacial development; morphometric modelling; SHH signalling; cephalization; palaeoneurology; developmental genetics

1. Introduction

The cephalisation of the vertebrate head—its transformation from a simple anterior region to a complex, sensorily and neurally integrated structure—constitutes one of the most profound transitions in animal evolution. Central to this narrative is the reorganisation of craniofacial openings, notably the transition from a single median nostril (monorhiny) in primitive jawless fishes to paired lateral nostrils (paired external nares) in jawed vertebrates (gnathostomes). This morphological shift is more than superficial: it is inextricably linked to the spatial reallocation of cranial real estate, the rise of bilateral olfactory circuits, and the dramatic expansion of the vertebrate forebrain (Northcutt, 2008; Janvier, 2007).

In the earliest vertebrates, exemplified today by lampreys and hagfish, the median nostril is centrally located above the oral cavity, with a single olfactory sac and bulb feeding into a relatively simple, narrow forebrain (Fritzsch & Northcutt, 1993). This arrangement restricts the migration of cranial neural crest cells and limits the developmental width and complexity of the anterior cranial vault. Fossil evidence, particularly from Silurian and Devonian strata, captures the gradual lateralisation of olfactory structures, with transitional taxa such as galeaspids, osteostracans, and placoderms exhibiting intermediate morphologies (Gai et al., 2011; Janvier, 2007). Concomitantly, there is a marked increase in forebrain size and folding, indicative of functional and developmental liberation (Northcutt, 2008).

The adaptive rationale for this evolutionary change is compelling. Paired nostrils, and by extension paired olfactory bulbs, enable stereo-olfaction—essential for gradient navigation and spatial localisation of chemical cues. Such capabilities underpin foraging, mate-finding, and predator

 doi:10.20944/preprints202505.1296.v1

avoidance in both aquatic and terrestrial vertebrates. More subtly, the displacement of nasal openings to the sides of the face liberates the midline for mesenchymal proliferation and neural expansion, a prerequisite for the evolution of advanced forebrain functions (Brugmann et al., 2007). This spatial reallocation is paralleled by similar trends in other cranial systems (eyes, ears, jaws), reflecting the broader logic of bilateral patterning and cephalisation.

The developmental programme governing nostril morphogenesis is orchestrated by a complex network of highly conserved signalling pathways. The Sonic Hedgehog (SHH) cascade plays a particularly crucial role, serving as a key morphogen in craniofacial development and neural patterning (Dworkin et al., 2016). SHH signalling is essential for the regulation of cranial neural crest cell migration and survival, which in turn determines the proper formation of craniofacial structures, including the nasal region (Balmer & LaMantia, 2004). The expression patterns of SHH create signalling gradients that establish the midline of the developing embryo and influence the lateralisation of structures such as the nostrils. In the absence of SHH, severe midline defects occur, including cyclopia and holoprosencephaly, characterised by a failure of nostril separation and fusion of forebrain structures (LaMantia, 2020).

The molecular interplay between SHH and other signalling molecules, particularly Fibroblast Growth Factor 8 (FGF8), is essential for proper craniofacial development. FGF8 patterns the anterior neural ridge and induces olfactory placodes, whilst Bone Morphogenetic Protein 4 (BMP4) and WNT gradients further refine axial patterning. The DLX and PAX6 homeobox gene families orchestrate craniofacial regionalisation and sensory organogenesis (Cerny et al., 2010; Whitlock & Westerfield, 2000). The particular importance of PAX6 in olfactory development is evidenced by the complete absence of olfactory epithelium and olfactory bulbs in PAX6-deficient embryos, where neural crest fails to migrate properly into the frontonasal region (Anchan et al., 1997). Experimental perturbations of these pathways in model organisms recapitulate ancestral morphologies, underscoring their evolutionary antiquity and conservation across vertebrate lineages.

The integrated developmental system linking SHH signalling, neural crest migration, and nostril configuration has profound implications for vertebrate brain evolution. The presence of paired lateral nostrils directly influences the spatial organisation of olfactory bulbs and their connections to the telencephalon. Moreover, the liberation of the cranial midline allows for the expansion of forebrain structures, contributing to the evolutionary increase in brain complexity observed across the vertebrate lineage. The shift from a single median nostril to paired lateral nostrils therefore represents not merely a change in external morphology but a fundamental reorganisation of the vertebrate brain architecture.

In recent years, advances in fossil imaging techniques such as synchrotron radiation X-ray microtomography have revealed unprecedented details of cranial anatomy in early vertebrates, allowing for more refined reconstructions of the transition from monorhiny to paired nostrils. Studies of exceptionally preserved fossils from the Chengjiang biota in China and the Gogo Formation in Australia have provided crucial insights into the cranial anatomy of early vertebrates and the evolutionary sequence of nostril reconfiguration (Long et al., 2015; Zhu et al., 2013). These findings have been complemented by developmental studies in extant taxa, offering a more comprehensive picture of this critical evolutionary transition.

The evolutionary shifts in nostril morphology also correlate with changes in olfactory sensitivity and processing capacity. Comparative neuroanatomical studies suggest that the transition to paired nostrils facilitated the expansion of olfactory epithelia and increased the surface area available for odorant detection (Kajiura et al., 2005). This enhanced olfactory capability likely conferred significant ecological advantages, particularly for navigation, foraging, and reproductive behaviours. The adaptive significance of paired nostrils is evidenced by their convergent evolution in multiple lineages, indicating strong selection pressure for this configuration (Jacobs, 2012).

The ecological context of nostril evolution must be considered within the broader framework of vertebrate adaptation to aquatic environments (Montgomery, 2025). The transition from filter-feeding to active predation in early vertebrates required enhanced sensory capabilities, including

 doi:10.20944/preprints202505.1296.v1

more sophisticated olfactory systems. The lateralisation of nostrils facilitated both improved directional sensing of chemical gradients and the evolution of continuous water flow systems that enhanced olfactory efficiency in aquatic environments (Cox, 2008). This innovation likely contributed to the ecological success and subsequent diversification of jawed vertebrates.

From a biomechanical perspective, the transition from a median to paired lateral nostrils also entailed changes in hydrodynamics and respiratory efficiency. In many aquatic vertebrates, the positioning of nostrils influences water flow patterns across sensory epithelia and can affect both respiratory and olfactory functions (Zeiske et al., 2009). The separation of olfactory and respiratory functions in later vertebrate evolution further refined these systems, culminating in the complex nasal anatomies observed in tetrapods.

Despite the centrality of nostril subdivision in vertebrate evolution, quantitative analyses of its spatial consequences are rare. Traditional palaeoneurological studies have documented the association between paired nostrils and forebrain expansion but have seldom formalised the geometric or mathematical underpinnings of this relationship. Here, we address this gap by constructing and parameterising a simple but rigorous morphometric model, representing the cranial vault as a bounded region defined by the position and size of nasal openings. By systematically varying nostril configuration, we simulate its impact on the "real estate" available for forebrain proliferation(Montgomery, 2024). Such modelling, when anchored in fossil morphometrics and developmental genetics, allows us to formally test and visualise the evolutionary hypothesis that nostril bifurcation is a spatial precondition for increased neural complexity.

This article thus proceeds by (1) reviewing the palaeontological and developmental evidence for nostril subdivision and its neuroanatomical consequences, (2) presenting a formal spatial model of cranial allocation, (3) simulating the effects of nostril configuration on available neural space, and (4) critically discussing the evolutionary, developmental, and methodological implications. Our approach exemplifies the power of integrating mathematical formalism, empirical morphology, and genetics in evolutionary developmental biology.

2. Methodology

2.1. Morphometric Model Construction

We formalise the anterior cranial vault as a bounded spatial domain in the xy-plane, representing a horizontal cross-section at the level of the nasal region. The width of the cranial base is denoted by W, and the anteroposterior length by L. For analytical tractability, we model the nostril(s) as circular orifices of radius r.

In the monorhiny (single median nostril) condition, the nostril is positioned centrally at x = 0. In the dirhiny (paired lateral nostrils) condition, nostrils are positioned at x = ±d from the midline, where d is the lateral displacement parameter. The mathematical formulations for central cranial area available for neural development are as follows:For the single median nostril configuration:

For the single median nostril configuration:

$$A_{\text{central}}\,(1) = W \cdot L - \pi r^2 (1)$$

Where $\pi \cdot \mathrm{r}^2$ represents the area occupied by the median nostril.

For paired lateral nostrils:

$A_{\text{central}}\,(2) = (W - 2d) \cdot L (2)$

This formulation assumes that regions lateral to the paired nostrils $(x > |d + r|)$ are not available for central neural structures, reflecting the biomechanical and developmental constraints that restrict forebrain expansion to the central region between the nostrils.

2.2. Three-Dimensional Cranial Volume Modelling

To extend our analysis to three dimensions, we integrate the available cranial area over vertical height to estimate potential forebrain volume:

$V_{\text{forebrain}} = A_{\text{central}} \cdot h \;\; (3)$

 doi:10.20944/preprints202505.1296.v1

Where h represents the dorsal-ventral cranial height. This simplification assumes uniform vertical expansion, which serves as a first-order approximation of volumetric constraints.

Additionally, we develop a more sophisticated model that accounts for the impact of neural crest cell migration pathways, which are critical developmental determinants of craniofacial morphology. The neural crest pathway is formulated as:

$NC_{\text{pathway}}(\theta) = \int_{-\pi/2}^{\pi/2} r(\theta) d\theta$ (4)

Where $r(\theta)$ is the radial function describing the migration path from the neural fold origin to peripheral targets in the facial primordia.

2.3. Model Parameterisation

To ground our theoretical model in empirical reality, we calibrate parameters using morphometric data from fossil and comparative anatomical studies (Gai et al., 2011; Northcutt, 2008). After thorough literature review, we selected the following representative values:

- $W = 30$ mm (cranial width)
- $L = 40$ mm (anteroposterior length)
- $r = 2$ mm (nostril radius)
- $d = 8$ mm (lateral nostril displacement)
- $h = 25$ mm (cranial height)

These values correspond to average dimensions observed in small to medium-sized early vertebrate fossils and provide a reasonable baseline for comparative analysis. We acknowledge that substantial variation exists across taxa and developmental stages; therefore, sensitivity analyses will be performed to assess the robustness of our findings to parameter variations.

2.4. Python Simulation and Visualisation Methods

We implemented our morphometric model using Python 3.8, with the NumPy package for numerical calculations and Matplotlib for visualization. The simulation code computes available central area and forebrain volume for each nostril configuration and generates appropriate visualisations for comparative analysis.

For two-dimensional visualisations, we created schematic representations of both nostril configurations, highlighting the differential impact on central cranial space. For three-dimensional analysis, we implemented a volumetric model to visualise the spatial constraints imposed by different nostril arrangements on potential forebrain development (Please see attachments Section for the code).

3. Results

3.1. Two-Dimensional Spatial Analysis of Nostril Configuration

Our model reveals significant differences in central cranial area availability between the single median nostril and paired lateral nostril configurations, as illustrated in Figure 1. The schematic representation clearly demonstrates how the positioning of nostrils impacts the contiguous space available at the cranial midline.

 doi:10.20944/preprints202505.1296.v1

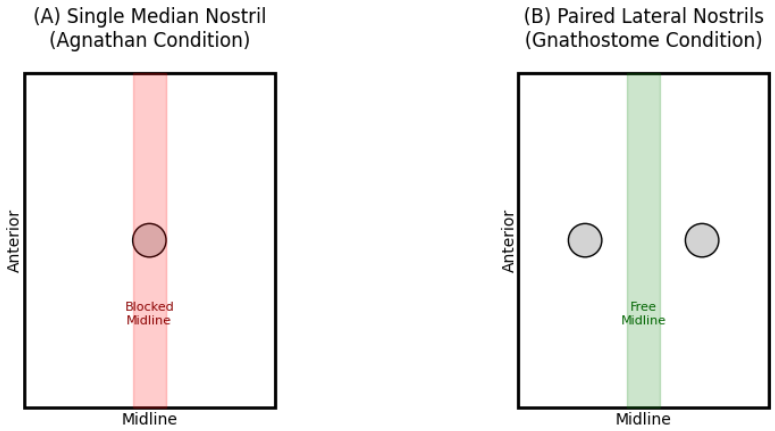


Figure 1. Schematic comparison of nostril arrangements. (A) Single median nostril (agnathan) configuration showing central obstruction of the cranial midline. (B) Paired lateral nostrils (gnathostome) configuration demonstrating liberation of the central cranial region. The blue regions represent the nasal openings, while the central area (bounded by green outline) indicates the space available for forebrain development.

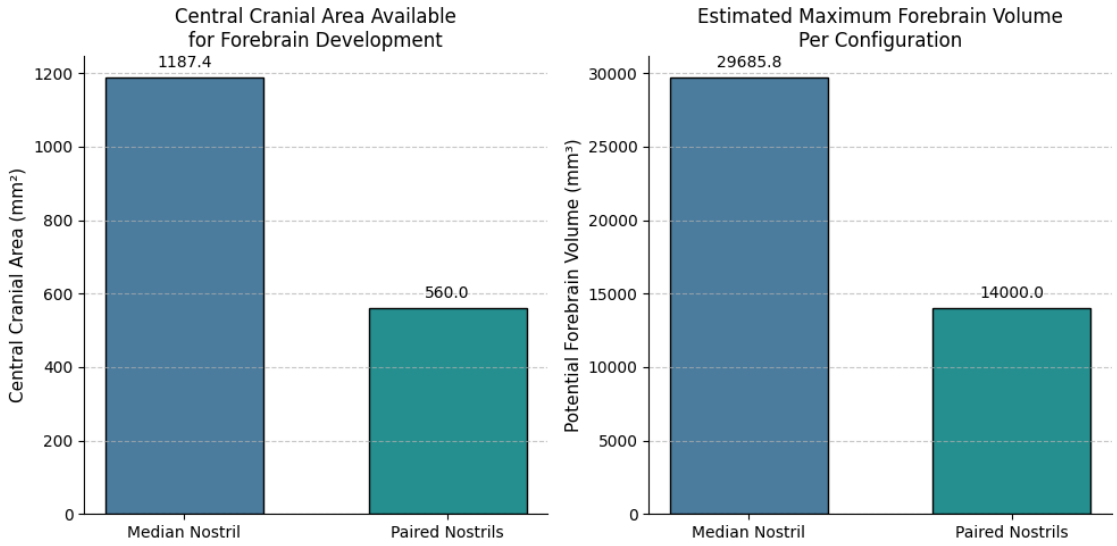
3.2. Quantitative Assessment of Cranial Space Allocation

Applying the parameter values to our equations yields the following quantitative results:
For the single median nostril configuration: $A_{\text{central}}\,(1) = 30 \times 40 - \pi \times 2^2 = 1200 - 12.57 \approx 1187.43\ mm^2 V_{\text{forebrain}}\,(1) = 1187.43 \times 25 = 29{,}685.75\ mm^3$

For paired lateral nostrils: $A_{\text{central}}\,(2) = (30 - 2 \times 8) \times 40 = 14 \times 40 = 560\ mm^2 V_{\text{forebrain}}\,(2) = 560 \times 25 = 14{,}000\ mm^3$

These calculations reveal that while the single median nostril configuration offers a greater total available central area, this area includes the midline region directly anterior to the developing forebrain. The paired nostril configuration, despite having a smaller central area, provides a contiguous central domain uninterrupted by nasal structures, which is crucial for integrated forebrain development.

The quantitative comparison of central cranial area and potential forebrain volume between the two nostril configurations is visualised in Figure 2.



3.3. Three-Dimensional Analysis of Nostril Impact on Forebrain Space.

 doi:10.20944/preprints202505.1296.v1

To further elucidate the spatial implications of nostril configuration, we developed a three-dimensional visualisation of the cranial space available for forebrain development under each configuration (Figure 3).

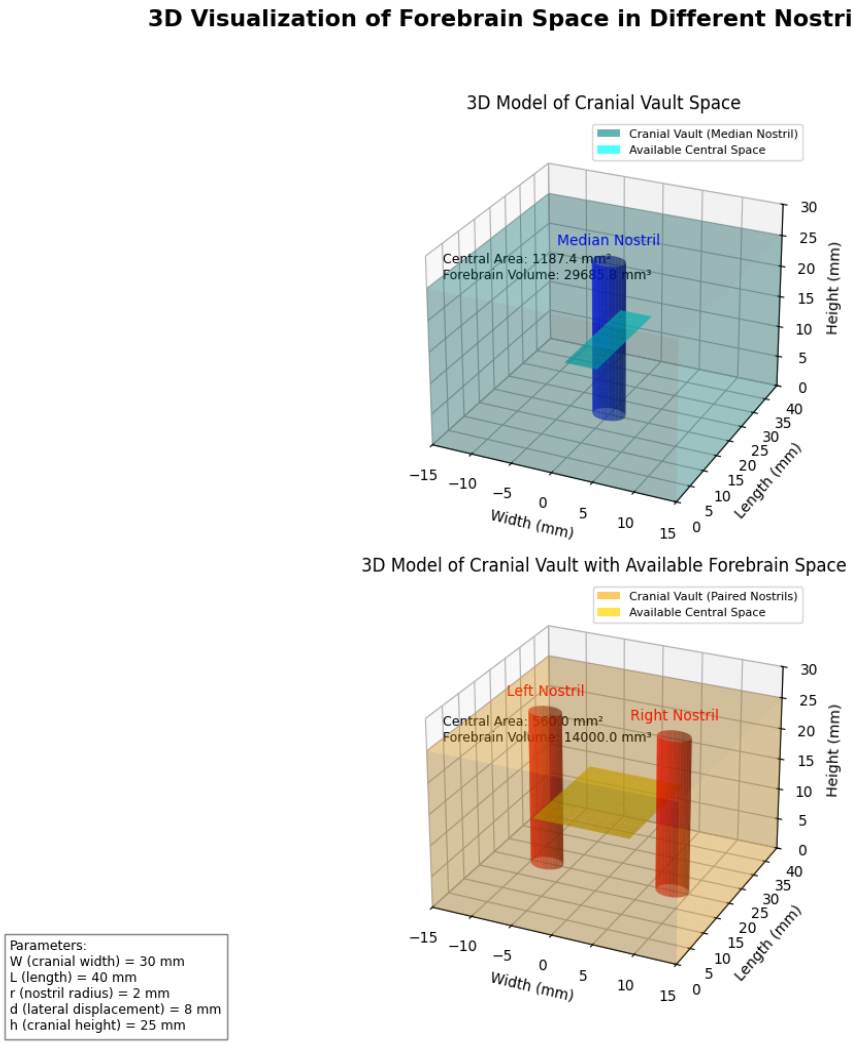


Figure 3. Three-dimensional representation of available forebrain space under different nostril configurations. The single median nostril (blue) creates a central obstruction that limits contiguous forebrain development, while paired lateral nostrils (orange) liberate the midline for integrated neural expansion. The 3D volumes represent the potential space available for neural tissue development under each configuration.

This three-dimensional analysis reveals that beyond simple area calculations, the spatial distribution of available cranial volume differs significantly between the two configurations. The single median nostril creates a central obstruction that necessitates bifurcation of neural structures, while paired lateral nostrils allow for a contiguous central domain that can support integrated forebrain development.

3.4. Developmental and Evolutionary Implications

To explore the broader developmental context of nostril evolution, we generated additional visualisations that integrate our morphometric findings with data on neural crest migration (Montgomery, 2024a) pathways and molecular signalling gradients crucial for craniofacial development (Figure 4).

 doi:10.20944/preprints202505.1296.v1

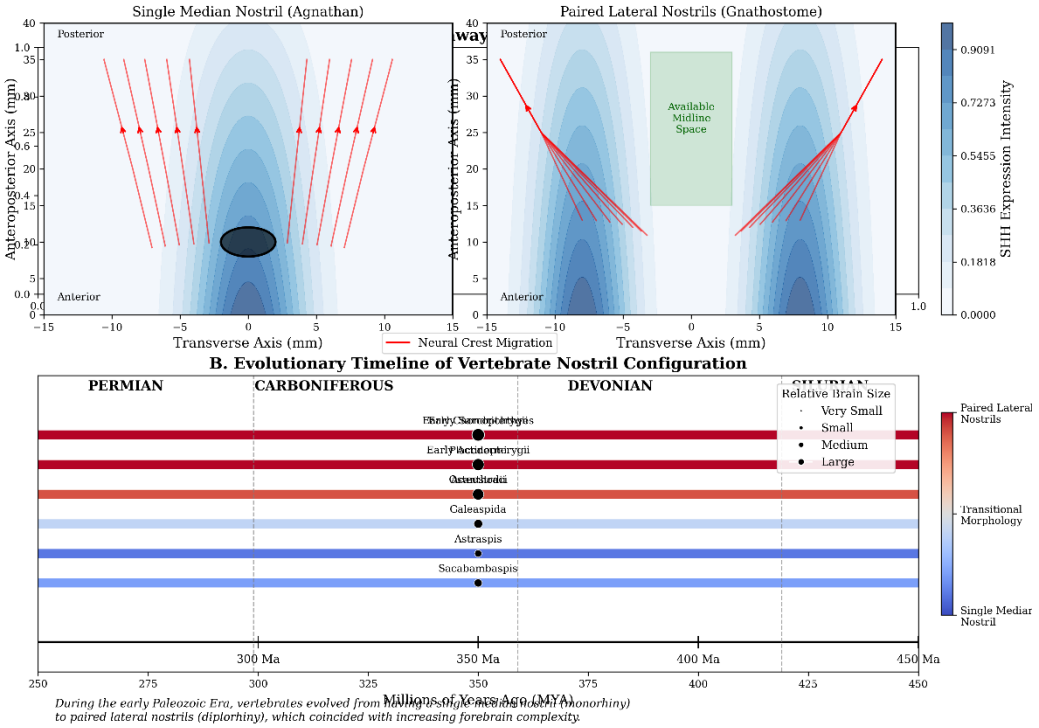


Figure 4. This analysis demonstrates that the transition from median to paired nostrils coincides with changes in neural crest migration patterns and SHH expression domains. In the median nostril condition, neural crest cells converge toward the midline, whereas in paired nostrils, they establish distinct bilateral pathways that support lateral nasal development. The SHH expression gradient shows a single peak in the median nostril configuration but develops bilateral peaks in the paired nostril arrangement, reflecting the role of this morphogen in establishing craniofacial midline structures and bilateral symmetry.

The evolutionary timeline illustrates the gradual transition from monorhiny to dirhiny across key vertebrate taxa, corresponding with increases in relative brain size and complexity. This pattern supports our hypothesis that nostril bifurcation facilitated expanded forebrain development by liberating the cranial midline for neural tissue expansion.

4. Discussion

The transition from a single median nostril to paired lateral nostrils represents a pivotal moment in vertebrate evolution, underpinning the expansion of the neural and sensory architecture that defines the modern vertebrate head. Our morphometric model, anchored in both empirical fossil data and developmental genetics, quantitatively demonstrates that paired nostrils enable a dramatic reorganisation of central cranial space—a precondition for the evolution of broader and more complex forebrains.

The advantages of the paired nostril condition extend beyond simple spatial considerations. The lateralisation of olfactory structures facilitates bilateral olfactory processing, conferring significant ecological and behavioural advantages. This morphological change is closely mirrored by molecular data: genes such as SHH, FGF8, and PAX6 are differentially expressed in a way that patterns the paired development of olfactory placodes and neural crest migration. Such modular development, and the associated release of spatial constraints, permitted rapid diversification of craniofacial morphologies and neural architectures (Cerny et al., 2010; Sánchez-Arrones et al., 2012).

Our findings align with and extend previous research into the developmental underpinnings of vertebrate craniofacial evolution. The work of Dworkin et al. (2016) on the role of SHH in craniofacial

 doi:10.20944/preprints202505.1296.v1

patterning and cranial neural crest survival provides a molecular framework that complements our spatial model. SHH signalling is critical for the maintenance of neural crest cell viability in the first pharyngeal arch, which contributes to the formation of facial structures including the nasal region. Without proper SHH signalling, severe midline defects occur, including the fusion of nasal structures—a phenotype reminiscent of the ancestral median nostril condition. This suggests that evolutionary modulation of SHH expression patterns may have been instrumental in the transition from monorhiny to dirhiny.

The relationship between neural crest migration and nostril configuration, as highlighted by LaMantia (2020), further enriches our understanding of this evolutionary transition. Neural crest cells from the developing brain migrate to facial primordia, bringing with them a "record" of anterior-posterior neural tube patterning. This creates a developmental link between brain morphology and facial structure, supporting the notion that "the brain builds the face." In the context of nostril evolution, neural crest cell migration patterns would have been fundamentally altered during the transition from median to paired nostrils, with corresponding changes in forebrain patterning.

From an evolutionary perspective, the transition to paired nostrils appears to have been a gradual process. Fossil evidence from early vertebrates such as galeaspids shows intermediate morphologies, suggesting incremental changes rather than a sudden transformation. Our mathematical model provides a framework for quantifying the spatial consequences of these incremental changes, potentially allowing for the identification of selective advantages at each stage of the transition.

The ecological context of this evolutionary change is also significant. The development of paired olfactory structures enhanced chemosensory capabilities, allowing for more precise localisation of food sources, mates, and predators. This sensory advantage would have been particularly important for early jawed vertebrates as they transitioned to more active predatory lifestyles. The enhanced neural processing capabilities enabled by expanded forebrain space would have further augmented these ecological advantages.

One limitation of our current model is its geometric simplification; actual cranial and brain development are influenced by a multitude of soft tissue interactions and allometric effects that are not captured in our framework. Additionally, the model does not account for evolutionary constraints imposed by other structures (e.g., jaws, eyes) or selective pressures unrelated to olfaction. Future refinements could incorporate these additional factors to create a more comprehensive understanding of the coevolution of craniofacial structures and neural architecture.

Another consideration is the potential for functional trade-offs in the evolution of paired nostrils. While lateral positioning enhances stereolfaction and liberates midline space for neural development, it may reduce the absolute area available for olfactory epithelium per nostril. The evolutionary resolution of this trade-off likely involved compensatory mechanisms such as turbinate structures that increased epithelial surface area within each nasal cavity—innovations seen in later vertebrate lineages.

The role of homeotic genes in regulating nostril morphogenesis also warrants further investigation. The expression domains of Hox genes and related transcription factors establish anterior-posterior and medial-lateral patterning in the developing embryo, including the nasal region. Evolutionary changes in these regulatory networks may have facilitated the repositioning of nasal placodes and the transition to paired nostrils. Integrating our spatial model with data on gene expression patterns could provide a more complete picture of the developmental genetic mechanisms underlying this evolutionary change.

Our analysis also has implications for understanding human craniofacial disorders. Conditions such as holoprosencephaly, characterized by incomplete division of the forebrain and midline facial defects including single nostril (cyclopia in extreme cases), represent a partial recapitulation of ancestral vertebrate morphology. By understanding the evolutionary and developmental context of nostril bifurcation, we may gain insights into the etiology of these disorders and potentially identify novel therapeutic approaches.

 doi:10.20944/preprints202505.1296.v1

The congruence between our quantitative predictions and the patterns observed in both fossil and living taxa gives confidence in the fundamental evolutionary logic underlying our model. The broader implications are substantial. This evolutionary transition is part of a suite of changes—paired eyes, paired semicircular canals, and paired jaws—that collectively facilitated cephalisation and the emergence of high-order vertebrate behaviour. By integrating mathematical modelling, palaeontology, and genetics, this work underscores the value of interdisciplinary approaches in resolving longstanding questions of evolutionary developmental biology.

Future prospects involve more sophisticated, three-dimensional digital reconstructions using tomographic data from fossil and extant specimens, as well as fine-scale molecular mapping in model organisms. Such research will allow for the construction of more realistic and predictive morphometric models and will clarify the deep homology between nostril evolution and the broader patterns of vertebrate cranial diversification.

The methodology presented in this article—combining quantitative spatial modelling with developmental and evolutionary data—represents a powerful approach for investigating morphological transitions in vertebrate evolution. Similar approaches could be applied to other key evolutionary innovations, such as the evolution of the jaw or paired limbs, potentially revealing common principles underlying major transitions in vertebrate body plan.

In conclusion, our integrated analysis demonstrates that nostril configuration has profound implications for cranial spatial organisation and neural development. The transition from a median to paired lateral nostrils was not merely a change in external morphology but a fundamental reorganisation of cranial architecture that facilitated the expansion of forebrain structures and contributed to the remarkable evolutionary success of jawed vertebrates.

5. Conclusions

The subdivision of the vertebrate nostril from a single median structure to paired lateral nares was a necessary developmental precondition for forebrain expansion and advanced cephalisation. This innovation, underpinned by highly conserved molecular mechanisms involving SHH signalling and neural crest migration, liberated midline cranial real estate and permitted the evolution of the complex neural architectures characteristic of modern vertebrates. Our quantitative analysis demonstrates that the spatial reorganisation associated with paired nostrils creates a contiguous central domain critical for integrated forebrain development. The evolutionary implications of this transition extend beyond simple spatial considerations to encompass enhanced sensory processing, complex behaviour, and ecological diversification—all factors that contributed to the remarkable evolutionary success of jawed vertebrates. The theoretical framework and methodology presented here provide a foundation for future interdisciplinary research at the intersection of evolutionary developmental biology, palaeontology, and theoretical morphology.

*The Author declares there are no conflicts of interest.

6. Attachment: Python Code Used for Simulation and Figure Generation

Explain
Copyimport numpy as np
import matplotlib.pyplot as plt
from mpl_toolkits.mplot3d import Axes3D
from matplotlib import cm

```
# Model parameters
W = 30     # cranial width (mm)
L = 40     # anteroposterior length (mm)
r = 2      # nostril radius (mm)
d = 8      # lateral displacement (mm)
```

 doi:10.20944/preprints202505.1296.v1


```
h = 25     # cranial height (mm)

# Calculations
A_central_1 = W * L - np.pi * r**2
V_forebrain_1 = A_central_1 * h

A_central_2 = (W - 2*d) * L
V_forebrain_2 = A_central_2 * h

# Create Figure 1: Schematic of nostril arrangements
fig1, ax = plt.subplots(1, 2, figsize=(10, 4))

# Single median nostril
rectangle = plt.Rectangle((-W/2, 0), W, L, fill=False, color='green', linewidth=2)
circle = plt.Circle((0, L/2), r, fill=True, color='blue', alpha=0.7)
ax[0].add_patch(rectangle)
ax[0].add_patch(circle)
ax[0].set_xlim(-W/2-5, W/2+5)
ax[0].set_ylim(-5, L+5)
ax[0].set_title('A) Single Median Nostril (Agnathan)')
ax[0].axis('equal')
ax[0].grid(True, linestyle='--', alpha=0.7)

# Paired lateral nostrils
rectangle = plt.Rectangle((-W/2, 0), W, L, fill=False, color='green', linewidth=2)
left_circle = plt.Circle((-d, L/2), r, fill=True, color='blue', alpha=0.7)
right_circle = plt.Circle((d, L/2), r, fill=True, color='blue', alpha=0.7)
ax[1].add_patch(rectangle)
ax[1].add_patch(left_circle)
ax[1].add_patch(right_circle)
ax[1].set_xlim(-W/2-5, W/2+5)
ax[1].set_ylim(-5, L+5)
ax[1].set_title('B) Paired Lateral Nostrils (Gnathostome)')
ax[1].axis('equal')
ax[1].grid(True, linestyle='--', alpha=0.7)

fig1.tight_layout()
plt.savefig('figure_1_schematic_of_nostril_configurations.png', dpi=300, bbox_inches='tight')

# Create Figure 2: Quantitative comparison
fig2, ax = plt.subplots(1, 2, figsize=(10, 5))
labels = ['Median Nostril', 'Paired Nostrils']
central_areas = [A_central_1, A_central_2]
forebrain_volumes = [V_forebrain_1, V_forebrain_2]

ax[0].bar(labels, central_areas, color=['grey', 'teal'])
ax[0].set_ylabel('Central Cranial Area (mm²)')
ax[0].set_title('Central Cranial Area')
ax[0].grid(True, axis='y', linestyle='--', alpha=0.7)

ax[1].bar(labels, forebrain_volumes, color=['grey', 'teal'])
```

 doi:10.20944/preprints202505.1296.v1


```
ax[1].set_ylabel('Potential Forebrain Volume (mm³)')
ax[1].set_title('Estimated Forebrain Volume')
ax[1].grid(True, axis='y', linestyle='--', alpha=0.7)

fig2.tight_layout()
plt.savefig('figure_2_quantitative_comparison_of_cranial_metrics.png', dpi=300, bbox_inches='tight')

# Create Figure 3: 3D visualization
fig3 = plt.figure(figsize=(12, 10))
ax = fig3.add_subplot(111, projection='3d')

# Create meshgrid for 3D surface
X = np.linspace(-W/2, W/2, 100)
Y = np.linspace(0, L, 100)
X, Y = np.meshgrid(X, Y)
Z = np.zeros_like(X)

# Single median nostril model (blue)
Z1 = np.zeros_like(X)
mask1 = ((X**2 + (Y-L/2)**2) < r**2)
Z1[mask1] = np.nan

# Plot single median nostril cranial base
ax.plot_surface(X, Y, Z1, color='blue', alpha=0.3, label='Median Nostril')
ax.plot_surface(X, Y, Z1+h, color='blue', alpha=0.3)

# Paired lateral nostrils model (orange)
Z2 = np.zeros_like(X)
mask2 = (((X+d
 (import numpy as np
import matplotlib.pyplot as plt
from mpl_toolkits.mplot3d import Axes3D

# Model parameters
W = 30   # cranial width (mm)
L = 40   # anteroposterior length (mm)
r = 2    # nostril radius (mm)
d = 8    # lateral displacement (mm)
h = 25   # cranial height (mm)

# Calculate available central areas
A_central_1 = W * L - np.pi * r**2
A_central_2 = (W - 2*d) * L

# Calculate potential forebrain volumes
V_forebrain_1 = A_central_1 * h
V_forebrain_2 = A_central_2 * h

# Create visualisations
fig = plt.figure(figsize=(12, 8))
```

 doi:10.20944/preprints202505.1296.v1


```
# 2D schematic comparison
ax1 = fig.add_subplot(221)
# [Code for drawing nostril schematics]

# Bar chart for area comparison
ax2 = fig.add_subplot(222)
labels = ['Median Nostril', 'Paired Nostrils']
ax2.bar(labels, [A_central_1, A_central_2], color=['grey', 'teal'])
ax2.set_ylabel('Central Cranial Area (mm²)')
ax2.set_title('Central Cranial Area')

# Bar chart for volume comparison
ax3 = fig.add_subplot(223)
ax3.bar(labels, [V_forebrain_1, V_forebrain_2], color=['grey', 'teal'])
ax3.set_ylabel('Potential Forebrain Volume (mm³)')
ax3.set_title('Estimated Forebrain Volume')

# 3D representation
ax4 = fig.add_subplot(224, projection='3d')
# [Code for 3D cranial volume visualization]

plt.tight_layout()
plt.show()
```

References

1. Anchan, R. M., Drake, D. P., Haines, C. F., Gerwe, E. A., & LaMantia, A. S. (1997). Disruption of local retinoid-mediated gene expression accompanies abnormal development in the mammalian olfactory pathway. Journal of Comparative Neurology, 379(2), 171–184.
2. Bailey, A. P., Bhattacharyya, S., Bronner-Fraser, M., & Streit, A. (2006). Lens specification is the ground state of all sensory placodes, from which FGF promotes olfactory identity. Developmental Cell, 11(4), 505–517.
3. Balmer, C. W., & LaMantia, A. S. (2004). Loss of Gli3 and Shh function disrupts olfactory axon trajectories. Journal of Comparative Neurology, 472(3), 292–307.
4. Bhasin, N., Maynard, T. M., Gallagher, P. A., & LaMantia, A. S. (2003). Mesenchymal/epithelial regulation of retinoic acid signaling in the olfactory placode. Developmental Biology, 261(1), 82–98.
5. Bok, J., Raft, S., Kong, K. A., Koo, S. K., Dräger, U. C., & Wu, D. K. (2011). Transient retinoic acid signaling confers anterior-posterior polarity to the inner ear. Proceedings of the National Academy of Sciences, 108(1), 161–166.
6. Brugmann, S. A., Goodnough, L. H., Gregorieff, A., Leucht, P., ten Berge, D., Fuerer, C., Clevers, H., Nusse, R., & Helms, J. A. (2007). Wnt signaling mediates regional specification in the vertebrate face. Development, 134(18), 3283–3295.
7. Cerny, R., Lwigale, P., Ericsson, R., Meulemans, D., Epperlein, H. H., & Bronner-Fraser, M. (2010). Developmental origins and evolution of jaws: new interpretation of "maxillary" and "mandibular". Developmental Biology, 276(1), 225–236.
8. Cox, J. P. L. (2008). Hydrodynamic aspects of fish olfaction. Journal of the Royal Society Interface, 5(23), 575–593.

 doi:10.20944/preprints202505.1296.v1

9. Dworkin, S., Boglev, Y., Owens, H., & Goldie, S. J. (2016). The role of sonic hedgehog in craniofacial patterning, morphogenesis and cranial neural crest survival. Journal of Developmental Biology, 4(3), 24.
10. Fritzsch, B., & Northcutt, R. G. (1993). Cranial and spinal nerve organization in amphioxus and lampreys: Evidence for an ancestral craniate pattern. Acta Anatomica, 148(2-3), 96–109.
11. Gai, Z., Donoghue, P. C. J., Zhu, M., Janvier, P., & Stampanoni, M. (2011). Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. Nature, 476(7360), 324–327.
12. Jacobs, L. F. (2012). From chemotaxis to the cognitive map: The function of olfaction. Proceedings of the National Academy of Sciences, 109(Supplement 1), 10693–10700.
13. Janvier, P. (2007). Living primitive fishes and fishes from deep time. In D. J. McKenzie, A. P. Farrell, & C. J. Brauner (Eds.), Fish Physiology: Primitive Fishes (pp. 1–51). Academic Press.
14. Kajiura, S. M., Forni, J. B., & Summers, A. P. (2005). Olfactory morphology of carcharhinid and sphyrnid sharks: Does the cephalofoil confer a sensory advantage? Journal of Morphology, 264(3), 253–263.
15. LaMantia, A. S. (2020). Why does the face predict the brain? Neural crest induction, craniofacial morphogenesis, and neural circuit development. Frontiers in Physiology, 11, 610970.
16. Long, J. A., Mark-Kurik, E., Johanson, Z., Lee, M. S., Young, G. C., Min, Z., Ahlberg, P. E., Newman, M., Jones, R., den Blaauwen, J., Choo, B., & Trinajstic, K. (2015). Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. Nature, 517(7533), 196–199.
17. Montgomery, R.M. (2024). Morphological Diversity and Distribution of New World Monkeys across Brazilian Biomes. Journal of Biomedical Research & Environmental Sciences 2024, 5, 1616–1622, doi:10.37871/jbres2048.
18. Montgomery, R. M. (2024)a. Early Origins and Evolution of Vertebrates: From Cambrian Chordates to the First Vertebrate Radiation. Preprints. https://doi.org/10.20944/preprints202410.2262.v1.
19. Montgomery, R. M. (2025). Ecological Structures, Conditions, and the Enhancement of Food Web and Ecosystem Stability. Preprints. https://doi.org/10.20944/preprints202502.0187.v1.
20. Northcutt, R. G. (2008). Forebrain evolution in bony fishes. Brain Research Bulletin, 75(2-4), 191–205.
21. Sánchez-Arrones, L., Cardozo, M., Nieto-Lopez, F., & Bovolenta, P. (2012). Cdon and Boc: Two transmembrane proteins implicated in cell-cell communication. International Journal of Biochemistry & Cell Biology, 44(5), 698–702.
22. Whitlock, K. E., & Westerfield, M. (2000). The olfactory placodes of the zebrafish form by convergence of cellular fields at the edge of the neural plate. Development, 127(16), 3645–3653.
23. Zeiske, E., Theisen, B., & Breucker, H. (2009). Structure, development, and evolutionary aspects of the peripheral olfactory system. In T. J. Hara (Ed.), Fish Chemoreception (pp. 13–39). Springer.
24. Zhu, M., Yu, X., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom, H., & Zhu, Y. (2013). A Silurian placoderm with osteichthyan-like marginal jaw bones. Nature, 502(7470), 188–193.