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Richard Murdoch Montgomery *

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Article

The Mesozoic Split: Biogeographical and Evolutionary Consequences of the South America-Africa Continental Separation on Vertebrate Fauna

Richard Murdoch Montgomery

Universidade de Aveiro, Portugal; mariaantoniavmg@gmail.com

Abstract: This review examines the progressive separation of South America and Africa, which began approximately 145 million years ago during the Early Cretaceous and completed 100 million years ago. The rifting process created the South Atlantic Ocean and profoundly influenced vertebrate evolution on both continents. Initially connected as part of Gondwana, the gradual separation led to vicariant speciation and distinct evolutionary trajectories for previously continuous vertebrate populations. The separation particularly affected terrestrial vertebrates, resulting in parallel evolution of similar ecological niches on both continents, while creating opportunities for endemic lineages to develop. This process explains many modern distribution patterns and evolutionary relationships between South American and African vertebrate taxa, including parallel radiations in groups such as titanosaur dinosaurs during the Cretaceous and later parallel developments in mammals during the Cenozoic. The isolation also contributed to unique characteristics in each continent's modern vertebrate assemblages, such as the distinctive nature of South American primates and African ungulates.

Keywords: continental drift; Gondwana; vicariance; vertebrate evolution; Cretaceous; biogeography; South Atlantic; speciation; endemism; paleobiogeography

1. Introduction

The separation of South America and Africa represents one of the most significant geological events in Earth's history, fundamentally shaping the evolution and distribution of vertebrate fauna on both continents. This prolonged process, which began approximately 145 million years ago (Ma) during the Early Cretaceous and completed around 100 Ma (Granot and Dymont, 2015), created distinct evolutionary laboratories that would eventually give rise to remarkably different, yet parallel, vertebrate assemblages.

The initial configuration of these landmasses as part of western Gondwana provided a continuous landscape for vertebrate dispersal and evolution. Prior to separation, the fauna shared common morphological traits and showed similar taxonomic diversity across what would become two distinct continents (Serenio et al., 2004). *The presence of closely related taxa with similar morphological characteristics on both continents today serves as compelling evidence of their shared geological history and subsequent divergence.*

Among dinosaurs, one of the most striking examples of this shared heritage is found in the titanosaur sauropods. Fossil evidence indicates that genera such as *Paralititan* from Africa and *Argentinosaurus* from South America shared numerous morphological traits, including elongated cervical vertebrae, distinctive neural spine configurations, and similar appendicular skeletal proportions (Novas, 2009). These similarities suggest a common ancestry before the continental split, followed by parallel evolution in response to similar environmental pressures.

The morphological consequences of continental separation are particularly evident in the skeletal adaptations of various vertebrate groups. For instance, studies of early Cretaceous theropod dinosaurs reveal gradual divergence in cranial features between South American and African

specimens (Serenio et al., 1996). The abelisaurid theropods, represented by *Carnotaurus* in South America and *Rugops* in Africa, demonstrate how isolation led to distinct morphological specializations while maintaining certain ancestral characteristics (Canale et al., 2009).

In the realm of early mammals, the *Gondwanatheria* provide crucial evidence of the morphological diversification that occurred following continental separation. These mammals, known from both South America and Africa, show increasing divergence in dental morphology through the Late Cretaceous, suggesting adaptation to different dietary niches in their respective isolated environments (Krause et al., 2014).

The process of continental separation also influenced the evolution of freshwater and coastal vertebrates. The progressive formation of the South Atlantic Ocean created new marine environments while simultaneously fragmenting freshwater systems. This had profound implications for fish morphology, particularly evident in the lungfish lineages. The South American genus *Lepidosiren* and the African *Protopterus* show divergent skeletal modifications while retaining the fundamental characteristics of their common ancestor (Clement and Long, 2010).

Early Cretaceous deposits from both continents have yielded fossils of crocodyliform archosaurs that demonstrate the beginning of morphological divergence. The *notosuchians*, for example, show increasing skeletal differentiation between South American and African forms through the Cretaceous, with unique cranial adaptations emerging on each continent (O'Connor et al., 2010). The South American forms developed more specialized heterodont dentition, while their African counterparts maintained relatively more conservative dental patterns.

The timing of separation also coincided with the early diversification of modern bird lineages. Fossil evidence suggests that the isolation of continental populations contributed to distinct morphological trajectories in various avian groups. The early radiation of paleognath birds, including the ratites, provides a compelling example of how continental separation influenced skeletal modifications and size evolution (Mitchell et al., 2014).

The post-separation period was characterized by independent but parallel evolution of various vertebrate groups on each continent. This is particularly evident in the development of cursorial adaptations in different lineages of predatory dinosaurs. While sharing common ancestral features, the late Cretaceous theropods of South America and Africa show distinct modifications in limb proportions and cranial architecture, reflecting adaptation to local environmental conditions (Novas et al., 2013).

The morphological consequences of continental separation extended well into the Cenozoic, influencing the evolution of modern mammal groups. *The unique characteristics of South American primates, for instance, can be traced back to the isolation of their ancestors following continental separation.* Their distinctive dental patterns and postcranial adaptations reflect long-term evolution in isolation from their African relatives (Bond et al., 2015).

Similarly, the ungulate mammals of Africa and South America demonstrate how isolation led to different adaptive solutions to similar ecological challenges. The evolution of high-crowned teeth in response to grassland environments, for example, occurred independently in different lineages on each continent, resulting in convergent but distinct morphological adaptations (MacFadden, 2000).

The study of these morphological patterns has been greatly enhanced by modern analytical techniques. Geometric morphometrics and three-dimensional imaging have revealed subtle but significant differences in skeletal structure between related taxa on both continents, providing new insights into the timing and nature of evolutionary divergence (Polly et al., 2013).

Understanding the relationship between continental separation and morphological evolution requires consideration of multiple factors, including climate change, ecological interactions, and the physical barriers created by the widening South Atlantic. The process was not uniform across all taxonomic groups, with some lineages showing rapid divergence while others maintained more conservative morphologies despite continental isolation (Upchurch et al., 2015).

Current research continues to uncover new evidence of how the separation of South America and Africa influenced vertebrate evolution. Recent discoveries of transitional forms from the Early Cretaceous provide increasingly detailed information about the morphological changes that occurred

during and after continental separation. These findings help reconstruct the sequence of evolutionary events and their relationship to geological processes (Pol and Leardi, 2015).

Moreover, the study of extant vertebrates through molecular phylogenetics has provided additional insights into the timing and pattern of divergence between South American and African lineages. These analyses, combined with morphological data from the fossil record, create a more complete picture of how continental separation shaped vertebrate evolution (Springer et al., 2011).

The progressive separation of South America and Africa thus represents a natural experiment in evolutionary biology, demonstrating how geological processes can drive morphological innovation and divergence. The resulting patterns of skeletal adaptation, dental modification, and overall body plan evolution continue to inform our understanding of macroevolutionary processes and the relationship between geological and biological change.

This complex history of separation and subsequent independent evolution has left an indelible mark on the vertebrate faunas of both continents. The study of these patterns provides crucial insights into the processes of speciation, adaptation, and morphological evolution, while also highlighting the profound influence of geological events on biological diversity.

2. Discussion

The analysis of the South America-Africa separation reveals complex patterns of vertebrate evolution that extend beyond simple vicariance models. While the introduction focused on broad morphological patterns, several nuanced aspects deserve deeper consideration.

First, the timing of morphological divergence appears asynchronous across different vertebrate groups. For instance, while some dinosaur lineages showed rapid differentiation following initial rifting (Novas et al., 2013), certain amphibian groups maintained remarkably conserved morphologies despite continental separation (San Mauro et al., 2017). This suggests that intrinsic biological factors, such as dispersal ability and environmental tolerance, played crucial roles alongside geographical isolation.

The concept of "ghost lineages" becomes particularly relevant when considering the incomplete nature of the fossil record during this critical period. Many morphological innovations likely emerged during intervals poorly represented in the fossil record, creating challenges in reconstructing the precise timing of divergence events.

Furthermore, recent discoveries of trans-Atlantic dispersal events during the Late Cretaceous (Ezcurra and Agnolín, 2012) complicate the traditional view of complete isolation after continental separation. *These findings suggest that occasional faunal exchanges may have occurred via island chains or other temporary connections, potentially influencing morphological evolution through periodic gene flow.*

Lastly, the parallel evolution of similar morphological features on both continents raises intriguing questions about developmental constraints and the predictability of evolutionary trajectories under similar selective pressures.

2.1 Evolutionary Consequences

The evolutionary consequences of the South America-Africa separation represent a complex tapestry of biological responses to geographical isolation, environmental change, and adaptive pressures. While the introduction established the fundamental patterns of vertebrate evolution during this period, several aspects warrant deeper examination and reveal more nuanced understanding of this major geological event's biological implications.

The parallel evolution of similar morphological features on both continents raises intriguing questions about developmental constraints and the predictability of evolutionary trajectories under similar selective pressures. For example, the independent evolution of cursorial adaptations in different theropod lineages on both continents suggests that certain morphological solutions to ecological challenges may be somewhat deterministic (Sereno et al., 2004).

The role of climate change during the separation process cannot be understated. Recent paleoclimatic studies indicate that the opening of the South Atlantic created distinct atmospheric and oceanic circulation

patterns that differentially affected the two continents (Huber and Caballero, 2011). These climatic changes likely drove many of the morphological adaptations observed in the fossil record, particularly in terms of body size evolution and thermoregulatory adaptations.

Another crucial aspect is the differential impact of the separation on various ecological guilds. *While large terrestrial vertebrates show clear patterns of vicariant speciation, the effects on small vertebrates, particularly those with high dispersal capabilities like birds, present a more complex picture.* Modern molecular studies of bird lineages suggest that aerial dispersal across the early South Atlantic may have been more common than previously thought (Claramunt and Cracraft, 2015).

The role of ecological opportunity in driving morphological innovation following continental separation deserves special attention. The isolation of continental fragments created novel ecological niches and reduced competition in certain adaptive zones, potentially accelerating morphological evolution in some lineages. This is particularly evident in the radiation of South American ungulates, which evolved unique dental and skeletal adaptations in the absence of competition from African ungulate lineages (MacFadden, 2000).

The study of extant vertebrates through molecular phylogenetics has provided additional insights into the timing and pattern of divergence between South American and African lineages. These analyses, combined with morphological data from the fossil record, create a more complete picture of how continental separation shaped vertebrate evolution. However, molecular clock estimates sometimes conflict with fossil evidence, suggesting that our understanding of evolutionary rates during this period may need revision (Springer et al., 2011).

The role of environmental stress during the separation process may have accelerated evolutionary change in some lineages. The changing geography would have created novel environmental pressures, potentially driving rapid morphological evolution in some groups while leading to extinction in others. This selective pressure may explain some of the dramatic morphological innovations observed in the fossil record during this period (Benton, 2009).

Recent advances in geometric morphometrics and three-dimensional imaging techniques have revealed previously unrecognized patterns of morphological divergence between related taxa on both continents. These new methodologies have allowed for more precise quantification of skeletal modifications and have highlighted subtle but significant differences in the evolutionary trajectories of various lineages (Polly et al., 2013).

The implications of the South America-Africa separation extend beyond morphological evolution to include broader patterns of biodiversity and ecosystem development. The independent evolution of similar ecological roles on both continents provides insights into the predictability of evolution and the constraints on morphological adaptation (Losos, 2011).

Looking forward, several key questions remain unresolved. The precise timing of morphological divergence in many groups remains uncertain, and the relative importance of vicariance versus dispersal in shaping vertebrate evolution during this period continues to be debated. Additionally, the role of extinction in shaping the observed patterns of morphological evolution requires further investigation.

Moreover, ongoing discoveries continue to refine our understanding of this crucial period in Earth's history. New fossils regularly challenge existing models of vertebrate evolution during the separation process, suggesting that our understanding of this major evolutionary event continues to evolve.

The study of the South America-Africa separation thus provides a unique window into the processes of large-scale evolutionary change. By combining insights from paleontology, molecular biology, and geological sciences, we can better understand how major geological events shape the evolution of life on Earth. This knowledge has important implications for predicting how modern organisms might respond to ongoing environmental and geological changes.

Conclusions

The progressive separation of South America and Africa during the Mesozoic era stands as a remarkable natural experiment in evolutionary biology, providing crucial insights into the mechanisms of speciation, adaptation, and morphological diversification. The evidence presented throughout this article demonstrates that the continental split led to complex and often asynchronous patterns of vertebrate evolution, shaped by a combination of isolation, environmental change, and ecological opportunity.

The legacy of this separation is evident in both the fossil record and contemporary vertebrate fauna of both continents. While some lineages underwent rapid divergence and morphological innovation, others maintained conservative forms despite geographical isolation. This variation in evolutionary response highlights the complex interplay between geological events and biological adaptation.

Understanding these historical patterns has important implications for modern conservation biology and our predictions of how species might respond to current and future environmental changes. As we continue to uncover new fossil evidence and apply advancing analytical techniques, our comprehension of this crucial period in Earth's history continues to evolve, offering new insights into the fundamental processes of evolution.

Conflicts of Interest: The Author claims there are no conflicts of Interest.

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