A Review on Why Some of the Reptilian Lineages are Relict Taxa?

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Abstract: ***The Earth has never remained environmentally or geologically stable since its origin. Plate tectonics, continental drift, climatic oscillations, sea-level fluctuations, geological catastrophes and associated ecological changes have repeatedly altered the distribution, diversification and extinction of several organisms. These processes have profoundly influenced the evolutionary history and biogeography of the so-called Class Reptilia. Nevertheless, several extant reptilian lineages represent highly distinctive remnants of formerly more diverse and geographically widespread evolutionary radiations. Such taxa are commonly referred to as evolutionary or phylogenetic relicts. The present review reveals why some reptilian lineages have remained comparatively conservative in their fundamental morphology while other reptilian taxa have undergone extensive diversification and innovation of morphologically novel traits. Particular attention is given to the tuatara (Sphenodon punctatus), phylogenetically primitive monitor lizard (lack of exposed external tympanum), Lanthanotus borneensis and the Gharial (Gavialis gangeticus) as examples of evolutionarily distinctive and unique surviving monotypic lineages, taxonomically known as monotypic taxa. The review discusses phylogenetic conservatism and ecological constraints with respect to niche segregation, ecological specialization, stabilizing selection, developmental as well as functional constraints, geographic isolation, extinction filtering, climatic change, ecological opportunity and historical contingency as possible factors contributing to relictuality. Importantly, morphological conservatism should not be interpreted as evolutionary inactivity. Fossil evidence demonstrates that Rhynchocephalians, for example, were once morphologically and ecologically diverse, and Sphenodon represents only the surviving component of that former adaptive radiation. Similarly, extant crocodilians constitute a small surviving fraction of a much more diverse crocodylomorph evolutionary history. Therefore, the apparent evolutionary conservatism of some living reptiles may partly reflect differential extinction rates and the survival of particular ecological and most adaptive phenotypes rather than an absence of evolutionary change. The term "living fossil" is consequently problematic when it is used to imply evolutionary stagnation. The concept of an evolutionary relicts or phylogenetic relicts provides a more appropriate framework for discussing surviving representatives of ancient and formerly more diverse lineages. Understanding reptilian relicts requires much better integration of evolutionary biology, palaeontology, ecology, biogeography, phylogenetics and finally conservation biology.***

Keywords: Reptilia; evolutionary relict; phylogenetic relict; phylogenetic niche conservatism; evolutionary stasis; morphological conservatism; extinction filtering; natural selection; macroevolution; Rhynchocephalia; Squamata; Crocodylia.

1. Introduction

The Earth on which we live has never remained geologically, climatically or ecologically stable throughout its history. Plate tectonics has repeatedly modified continental formations, oceanic connections, submersion of small islands and emergence of many terrestrial habitats, while climatic oscillations, sea-level fluctuations, volcanic activity and mass-extinction events have altered the distribution and ecological structure of biological communities. Consequently, the evolutionary history of organisms cannot be separated from the geological and environmental history of the planet.

Plate tectonics is particularly important in biogeography because continental fragmentation, splitting and tectonic movements can promote geographic isolation, vicariance and subsequent population divergence, while formation of new land bridge connectivity may also facilitate and enhance species dispersal. Such geophysical processes have contributed substantially to the distribution and species diversification of vertebrate lineages.

A fundamental question therefore arises: if evolutionary change is continuous, why do some extant reptilian lineages appear remarkably conservative in their fundamental body plans while other lineages have undergone extensive morphological and ecological diversification?

Examples frequently discussed in this context include the Rhynchocephalian *Sphenodon punctatus*, the Anguimorph *Lanthanotus borneensis*, and the Gharial *Gavialis gangeticus*. These taxa possess highly distinctive combinations of morphological traits which includes ecological and phylogenetic characteristics and represent surviving branches of evolutionary more diverse lineages in the past. The tuatara, for example, is the sole surviving representative of a formerly diverse Mesozoic Rhynchocephalian radiation. Fossil evidence demonstrates that Rhynchocephalians exhibited substantial morphological and ecological disparity during the Mesozoic.

The persistence of such lineages raises important questions concerning evolutionary conservatism, stabilizing selection, ecological constraint, phylogenetic niche conservatism, extinction filtering and evolutionary stasis. These concepts are particularly relevant to understanding macroevolutionary patterns within Reptilia.

Evolutionary change and biological stability

The statement that "**change is the only constant**" has considerable relevance to evolutionary biology, but it should not be interpreted to mean that every lineage must undergo continuous and conspicuous morphological transformation.

Evolution occurs through changes in populations over generations, but the rate and direction of evolutionary changes are not uniform among lineages. Some populations may undergo rapid morphological diversification, whereas others may retain relatively similar and stable phenotypes over long geological intervals.
Consequently, evolutionary history can involve both:
1) Rapid evolutionary innovation (of novel traits) and adaptive radiations; and
2) Prolonged periods of relative morphological conservatism.

So morphological conservatism should therefore not be equated with evolutionary stagnation.

Reptilia and phylogenetic interpretation
Reptilian diversity is deeply embedded within the evolutionary phylogenetics of the clade Amniota. In traditional classifications, **"The term 'Reptilia' has historically been used in a narrower, traditional sense to refer to non-mammalian amniotes, often excluding Aves. In a broader phylogenetic context, however, Reptilia encompasses the diverse evolutionary radiation of Sauropsid amniotes, including extant and extinct lineages such as Testudines, Lepidosauria, Crocodylia, terrestrial non-avian Dinosauria, volant Pterosauria, aquatic Ichthyosauria, Sauropterygia and Mosasauridae. Under a phylogenetic definition, Aves are also nested within Reptilia through Dinosauria and therefore cannot be excluded from a truly clade-based concept of Reptilia."** In a modern phylogenetic Cladistics, however, taxonomic definitions should be based on explicit clade concepts rather than on typical traditional Linnean taxonomic hierarchy.

A clade comprises an ancestor and all of its descendants. **Synapomorphies** are shared evolutionary novel derived character traits that help to understand monophyletic groups in a clade, whereas **symplesiomorphies** are shared ancestral characters and generally do not provide evidence for exclusive evolutionary relationships between taxa.

This distinction is particularly important when discussing "evolutionary primitive" and comparatively recently evolved reptiles. An extant taxon may retain some ancestral character states while simultaneously possessing numerous derived characters. Consequently, describing an entire lineage as "primitive" can obscure its actual evolutionary history. The same principle applies to relict taxa.

An evolutionary relict is not an ancestral species living in the present.
Rather, it is a **surviving relict lineage** that has persisted after the extinction many of their sister taxa.

Speciation, geographic isolation and macroevolution
Geographic isolation has played an important role in the diversification of many reptilian groups. Allopatric divergence may occur when populations become separated by geographical barriers, whereas peripatric divergence represents a particular form of geographic isolation involving small peripheral populations.

Parapatric divergence may occur when neighbouring populations experience different selective environments despite some degree of gene flow. Sympatric speciation, although well documented in several groups of organisms, is more difficult to demonstrate conclusively in many reptilian radiations and should not be assumed to have played either a major or minor role without lineage-specific evidence.

It is therefore preferable to consider speciation as a multifactorial process involving:
- Geographic isolation; ecological differentiation; sexual selection; genetic drift; natural selection; reproductive isolation; hybridization and introgression; environmental heterogeneity; and historical contingency.

These processes operate at the population and species levels, while their accumulated consequences contribute to macroevolutionary patterns such as adaptive radiation, extinction, morphological disparity and clade diversification.

Natural selection and evolutionary conservatism
Darwinian natural selection remains one of the central mechanisms explaining adaptation. Natural selection can alter the frequency of heritable phenotypic variation when particular traits influence survival or reproductive success.

However, natural selection does not necessarily produce continuous directional morphological transformation.

Where an existing phenotype performs efficiently under relatively stable ecological conditions, stabilizing selection may favour intermediate or functionally optimal phenotypes and reduce the frequency of extreme variants. This may contribute to morphological conservatism.

It is therefore inappropriate to state that natural selection is not important in macroevolution. Rather, macroevolutionary patterns emerge from the synergistic cumulative interaction of microevolutionary processes with speciation, extinction, developmental constraints, ecological opportunity and evolution of evolvability.

Evolutionary stasis and the fossil record
The concept of evolutionary stasis describes relatively limited overall morphological changes within a lineage over a particular geological interval. Stasis, however, does not imply the complete absence of genetic or physiological evolution.

Furthermore, the fossil record should not be interpreted as a continuous sequence of morphological transitions for every lineage. Fossilization is highly incomplete and geographically and temporally biased.

Punctuated equilibrium provides one model for explaining certain patterns in the fossil record, in which morphological change is concentrated around speciation events and followed by comparatively prolonged periods of morphological stability. However, punctuated equilibrium should not be used as a universal explanation for the absence of transitional fossils in the geological records.

Different lineages may exhibit different evolutionary tempos, including gradual change, episodic change, stasis or combinations of these patterns.

Why are some reptilian lineages relict?

Several interacting processes may explain why particular reptilian lineages survive while their close sister taxa become extinct.

Phylogenetic niche conservatism

Phylogenetic niche conservatism describes the tendency of ecological characteristics to remain stable with respect to other related lineages over evolutionary time. A lineage may therefore retain aspects of its ancestral ecological niche while undergoing genetic and phenotypic evolution. Such conservatism may be promoted by ecological specialization, physiological limitations, developmental constraints and environmental stability.

Ecological specialization

Highly specialized organisms may persist successfully when their ecological requirements remain available. However, specialization may simultaneously increase extinction risk when environments change rapidly. Thus, ecological specialization can have a dual evolutionary consequence: high ecological efficiency under stable conditions but increased vulnerability under environmental disruption.

Stabilizing selection

Where an existing morphology remains functionally effective, stabilizing selection may reduce the persistence of extreme phenotypes.

This can produce relative morphological conservatism without preventing evolutionary change.

Developmental and functional constraints

Developmental as well as functional integration can constrain the range of viable morphological transformations. Strong integration among skeletal, muscular, respiratory and locomotor systems may make major alterations to an established body plan difficult without simultaneous changes in several associated traits.

Geographic isolation and ecological refugia

Geographic isolation can protect surviving populations from competition and environmental changes occurring elsewhere.

Isolated islands, wetlands, river systems, forest patches and other ecological refugia may therefore act as reservoirs in which ancient evolutionary lineages may persist.

Extinction filtering

Perhaps the most important factor is differential extinction rates. A formerly diverse radiation may contain numerous lineages, but geological and ecological changes can eliminate most of them. The few surviving lineages may consequently appear exceptionally conservative when viewed only from the perspective of modern biodiversity. The present-day diversity of a lineage therefore represents a survivorship filte**r** imposed by its evolutionary history.

***Sphenodon punctatus*: an evolutionary relict**

The tuatara provides perhaps the clearest example of reptilian evolutionary relicts or phylogenetic relicts.

Sphenodon punctatus is the only living representative of Rhynchocephalia, a group that was considerably more diverse and widespread during the Mesozoic. Fossil Rhynchocephalians demonstrate substantial variation in skull morphology, feeding adaptations, body size and ecological specialization. Therefore, the tuatara should not be interpreted as an unchanged Mesozoic reptile. Rather, it is the surviving relict lineage of an ancient and formerly diverse radiation. This distinction is crucial. The fossil record does not support the simplistic proposition that *Sphenodon* has remained morphologically unchanged for more than 200 million years. Indeed, comparative analyses of rhynchocephalians have demonstrated substantial morphological disparity within the group and have challenged the traditional "living fossil" interpretation. Consequently: Sphenodon is best understood as an evolutionary or phylogenetic relict rather than as an unchanged ancestral reptile.

***Lanthanotus borneensis* and varanoid relictuality**

Lanthanotus borneensis, represents another highly distinctive surviving Anguimorph lineage. *Lanthanotus* and *Varanus* are closely related within the varanoid/anguimorph radiation, although the precise phylogenetic placement of fossils and extant varananoid taxa has varied among analyses. The evolutionary significance of *Lanthanotus* lies not simply in its apparently unusual morphology but in its representation of a deeply distinctive surviving lineage. Its restricted range dispersal and ecological specialization make it particularly interesting for understanding how geographic isolation, ecological constraints, species specialization and extinction can contribute to the persistence of evolutionarily distinctive taxa. It should nevertheless be emphasized that *Lanthanotus* is not "primitive" in an evolutionary sense. It possesses its own derived morphological and physiological characters through ecological adaptation.

Gavialidae and crocodilian evolutionary conservatism

The Gharial, *Gavialis gangeticus*, provides a particularly interesting example of ecological and morphological specialization among extant Crocodilians. Its highly elongated and narrow snout represents (longirostral skull) a specialized feeding morphology rather than evidence of evolutionary primitiveness. Crocodilian evolutionary history further demonstrates why extant morphological conservatism should be interpreted cautiously. Crocodylomorpha historically contained a much broader range of ecological and morphological forms than the living crocodilian fauna. Consequently, the relatively restricted modern diversity of Crocodylia partly reflects substantial extinction and ecological filtering. The apparent conservatism of living crocodilians therefore represents both retention of an effective functional morphology and survival following extensive lineage extinction.

Relict taxa versus "living fossils"

The term "living fossil" has historically been applied to organisms such as *Sphenodon*, but the term can be misleading when it implies that an extant species is literally equivalent to a fossil lineage. A living organism is not a fossil. Moreover,

Paper ID: SR26825114241 DOI: https://dx.doi.org/10.21275/SR26825114241

evolutionary studies of Rhynchocephalia demonstrate that the fossil relatives of *Sphenodon* were considerably more diverse and morphologically disparate than the extant tuatara.

The terminology "evolutionary relict" or "phylogenetic relict" is therefore preferable when the intention is to emphasize the survival of an evolutionary distinctive lineage. A relict is not an evolutionary failure.

It is a lineage that has survived the extinction and transformation of much of its former evolutionary radiation.

Mass extinction and evolutionary opportunity

Mass-extinction events can profoundly restructure ecosystems by eliminating large numbers of competing lineages. Following extinction events, surviving lineages may experience ecological niche expansion to diversify into previously occupied niches known as morphospaces. Conversely, lineages that survive mass extinctions but fail to diversify may become disproportionately isolated representatives of ancient clades and became depauperate taxa. Thus, both adaptive radiation and relictuality may be alternative outcomes of the same evolutionary perturbation. One surviving lineage may diversify extensively, whereas another may persist within a relatively narrow ecological domain.

The role of ecological and evolutionary specialization

The persistence or survival of relict taxa may largely depend upon the balance and calibration between ecological specialization and environmental stability. A specialized lineage may possess highly efficient adaptations to a particular ecological niche. If that niche persists, the lineage may survive with comparatively limited changes to its fundamental morphology. However, if environmental conditions change rapidly, specialization may become an evolutionary challenge.

This relationship can be represented conceptually as: Environmental stability → ecological persistence → stabilizing selection → morphological conservatism.
whereas: Environmental disruption or change → ecological extinction → diversification or lineage loss. Consequently, the same evolutionary mechanisms that promote persistence under one set of environmental conditions may increase extinction risk under another.

Epigenetics and phenotypic plasticity

The capacity of organisms to respond phenotypically to environmental variation may also influence long-term persistence.

Phenotypic plasticity can allow populations to tolerate environmental heterogeneity without immediate genetic fixation of every phenotypic response. Epigenetic mechanisms may contribute to environmentally responsive gene regulation and potentially influence phenotypic variation across generations. Nevertheless, epigenetics should not be presented as a universal explanation for the survival of relict taxa. Its contribution must be demonstrated independently in each lineage.

Conservation implications

Many evolutionary relicts possess restricted geographical distributions or range extension and low extant species diversity. Such characteristics can make them especially vulnerable to environmental disturbance. The extinction of the final surviving lineage of an ancient clade represents not merely the loss of a species but the loss of an entire branch of evolutionary history.

Consequently, conservation priorities should consider phylogenetic diversity in addition to species richness.

The conservation of *Sphenodon*, *Lanthanotus*, *Gavialis* and other evolutionarily distinctive reptiles is therefore important because these taxa represent unique evolutionary histories that cannot be brought back once lost.

2. Conclusion

The existence of relict reptilian taxa demonstrates that evolutionary change does not proceed at a uniform rate across all lineages.
Some reptilian lineages have undergone spectacular adaptive radiations, whereas others have persisted by retaining comparatively conservative fundamental body plans with respect to their morphology. This difference should not be interpreted as evidence that evolution has stopped and not at all happening.

Rather, reptilian relictuality is probably produced by a complex interaction of phylogenetic niche conservatism, stabilizing natural selection, ecological specialization, developmental and functional constraints, geographic isolation, environmental stability, historical contingency and differential extinction rates.

The fossil record is particularly important because modern biodiversity represents only the surviving fraction of ancient evolutionary diversity. Rhynchocephalia provides a clear example: the living *Sphenodon* is not an unchanged representative of an ancestral reptile but the surviving member of a formerly diverse Mesozoic radiation.

Similarly, the modern crocodilian fauna represents only a small surviving component of a historically much more diverse crocodylomorph radiation.

Therefore, the term evolutionary or phylogenetic relict is more informative than "living fossil" when describing such taxa. Relictuality should be understood not as evolutionary stagnation but as long-term persistence of a lineage following extensive evolutionary, ecological and extinction-driven restructuring of its surrounding biota.

In this context, evolutionary relicts are not organisms that have escaped evolution. They are organisms whose evolutionary histories have been shaped by the unusual combination of persistence, constraint, specialization and survival.

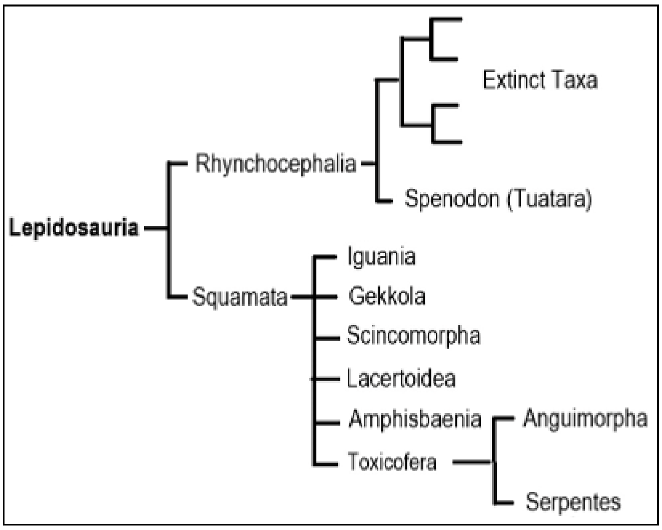

Figure 1: Showing a simplified hypothetical Clade Rhynchocephalia and its diversified extinct branches and extant remnant tuatara.

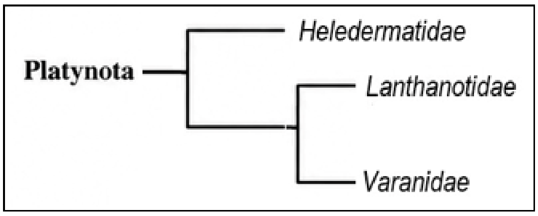

Figure 2: Showing a simplified hypothetical Clade Platynota also known as Anguimorpha and the probable Cladistic position of Lanthanotidae and its immediate phylogenetic or evolutionary relationships with much diverse Varanidae or monitor lizards

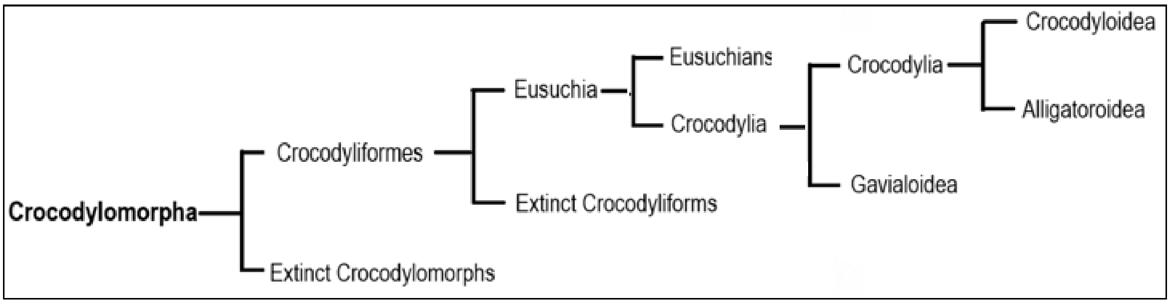

Figure 3: Showing a simplified hypothetical Clade of the extinct Eusuchians and extant much diverse Crocodilian Clade and its probable phylogenetic or evolutionary relationship with relatively much conserved Gavialidae.

Acknowledgments

We thank our project in-charge and co project in-charge, Centre for Environmental Management of Degraded Ecosystems (CEMDE), Department of Environmental Studies, University of Delhi, India, and the Delhi Development Authority (DDA) for institutional and financial support. We are thankful to the Director National Museum of Natural History (NMNH), New Delhi, India. We provide special gratitude to Mr. H. M. Mukherjee, former Senior Publication Officer, Botanical Survey of India (BSI). Finally, we thank Miss. Reysuka, Palaeontologist and Dinosaur Palaeobiologist from Tokyo, Japan, for her kind enthusiasm and support and little master Bihan for his enduring curiosity and profound interest in dinosaur evolution and extinction.

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