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Multidisciplinary and interdisciplinary uses and approaches to vertebrate biostratigraphy

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Summary

Vertebrate biostratigraphy is essential to characterizing both marine and terrestrial strata by their fossil content. Calibrating biostratigraphy is an iterative and multidisciplinary process that supplies numeric ages necessary for calculating rates of change in phylogenetic processes, refining studies of evolutionary adaptation to paleoenvironmental change, and constraining molecular clocks.

Keywords: Vertebrate, biostratigraphy, paleoenvironment, biochronology

In its simplest form, vertebrate biostratigraphy is the characterization of strata by their vertebrate fossil content. Relative dating schemes based on vertebrate biostratigraphy have very specific regional to continent-scale nomenclatures that are not widely employed across disciplines and are less useful in communication than the numeric designation of age. However, vertebrate biostratigraphy is the most useful system of organizing the vertebrate fossil record in terms of time and place of occurrence such that absolute dating techniques can be applied, and patterns of evolution, biogeography, and paleoenvironment can be explicitly addressed. The identity of a fossil, its age, and its place of occurrence are the primary data that only this science can provide. While there remains a central place for new discoveries, the existing data of vertebrate biostratigraphy is being mined and applied to multidisciplinary and interdisciplinary studies including large-scale phylogenetic analysis, molecular clock calibrations, global patterns, major transitions, paleoenvironments, and paleoecology. Most of these studies utilize breakthrough innovations that have improved precision in bioinformatics, absolute dating techniques, and geochemical sampling. Such broad studies are important because they integrate vertebrate paleontology with molecular biology and with paleoclimate and environmental evolution at levels that were not possible previously, and which are important with respect to questions that are asked across disciplines.

Development of robust timescales of increasing precision is an iterative process. The introduction of magnetic polarity stratigraphy had a profound effect on the chronology of vertebrate biostratigraphy even though it provides no numeric age by itself and cannot be correlated without constraints usually provided by paleontology or by quantitative methods. The Siwalik Group of Pakistan was one of the first long sections in which mammalian biostratigraphy and magnetostratigraphy were combined to provide a precise chronology for faunal change, most recently summarized by Flynn *et al.* (2013). Other complimentary techniques iteratively improving chronology are isotopic chemostratigraphy and cyclostratigraphy based on Milankovitch cycles. Orbital cyclicity and rates of sea floor spreading have improved precision in magnetostratigraphy.

Absolute dating is continually improving in precision, developing new methods, and discovering new datable samples. For example, new and precise chemical abrasion-thermal ionization U-Pb single crystal zircon ages from the Beaufort Group of the Permian Karoo constrain the ages of the *Pristerognathus*, *Tropidostoma*, and *Cistacephalus* zones (261-255 Ma; Rubidge *et al*., 2013). Dating of detrital zircons have proven to be extremely useful in geological studies and the evolution of sedimentary basins (e.g., Roberts *et al.,* 2012), but they may also be useful in providing age constraints of fossils, especially in frontier areas, for example in complex geological terranes. These may constrain the age of resulting sediments and limit the geographic origin of strata as in the age and paleogeographic placement of the Poul Creek Formation, Alaska (24-29 Ma; Perry *et al*., 2009), which contains fossil whales. Dating of radioisotopes in sedimentary systems is an active area of research.

Within the marine realm, during the Cretaceous long normal quiet zone (C34, about 35 million years in duration from early Aptian to late Santonian), an interval in which paleomagnetic stratigraphy is not particularly useful, our group in Angola has determined the carbon isotopic stratigraphy of bivave shells in relation to a dated basalt and identified Oceanic Anoxic Event II at the Cenomanian-Turonian boundary. This has allowed the alignment of vertebrate biostratigraphy with the carbon curve and has brought the correlation of occurrences of some mosasaur species into question. The use of eustatic sea level curves and sequence stratigraphy has also had some utility in establishing vertebrate chronology in the marine realm, especially in the Western Interior Seaway of North America and in Europe

In strictly molecular studies of phylogeny, the only method of calibration other than internal statistical methods, requires the tangible evidence of the fossil record. Parham *et al.* (2012) recently outlined a set of criteria necessary for justified calibrations based on fossils, including reference to specific specimens, apomorphy based diagnoses of taxa, explicit statements regarding morphological and molecular data sets, locality and stratigraphic level, and details of numeric age assignment. The last two criteria are specifically contributed by vertebrate biostratigraphy.

Many phylogenetic hypotheses include ghost lineages that predict the presence of specific clades that are as yet unrepresented by fossils in the predicted earlier phases of their history, based on the presence of their sister clades. Ghost lineages represent a model required by the hypothesis derived from the favored cladogram. That model can involve both time and place. The challenge, and the stimulation, is to reconcile the field data of fossils with the predictions of the model both in terms of absolute dating and in the generation of new specimens, and to evaluate the hypotheses of the phylogenetic analysis, especially as new character data are acquired. These are tests of the completeness of the fossil record, of the fidelity of the phylogenetic analysis, and they are fundamental to understanding the rates at which molecules evolve.

Phylogenetic studies utilizing large databases incorporating both morphology and molecular data provide both hypotheses of relationships and models of biogeography. O'Leary *et al.* (2013) incorporated 4541 phenomic characters for 86 fossil and living species of placental mammals, producing a phylogenetic analysis temporally calibrated by fossils. Cladistic relationships from that analysis indicate the afrotheres existed in the Paleocene of North and South America and results in ghost lineages relevant to Africa. This conclusion presents both a prediction and an unresolved quandary as to the timing of the first afrotherian presence in Africa given Late Cretaceous and Paleocene continental geography.

Fossil vertebrate species in general have morphological characters that reflect their habits and diet, informing of their ecology. Patterns of diversity among species and evolutionary changes within lineages reflect environmental change. These sorts of studies are also advancing. Philip Gingerich, his students and colleagues, have documented global climate change, the Paleocene-Eocene Thermal Maximum (55.65-55.93 Ma, refined by astronomical calibration), in the Bighorn Basin, USA, a breakthrough that came about with the discovery of a thin interval of strata containing dwarf mammals (Gingerich, 2010). The stratigraphically controlled and calibrated biostratigraphy of the Siwalik Group, Pakistan, provided fundamental evidence for the Miocene shift in C3 to C4 plant dominance. Now, applying laser ablation GC-IRMS to the molars of fossil mice, Kimura

(2013) has tied the change in diet to the change in tooth ecomorphology through this temporally constrained sequence (14.1-6.5 Ma). This is a significant contribution because the small home range of rodents insures that the diet is obtained in a small area, the isotope values in the teeth tie an independent determination of diet to specific species through time, and rates of change between lineages can be directly compared. On a broader geographic scale, patterns of diversity and ecology are being evaluated from a statistical perspective (e.g., Benson & Upchurch, 2012) and regional patterns of climate over millions of years are being resolved by patterns of mammalian diversity (e.g., Fortelius *et al*., 2002). Ecological explanations of evolutionary patterns are being explored, for example, the Carboniferous diversification of tetrapods in response to rainforest collapse. In the Late Cretaceous, the distribution and evolutionary pattern of mosasaur diversity, disparity, and dental isotopic values compared to sea level, sea surface temperature, and $\delta^{13}C$ values throughout their 30 million years of existence indicate a highly productive ocean and top-down evolutionary selection pressure in which the abundance of food resources was not a limiting factor (Polcyn *et al*., *in* press).

There are more interdisciplinary methods and applications of vertebrate biostratigraphy than can possibly be covered here, but the examples provided speak to the vibrancy and innovation of the field. It is certain that fieldwork remains a vital component, not only in frontier areas, but also in established areas where new fossils can elucidate previously unseen patterns. The search for global patterns requiring large databases dictates that all vertebrate fossils collected in biostratigraphic context are significant. No vertebrate fossil from any locality is without meaning for the history of life on Earth, for the environments in which it continues to evolve, and for the geological processes that provide the planetary context of the origin and evolution of life.

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