

基于碳、氧同位素分析的翼龙类生态学

The Ecology of Pterosaurs Based on Carbon and Oxygen Isotope Analysis*

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Since their discovery, pterosaurs have prompted much discussion about their ecology and feeding habits. Most pterosaur specimens are known from marine deposits (Kellner, 2003), though this may represent a bias towards preservation rather than necessarily a habitat choice. Recent discoveries of terrestrial deposits (e.g. the Yixian Formation) have also yielded numerous pterosaurs and our knowledge of their diversity has increased dramatically in recent years. As flying animals, pterosaurs were clearly likely to occasionally, or even often, become preserved in a locality far from where they habitually lived. Therefore, the recovery of a pterosaur in a marine setting does not necessarily mean that this was where it spent most of its time, merely where the carcass ended up.

Some pterosaurs are notably controversial in this aspect. Specimens of the Brazilian tapejarids are known from the marine lagoons of the Araripe Basin (Unwin & Martill, 2007), yet several studies have suggested that they were frugivores or nectivores (Wellnhofer & Kellner, 1991) – an impossibility for a marine animal. Similarly, a recent comprehensive study of the azdarchids (Witton & Naish, 2008) suggests that these were primarily terrestrial predators, though they are also known from marine deposits.

Background to stable isotopes

The aim of this study was to try to establish the typical environments inhabited by various pterosaur taxa by means of stable isotope analysis of biogenic apatite of bones and teeth along with the surrounding matrix sediment. Isotope data of the pterosaur skeletal apatite may yield new evidence to help determine pterosaur habitat preference and preferred diet if original compositions are preserved. This geochemical approach is based on significant oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope differences that exist between water (fresh versus seawater) and food (terrestrial versus marine). These systematic differences in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values were ingested by pterosaurs with their

drinking water and food respectively, and incorporated into their skeletal apatite. $\delta^{18}\text{O}$ values are mainly controlled by variations in the compositions of drinking and food water, as well as by differences in physiology and ecology (Kohn 1996). $\delta^{13}\text{C}$ values reflect the isotope composition of the diet (DeNiro & Epstein 1978). Stable isotopes may thus allow us to distinguish the exploitation of terrestrial or marine water and food resources and thereby to characterize whether pterosaurs were preferentially living in the terrestrial or marine realm regardless of the locality in which they were preserved.

For this purpose the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of the structural carbonate in the apatite and the phosphate oxygen ($\delta^{18}\text{O}_{\text{PO}_4}$) composition were analyzed for pterosaur bone and tooth samples. Tooth enamel is the skeletal tissue with the best preservation potential of original stable isotope compositions and may preserve original compositions even back to Mesozoic times (Fricke et al. 2008). In contrast bone is prone to diagenetic alteration (Kolodny et al. 1996; Trueman et al. 2003). However, because pterosaurs often lack teeth, or are too valuable for destructive sampling, bone samples were primarily analyzed instead. The aim was to see if original isotope compositions were at least partially preserved and may still allow for inferences about pterosaur habitats. To characterize the taphonomic setting and to check for isotope exchange between embedding sediment and isotopic compositions of the fossils the sedimentary carbonate was also analyzed.

To investigate the ecological habits of pterosaurs we took samples of bones and, where possible, teeth, from a number of Jurassic and Cretaceous pterodactylid specimens from across the world. Despite the controversy over taxa such as the azdarchids and tapejarids, other taxa are well supported as being based in marine environments (e.g. *Pterandon* where most specimens are found in locations that were many kilometres out to sea in the Cretaceous) or terrestrial environments (e.g. *Dsungaripterus* found many kilo-

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metres inland). These taxa can provide a baseline for comparison with those whose status are contested.

Isotope results and discussion

Two pterosaur tooth and eight bone specimens from marine and terrestrial settings were analyzed for their carbon and oxygen isotope compositions (Table 1). Further specimens are currently undergoing analysis. The measured isotope ratios are expressed as delta-values ($\delta = (R_{\text{Sample}}/R_{\text{Standard}} - 1) \times 10^3$ with $R = {}^{18}\text{O}/{}^{16}\text{O}$ or ${}^{13}\text{C}/{}^{12}\text{C}$) in permil (‰) relative to the international standards V-SMOW and V-PDB for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values respectively. $\delta^{18}\text{O}_{\text{PO}_4}$ values for all specimens range from 13.6 to 21.6‰ V-SMOW. This huge range of 8‰ indicates either (1) the consumption of water from isotopically distinct sources or (2) the fossilisation and alteration of the skeletal apatite in diagenetic fluids with different $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values.

Tapejaridae (20.9 to 21.6‰) and Ornithocheiridae (19.8 to 20.1‰) have the highest $\delta^{18}\text{O}_{\text{PO}_4}$ values, similar to those known from marine vertebrates. *Pteranodon* has an intermediate value of 17.8‰. The dsungaripteroids have the lowest values ranging from 13.6 to 15.1‰. Such low values are clearly in accordance with a freshwater consumption and/or fossilisation.

Higher $\delta^{18}\text{O}_{\text{PO}_4}$ values may either indicate consumption of meteoric water with higher $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values in much warmer climate settings, for example from evaporatively ${}^{18}\text{O}$ -enriched freshwater bodies or consumption of seawater. Given the taphonomic setting of Tapejaridae, Ornithocheiridae, and *Pteranodon* as well as inferred lifestyles, the latter possibility seems more likely. The preliminary $\delta^{18}\text{O}_{\text{PO}_4}$ data as well as the ${}^{18}\text{O}_{\text{CO}_3}$ of the structural carbonate in the skeletal apatite indicate differences between the pterosaur specimens analyzed so far that seem consistent with

the environments in which they were found (Table 1). However, it has yet to be demonstrated that these isotope signatures in the pterosaur bones reflect biogenic and not taphonomic values. This is difficult because primary and diagenetic isotope signatures can be similar if a pterosaur lived and died in the same environmental setting.

The $\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{13}\text{C}$ values of the skeletal remains are often similar to those of the carbonate in the embedding sediment. This may hint at an isotopic exchange of the carbonate between bone and the sediment. However, the $\delta^{13}\text{C}$ values of enamel and even the dentine samples of two Ornithocheiridae teeth (−0.19 to −2.0‰) are about 8‰ higher than a bone specimen (−9.6‰) of the same taxon and the embedding sediment (−8.5‰). This seems to argue against a complete alteration of the isotope composition of the structural carbonate in these tooth specimens and thus at least a partial preservation of $\delta^{13}\text{C}$ values in dental tissues. All pterosaur specimens cover a large range of $\delta^{13}\text{C}$ values from −0.2 to −11.8‰ V-PDB. High values are more in agreement with the consumption of marine food resources whereas values at the lower end of this range are comparable to those of vertebrates feeding on terrestrial C_3 plants. However, it is difficult to determine if these $\delta^{13}\text{C}$ values are still original values and reflect genuine dietary differences. Preservation of taxon-specific isotope differences reflecting different food and water sources would be the best way to test this.

Thus more results, especially from tooth enamel samples, are necessary to determine with more confidence if the isotopic differences observed between the different pterosaur taxa are related to their feeding ecology and drinking behaviour and hence habitats, or if they just reflect taphonomic signatures. Results are currently uncertain, but the process has begun.

Table 1 Pterosaur taxa from which skeletal remains are analyzed for stable isotope compositions

Taxon	Locality	Environment type	Environment inferred from isotope analysis
Tapejaridae indet.	Santanta Fm.	Marine	Marine
<i>Dsungaripterus sp.</i>	Tugulu	Terrestrial	Terrestrial
<i>Dsungaripterus sp.</i>	Tugulu	Terrestrial	Terrestrial
<i>Dsungaripterus sp.</i>	Tugulu	Terrestrial	Terrestrial
<i>Pteranodon</i>	Niobrara	Marine	Marine/Terrestrial?
Ornithocheiridae indet.	Cambridge Greensand	Marine	Marine

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