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Palaeoecology, migration behavior, and reproductive pattern of Palaeozoic to Mesozoic freshwater sharks revealed by stable and radiogenic isotopes

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The biogenic fluor-apatite in shark teeth is regarded as a valuable, diagenetically resistant geochemical archive of the ambient water chemistry and temperature at the time of tooth formation. It represents a geochemical "snapshot" of the aquatic environment where the tooth was formed not where it was deposited. It is promoted by the fast and lifelong lasting tooth replacement in all sharks, fossil as well as extant ones. Since the palaeoecology of Late Palaeozoic and Early Mesozoic xenacanthiform and hybodontiform sharks from predominantly European basins is controversial, the tooth oxygen and strontium isotope composition is used here to differentiate between marine and freshwater signatures with respect to the hydrological cycle (Fig. 1) and the Phanerozoic strontium seawater curve in order to decipher whether they had a migratory or stationary freshwater lifestyle. Altogether, 430 $\delta^{18}O_P$ values and 175 $^{87}Sr/^{86}Sr$ ratios derived from teeth of several fossil shark taxa of several time slices from altogether 50 sites have been analysed for significance with regard to palaeoenvironmental conditions and potential migration behaviour. Tooth preservation was ascertained by cathodoluminescence microscopy.

The Palaeozoic (Late Carboniferous–Early Permian) tooth samples yield low $\delta^{18}O_P$ and high $^{87}Sr/^{86}Sr$ values typical for freshwater settings. Some deviating $\delta^{18}O_P$ values from Spain and Germany can be attributed to significant evaporative enrichment of ^{18}O in the ambient water. Overall, this suggests a fully freshwater-adapted lifestyle for a variety of xenacanthiform and hybodontiform shark taxa in Late Palaeozoic European basins.

The Latest Triassic (Rhaetian) tooth samples from bone beds of the Central European Basin indicate a shift from marine to brackish conditions in the south and west of the shallow epicontinental Rhaetian Sea towards extensively brackish conditions with low salinities in the eastern part due to massive fluviatl influx. Here, the $\delta^{18}O_P$ values indicate euryhaline adaption of hybodontiform sharks without a basin-wide migration pattern. Differences between taxa from the same site might indicate some degree of niche partitioning.

The evaluation of the $\delta^{18}O_P$ and $^{87}Sr/^{86}Sr$ datasets provided here proves its worthwhile use in order to contribute to long-lasting palaeobiological controversies. Therefore, further isotope investigations of fossil shark remains show considerable potential for growth in understanding regarding palaeoecolgy, palaeoenvironment conditions as well as palaeoclimatology, in marine and non-marine areas.

Moreover, the oviposition strategies (habitat shift, nursery areas, site fidelity) inferred from fossil egg capsule and hybodontiform shark teeth from a Middle Triassic site in Central Asia are remarkably similar to those of modern relatives suggesting that the reproductive patterns seen in extant sharks originated well before the Cenozoic. The results unequivocally prove oviparous behaviour of hybodontiform sharks in freshwater unknown in extant sharks.

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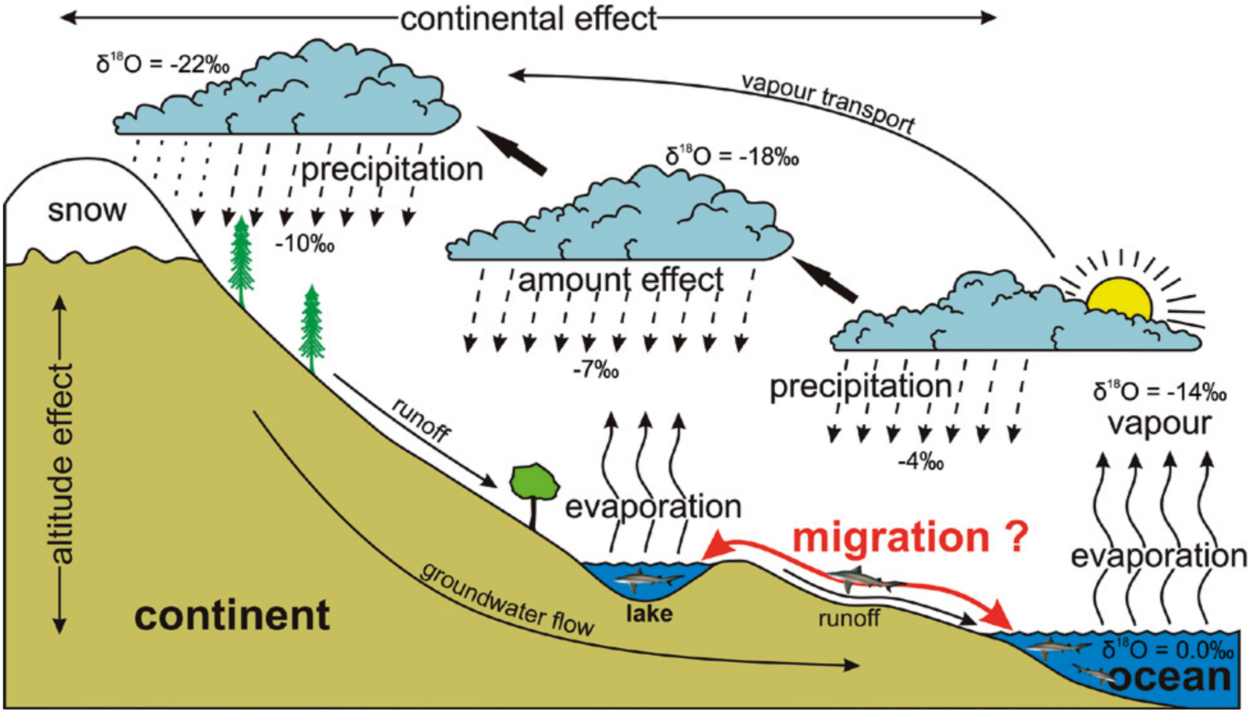

Fig. 1. Background of the interpretations is the present day hydrological cycle, which schematically comprises of evaporation, atmospheric vapor transport, precipitation and subsequent return of meteoric waters to the ocean, combined with an isotopic fractionation (Rayleigh distillation). It results in a variation of $^{18}O/^{16}O$ ratios in natural compounds depending on latitude, altitude, distance to the ocean, climate, and amount of precipitation. One would expect that sharks in case of migratory behaviour would mirror the distinct oxygen isotope composition of the different environments in their tooth enameloid.