



## Oxygen and strontium isotopes from fossil shark teeth: Environmental and ecological implications for Late Palaeozoic European basins



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### ABSTRACT

Fossil shark remains occur in both marine and nonmarine Late Palaeozoic deposits, therefore their palaeoecology is controversial. The oxygen and strontium isotopic composition of biogenic fluorapatite in 179 teeth, scales and spines predominantly of hybodontid (*Lissodus*) and xenacanthiform (*Orthacanthus*, *Xenacanthus*, *Bohemiacanthus*, *Triodus*) sharks from various Late Carboniferous (Moscovian) to Early Permian (Artinskian) basins of Europe are used as ecological tracers to decipher diadromous or obligate freshwater lifestyle of the investigated taxa. The  $\delta^{18}\text{O}_\text{p}$  values of the different shark teeth range from 11.7 to 20.2‰ within the different basins with mean values of  $16.9 \pm 0.5\%$  for the Bohemian Massif,  $16.2 \pm 0.8\%$  for eastern Germany,  $18.2 \pm 1.0\%$  for southwestern Germany,  $18.5 \pm 0.7\%$  for southern-central Spain,  $17.6 \pm 0.4\%$  for Sardinia, and  $16.6 \pm 0.5\%$  VSMOW for the French Massif Central. The tooth  $\delta^{18}\text{O}_\text{p}$  values from the basins are mostly depleted by 1–5‰ relative to those of shark teeth from contemporaneous marine settings. Oxygen isotope signatures of co-occurring taxa do not show systematic differences excluding habitat effects for different shark groups. However, distinctly higher  $\delta^{18}\text{O}_\text{p}$  values from Puertollano and Saar-Nahe can be attributed to significant evaporative enrichment in  $^{18}\text{O}$  of the ambient water in the ancient lacustrine environments due to a warm and dry climate and sufficient residence time in the basins. The strontium isotopic composition of the teeth varies between 0.70824 and 0.71216 with a mean value of 0.71031. These  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios are always more radiogenic in comparison to the  $^{87}\text{Sr}/^{86}\text{Sr}$  record of seawater of their stratigraphic age. Overall, the investigated tooth samples yield low  $\delta^{18}\text{O}_\text{p}$  and high  $^{87}\text{Sr}/^{86}\text{Sr}$  values deviating from bioapatite values expected for contemporaneous marine vertebrates and typical for freshwater settings. This indicates a fully freshwater adapted lifestyle for a variety of fossil shark taxa in Late Palaeozoic European basins.

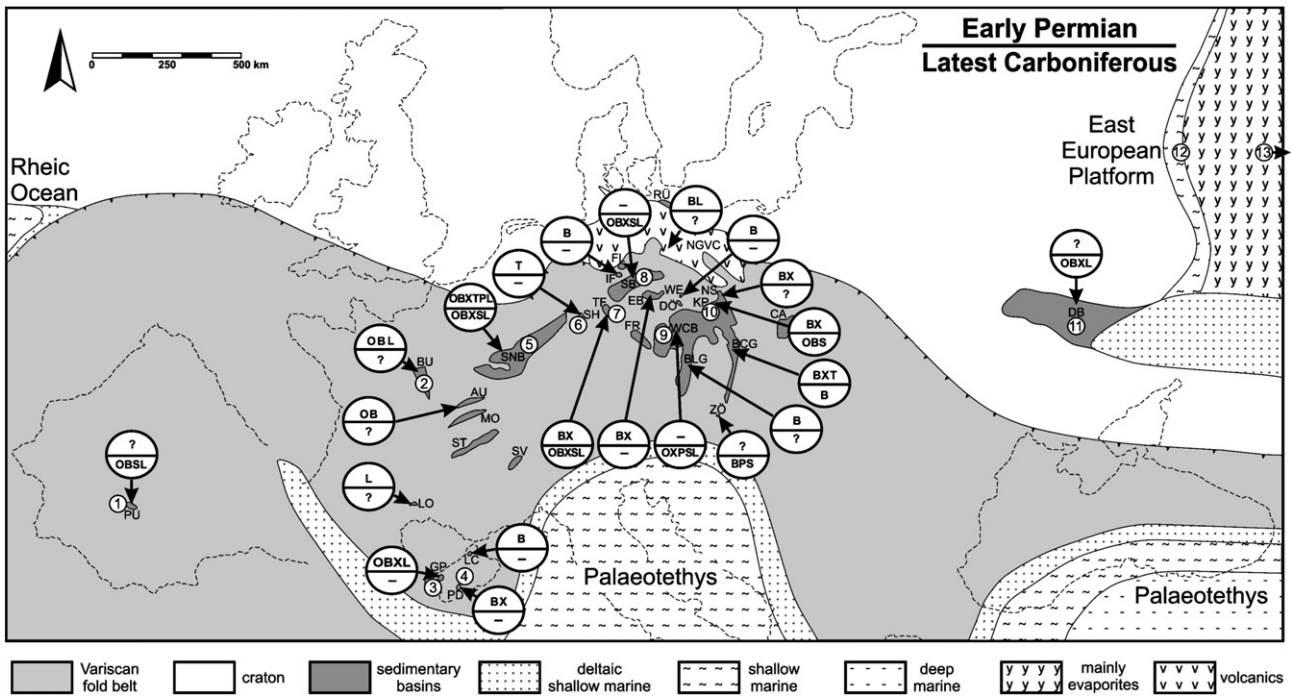
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### 1. Introduction

Fossil shark remains are abundant in Late Carboniferous and Early Permian deposits of continental basins of Europe being mostly represented by isolated teeth (e.g., Schneider, 1985; Hampe, 1994; Soler-Gijón, 1997; Štamberg and Zajíc, 2008; Fischer et al., 2010). Analyses of the spatial taxa distribution revealed a highly diverse, widespread, and uniform shark-association within the European basins during the latest Carboniferous (Gzhelian) (Schneider and Zajíc, 1994; Schneider et al., 2000) that became increasing patchy during the Early Permian (Fischer et al., 2010; Fig. 1). According to this observation, nearly all Carboniferous basins were connected by a

complex drainage system that gave aquatic vertebrates the possibility for exchange. However, the presence of shark remains in continental basins together with contradicting facies interpretations of sedimentary deposits led to different interpretations concerning a marine influence during the late Palaeozoic in Europe. Two contrary assumptions exist about the palaeoecology of these ancient shark communities. On one hand, they are considered to have been euryhaline fishes in marginal marine coastal, lagoonal to estuarine influenced environments (Soler-Gijón, 1999; Schultze and Soler-Gijón, 2004; Schultze, 2009; Carpenter et al., 2011). This view is based on the record of several members of specific fossil shark families from marine strata, their global occurrence, and the marine restriction of extant shark egg capsules as well as analogies with modern diadromous sharks (see also Soler-Gijón, 1993, 1997). The similarity of aquatic shark faunas in different European basins is explained by those authors assuming

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**Fig. 1.** Palaeogeographic overview map of important Latest Carboniferous and Early Permian basins of Europe (modified from Roscher and Schneider, 2006) with the currently known palaeobiogeography of xenacanthiformes, hybodontids, sphenacanthids (modified from Schneider and Zajíc, 1994; Fischer et al., 2010). Numbers in the circles refer to the localities in Figs. 2, 4, 5, and Tables 1–3. Shark taxa: B – *Bohemiacanthus*, L – *Lissodus*, O – *Orthacanthus*, P – *Plicatodus*, S – *Sphenacanthus*, T – *Triodus*, and X – *Xenacanthus*; below the horizontal line – occurrences during Stephanian C (late Gzhelian–early Asselian), and above the horizontal line – occurrences during Rotliegend (middle Asselian–early Artinskian). Basins: AU – Autun basin, BLG – Blanice Graben, BCG – Boskovicze Graben, BU – Bourbon l'Archambault basin, CA – Carpathian basin, DB – Donetsk basin, DÖ – Döhlen basin, EB – Erzgebirge basin, FL – Flechting Block, FR – Franconian basin, GP – Guardia Pisano basin, IF – Ilfeld basin, KP – Krkonoše Piedmont basin, LC – Lu Caparoni basin, LO – Lodève basin, MO – Montceau les Mines basin, NGVC – North German Volcanite Complex, NS – North Sudetic basin, PD – Perdasdefogu basin, PU – Puertollano basin, RÜ – Rügen, SB – Saale basin, SH – Spredlinger Horst, SNB – Saar–Nahe basin, ST – St. Etienne basin, SV – Salvan–Doréaz basin, TF – Thuringian Forest basin, WCB – Western and Central Bohemian basins, WE – Weissig basin, and ZÖ – Zöbingen.

marine conditions prevailing throughout these basins allowing migration along marine seaways. In contrast, the second hypothesis negates any marine influence, and assumes the full adaption of these sharks to an obligate freshwater lifestyle (Schneider and Zajíc, 1994; Schneider et al., 2000) based on sedimentological criteria as well as palaeogeographical and ecological arguments (see also Schneider and Reichel, 1989; Schneider, 1996; Boy and Schindler, 2000; Fischer et al., 2010). Accordingly, faunal exchange between basins is assumed to have occurred mainly within drainage systems, albeit faunal exchange between river mouths via coastal waters is not completely excluded (Schindler and Hampe, 1996; Schneider et al., 2000).

Analyses of the phosphate oxygen ( $\delta^{18}O_p$ ) and strontium ( $^{87}Sr/^{86}Sr$ ) isotope compositions of shark teeth are a worthwhile geochemical approach to address this controversy, and test the two different models for the shark palaeoecology and hence basin hydrography. Biogenic fluorapatite of fossil shark tooth enameloid is considered a valuable palaeoecological and palaeoenvironmental archive (e.g., Kolodny and Raab, 1988; Kolodny and Luz, 1991; Koch et al., 1992; Vennemann and Hegner, 1998; Kohn and Cerling, 2002; Lécuyer et al., 2003; Kocsis et al., 2007, 2009; Zacke et al., 2009; Tütken et al., 2011) due to the preservation of the aqueous conditions (i.e. isotope composition of the ambient water) at the time of tooth formation (Longinelli and Nuti, 1973; Kolodny et al., 1983; Schmitz et al., 1991; Vennemann et al., 2001). Contrary to other vertebrate bioapatites, shark teeth possess several advantages as palaeoenvironmental archives: (1) they are the most common phosphatic vertebrate remains in aquatic sediments with a wide spatial and stratigraphical distribution since the Devonian (Ginter et al., 2010), (2) the body temperature is related to the ambient water temperature because of shark ectothermy (Speers-Roesch and Treberg, 2010), (3) the body fluid of aquatic animals is in isotopic equilibrium with the ambient water contrary to

semi-aquatic and terrestrial vertebrates, whose body waters are enriched in  $^{18}O$  by up to 2‰ (Amiot et al., 2007; Bernard et al., 2010), (4) the  $\delta^{18}O_p$  of the tooth enameloid seems to be independent from metabolic fractionation effects (the so-called vital effects) (Kolodny et al., 1983), (5) no taxon-specific fractionation for sharks is reported (Vennemann et al., 2001), and (6) shark enameloid consists mainly of stable fluorapatite ( $Ca_5(PO_4)F$ ) with inferior amounts of hydroxyl- and carbonate apatite (Vennemann et al., 2001; Enax et al., 2012) compared to the metastable carbonate containing hydroxylapatite of bones. In addition, the fluorapatite of shark teeth has been considered to be more robust against diagenetic alteration than either dentine or bone because of its high degree of mineralisation, large apatite crystal size, the low content of organic compounds, and the strong chemical bond between phosphorus and oxygen (Kohn et al., 1999; Sharp et al., 2000; Kohn and Cerling, 2002; Enax et al., 2012). Hence original  $\delta^{18}O_p$  values are likely preserved in fossil shark teeth. The rapid, lifelong tooth replacement in sharks takes place within days to weeks (Berkovitz, 2000; Botella et al., 2009b). This makes their teeth short-term recorders of the isotope composition and temperature of the ambient water, in which the teeth were mineralised. Thus, tooth apatite of shark teeth formed in thermally and geochemically different water masses vary in  $\delta^{18}O_p$  and  $^{87}Sr/^{86}Sr$  between marine and freshwater environments (Schmitz et al., 1991; Kohn et al., 1999; Koch, 2007), which enables the tracking of euryhaline or obligate habitat preferences in fossil species (Kocsis et al., 2007; Klug et al., 2010; Fischer et al., 2011, 2012).

Besides teeth, chondrichthyan scales as well as spines provide further material for study since they are also covered by a hyper-crystalline cap on their exposed parts (Reif, 1978; Cappetta, 1987). In particular, spines (fin spines in hybodontids, head/dorsal spines in xenacanthiformes) as lifelong growing, nonreplaced hard tissues comprise an as yet unexplored isotopic time series of a shark's entire life, in addition to the short-term 'geochemical snapshots' from teeth

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