Biogeosciences

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EGU

Stable isotope study of a new chondrichthyan fauna (Kimmeridgian, Porrentruy, Swiss Jura): an unusual freshwater-influenced isotopic composition for the hybodont shark *Asteracanthus*

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Abstract. Chondrichthyan teeth (sharks, rays, and chimaeras) are mineralized in isotopic equilibrium with the surrounding water, and parameters such as water temperature and salinity can be inferred from the oxygen isotopic composition ($\delta^{18}O_p$) of their bioapatite. We analysed a new chondrichthyan assemblage, as well as teeth from bony fish (Pycnodontiformes). All specimens are from Kimmeridgian coastal marine deposits of the Swiss Jura (vicinity of Porrentruy, Ajoie district, NW Switzerland). While the overall faunal composition and the isotopic composition of bony fish are generally consistent with marine conditions, unusually low $\delta^{18}O_p$ values were measured for the hybodont shark *Asteracanthus*. These values are also lower compared to previously published data from older European Jurassic localities. Additional analyses on material from Solothurn (Kimmeridgian, NW Switzerland) also have comparable, low-^{18}O isotopic compositions for *Asteracanthus*. The data are hence interpreted to represent a so far unique, freshwater-influenced isotopic composition for this shark that is classically considered a marine genus. While reproduction in freshwater or brackish realms is established for other hybodonts, a similar behaviour for *Asteracanthus* is proposed here. Regular excursions into lower salinity waters can be linked to the age of the deposits and correspond to an ecological adaptation, most likely driven by the Kimmeridgian transgression and by the competition of the hybodont shark *Asteracanthus* with the rapidly diversifying neoselachians (modern sharks).

1 Introduction

Chondrichthyan remains are common in the Mesozoic fossil record of Western Europe, and in many different palaeoenvironmental settings (e.g. lagoonal, open marine, reduced salinity) (Duffin and Thies, 1997; Müller, 2011; Underwood, 2002). Their teeth are predominantly composed of fluorapatite, the most resistant variety of apatite (Vennemann et al., 2001) and are continuously shed and replaced, except in chimaeras (Cappetta, 2012; Stahl, 1999). In addition to their abundance, their mechanical and chemical resistance make them an ideal material for stable isotope analyses. They mineralize in isotopic equilibrium with the surrounding water, hence their primary oxygen isotopic composition ($\delta^{18}O_p$) reflects that of the ambient water at a given temperature when they formed (Kolodny et al., 1983; Longinelli and Nuti, 1973). This makes them a valuable palaeoenvironmental proxy, used in numerous studies (e.g. Kocsis et al., 2007; Lécuyer et al., 2003; Vennemann et al., 2001).

This research is based on fossil material – mainly chondrichthyans – found between 2000 and 2011 during
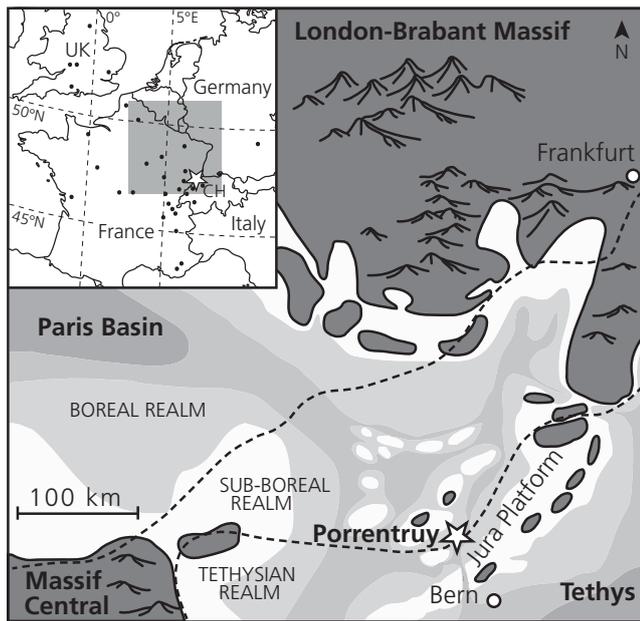
Figure 1. Palaeogeographical map of the study site and surroundings (Late Kimmeridgian, modified from Comment et al., 2011). CH = Switzerland, palaeolatitude of Porrentruy = ∼ 30° N. Emerged land is outlined, darker grey corresponds to deeper water. Upper left corner: present-day geographical position of Porrentruy (⋆) and other European sites (●) of previously published studies and providing geochemical data compared in Fig. 5. The shaded square delimits the area detailed in the palaeogeographical map.

controlled palaeontological excavations conducted by the Paléontologie A16 team (PAL A16, canton of Jura, NW Switzerland). All fossiliferous sites are located in the vicinity of Porrentruy (Ajoie district) and are related to the building of the Trans-Jura highway (A16). The Ajoie region is part of the Tabular Jura (Marty et al., 2007), mainly consisting of subhorizontal Mesozoic (Oxfordian and Kimmeridgian) strata.

During the Kimmeridgian, the Ajoie region was a shallow-marine carbonate platform at a palaeolatitude of about 30° N (Marty, 2008) and surrounded by the Central and London Brabant massifs, the Tethys, and the Paris Basin (Fig. 1). The palaeoclimate was semi-arid with high seasonality (Philippe et al., 2010; Waite et al., 2013). The platform had a very complex morphology due to the basement structure and sea-level changes occurred during its depositional history. These processes induced several episodes of emersion suggested by numerous dinosaur footprints (Marty, 2008; Marty et al., 2007) and hardgrounds, followed by erosion and reworking. Lateral changes in water depth potentially occurred at a very local scale (Jank et al., 2006; Waite et al., 2013). The record of ammonites typical of the boreal and Tethyan domains show that the study area was influenced by water masses from both the Tethys and Paris Basin (Colombié and Rameil, 2007; Comment et al., 2011).

Based on phosphate oxygen isotope analyses obtained from this Late Jurassic chondrichthyan fauna, this study proposes answers to the following questions: (1) is there any unexpected isotopic composition for the associated marine fauna recorded in Porrentruy? (2) Are the Porrentruy isotopic data unique so far, or comparable to other European localities? (3) What do we learn about the palaeoecology of the hybodont shark *Asteracanthus* based on the isotopic composition?

2 Material and methods

The chondrichthyan dental material of the PAL A16 collection is rich and diverse, comprising more than 2000 fossils. Sharks and rays (subclass Elasmobranchii) are represented by the hybodont sharks – the extinct sister group of modern sharks (Maisey et al., 2004) (order Hybodontiformes: "*Hybodus*", *Planohybodus*, *Asteracanthus*) – the modern sharks (subcohort Neoselachii, order Carcharhiniformes: *Palaeoscyllium*, *Corysodon*; order Heterodontiformes: *Heterodontus*, *Paracestracion*; order Protospinaciformes: *Protospinax*; order Squatiniformes: *Pseudorhina*) and rays (superorder Batomorphii, order Rajiformes: *Belemnobatis*, *Spathobatis*). Chimaeras (superorder Holocephali (*sensu* Stahl, 1999), order Chimaeriformes: *Ischyodus*) are also present. The investigated material comes from the Kimmeridgian Reuchenette Formation and more precisely from the latest Early Kimmeridgian (*Cymodoce* ammonite zone, Banné Marls) and up to the Late Kimmeridgian (*Mutabilis* ammonite zone, *Corbis* Limestones and *Eudoxus* ammonite zone, lower *Virgula* Marls) (Fig. 2). Except for *Asteracanthus* and *Ischyodus* remains that are of a considerable size and were collected directly on the field, the material consists predominantly of microfossils resulting from sediment sieving.

The oxygen isotopic composition of phosphate from biogenic apatite was measured on rays, the chimaeroid *Ischyodus* and the hybodonts *Asteracanthus* and *Hybodus*. Bioapatite of bony fish Pycnodontiformes was also analysed for comparison. Stratigraphically, samples were selected from different beds in order to cover all units of the studied section (Fig. 2). Additionally, Kimmeridgian material from the neighbouring Natural History Museum of Solothurn was analysed for comparison.

The best mineralized part of the teeth, the enameloid, was isolated in Pycnodontiformes and *Asteracanthus* (Fig. 3). From eleven of the *Asteracanthus* teeth, dentine was also analysed in parallel to examine any isotopic differences between the tissues. In the case of chimaeroid dental plates the densest parts were selected. For the very small material (1–5 mm) – as in rays and *Hybodus* – several isolated teeth were analysed together as bulk samples of enameloid and dentine. Due to the small size, only the outer aspect of this material was sampled as it was visibly the best preserved, i.e. not
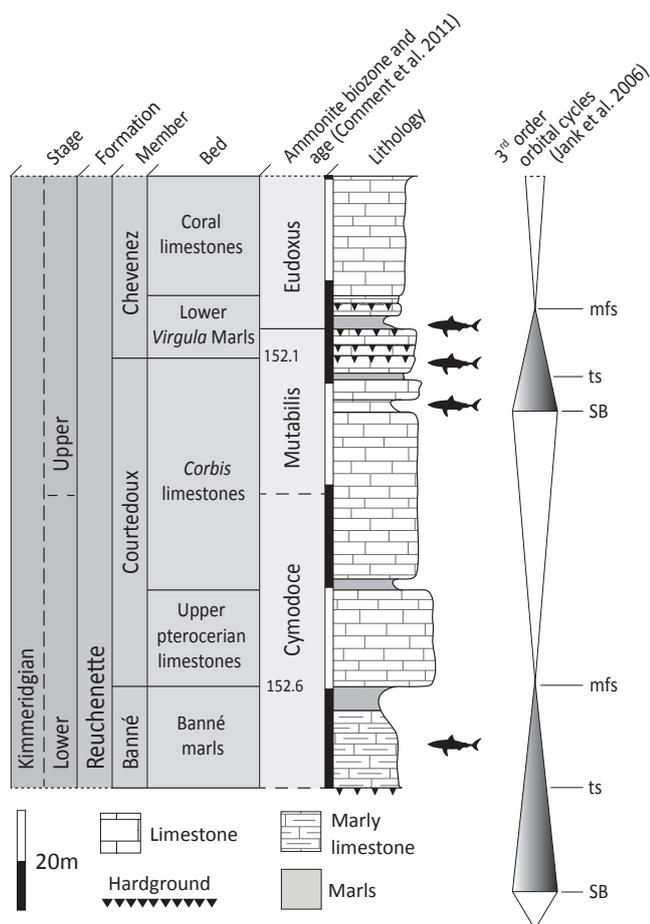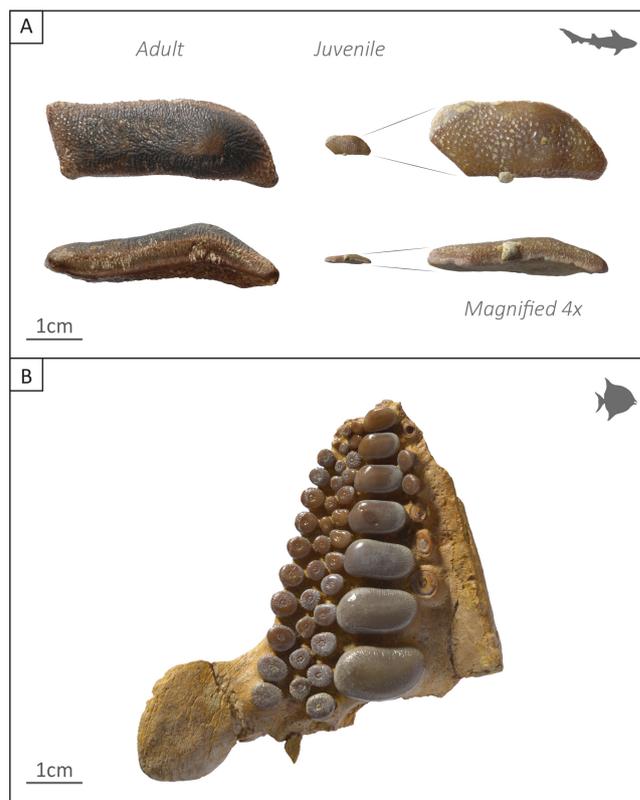
Figure 2. Simplified stratigraphic profile of the Porrentruy area with third order orbital cycles and section yielding the studied chondrichthyan material. Numbers indicate geological age in millions of years. SB = sequence boundary, ts = transgressive surface, mfs = maximum flooding surface.

Figure 3. Fossil material from the study site of Porrentruy. **(a)**: teeth of *Asteracanthus*. Left: adult specimen (SCR010-1125). Right: juvenile specimen (SCR004-221) to scale and magnified. Occlusal (top) and lateral (bottom) views. **(b)**: left prearticular bone of Pycnodontiformes with teeth (specimen SCR010-1204). Photographs by PAL A16.

worn-out teeth and/or with ornamentation well defined and light-grey in colour. After manual removal of the largest part possible of the root, the most dentine-free teeth were used for analysis.

From the Porrentruy material, 38 samples of *Asteracanthus* teeth (27 enameloid and 11 dentine), 7 of *Ischyodus* dental plates and 13 of Pycnodontiformes teeth were analysed; in addition, 4 bulk samples for *Hybodus* and 3 for rays were investigated. From the Solothurn material, enameloid of 9 *Asteracanthus* and 3 Pycnodontiformes teeth were added for comparison. Altogether, a total of 77 analyses were made.

The sample powders (at least 2 mg per sample) were pretreated following the procedure of Koch et al. (1997), and the PO_4^{3-} ion of the apatite was separated and precipitated as silverphosphate (e.g. Kocsis, 2011; O'Neil et al., 1994). NBS–120c phosphorite reference material was processed in parallel with the samples. Generally, triplicates of each sample were analysed together with two in-house phosphate stan-

dards (LK–2L: 12.1 ‰ and LK–3L: 17.9 ‰) to correct the results. The samples were analysed in a high-temperature conversion elemental analyser (TC/EA) coupled to a Finningan MAT Delta Plus XL mass spectrometer at the University of Lausanne after the method described in Vennemann et al. (2002). The data are expressed in permil and reported as $\delta^{18}O_p$ on the VSMOW scale (Vienna Standard Mean Ocean Water). The overall analytical error is taken as 0.3 ‰, however individual samples often reproduced better. For the NBS-120c an average value of 21.3 ± 0.3 ‰ ($n = 6$) was obtained. This is somewhat lower than the mean reported value of 21.7 ‰ (e.g. Halas et al., 2011), but no correction was applied to the values measured as the small offset is thought to be due to heterogeneity in the sedimentary phosphorite and its different response to pretreatments compared to the enameloid of the teeth sampled.

The oxygen isotope composition of unaltered fish teeth ($\delta^{18}O_p$) is a function of both water temperature and isotopic composition of ambient water ($\delta^{18}O_w$) during tooth growth (Kolodny et al., 1983; Lécuyer et al., 2013; Longinelli and Nuti, 1973). Here below is the phosphate fractionation equa-

tion of Lécuyer et al. (2013) used for calculating the temperature of sea water:

$$T(^{\circ}C) = 117.4(\pm 9.5) - 4.50(\pm 0.43) \cdot (\delta^{18}O_p - \delta^{18}O_w). \quad (1)$$

For marine fauna, the global, average seawater isotopic composition ($\delta^{18}O_w$) can be used as an approximation that is assumed to be equal to -1 ‰ for the ice-free Late Jurassic seawater (e.g. Shackleton and Kennett, 1975).

3　Results

For the Porrentruy samples, the bioapatite oxygen isotope compositions have a range between 17.0 and 21.9 ‰, with an overall average value of 18.8 ± 0.9 ‰ ($n = 65$). These values can be grouped into three ranges: (1) values of bulk samples (*Hybodus* and rays) and *Ischyodus* that are between 18.5 and 19.8 ‰ (average 19.2 ± 0.4 ‰, $n = 14$); (2) enameloid values of *Asteracanthus*, averaging 18.1 ± 0.6 ‰ (17.0–19.7 ‰, $n = 27$) and (3) those of Pycnodontiformes with an average of 19.8 ± 1.0 ‰ (18.2–21.9 ‰, $n = 13$). The average value of 18.9 ± 0.8 ‰ (17.7–20.0 ‰, $n = 11$) in the *Asteracanthus*' dentine is significantly different from the equivalent enameloid sampled from the same teeth demonstrated by Student's t test: $t(20) = 2.98$, $p < 0.01$.

For the Solothurn comparison material, an average of 18.7 ± 0.9 ‰ ($n = 9$) and 19.4 ± 0.7 ‰ ($n = 3$) was obtained for *Asteracanthus* and Pycnodontiformes teeth respectively.

All of the data are available and detailed in the Supplement.

4　Associated fauna and palaeoecology

The associated fauna of the Porrentruy material is characteristic of a coastal marine environment, with notably a rich marine bivalve assemblage, sea urchins and over 600 ammonites (Comment et al., 2011; Marty and Billon-Bruyat, 2009). Among vertebrates, coastal marine turtles (Plesiochelyidae) (Anquetin et al., 2014; Püntener et al., 2014, 2015) and crocodilians (Thalattosuchia) (Schaefer, 2012) are common.

During the Late Jurassic, modern sharks were expanding and diversifying, while hybodonts were declining and restricted more to environments of reduced salinity, or even freshwater, where modern sharks were less represented (Kriwet and Klug, 2008; Rees and Underwood, 2008; Underwood, 2002). In our assemblage however, hybodonts and rays clearly dominate (86 % of the dental material). This suggests that conditions are still favourable to hybodonts in Porrentruy, unlike in neighbouring localities from southern Germany (Nusplingen, Solnhofen) or France (Cerin), where hybodonts are scarce or absent. Our chondrichthyan assemblage (see Sect. 2) is rather similar to that in northern Germany (e.g. in Oker) (Duffin and Thies, 1997; Thies, 1995), also dominated by hybodonts and rays. There, the fauna is associated with conditions of reduced salinity (Underwood and

Rees, 2002; Underwood and Ward, 2004; Underwood, 2002, 2004). The chimaeroid *Ischyodus* must also be regarded as one of the most abundant chondrichthyans, even if representing only 3 % of the remains. Indeed, its nonrenewable and less resistant dentition and the relatively low amount of dental elements per individual (six dental plates against hundreds to thousands of teeth for sharks and rays) (Stahl, 1999) easily lead to an underestimate of its abundance. Interestingly, most of the few modern sharks (Neoselachii) of our assemblage (i.e. *Heterodontus*, *Palaeoscyllium*, *Protospinax*, *Pseudorhina*) are thought to have had a benthic lifestyle (Underwood, 2002; Underwood and Ward, 2004), supporting a well-oxygenated bottom water, which is also indicated by the invertebrate fauna.

5　Discussion

5.1　$\delta^{18}O_p$ values from the Porrentruy material: palaeoecological indications

Values of bulk samples (*Hybodus* and rays) and *Ischyodus* have a similar range and could reflect either a similar habitat for these groups, or a similar diagenetic alteration. Since they correspond to dentine-bearing samples – i.e. tissues that are more easily altered than enameloid – and given that the dentine samples of *Asteracanthus* tend to similar values, the least resistant tissue of all these specimens could have been affected by alteration during diagenesis. Diagenetically altered isotopic values for dentine or bone are expected in fossil samples (see Lécuyer et al., 2003; Sharp et al., 2000; Pucéat et al., 2003). Therefore, in order to discuss ancient ecological parameters, we focus on enameloid samples in the rest of the text.

The isotopic compositions of Pycnodontiformes and *Asteracanthus* enameloid samples are considered not to have been altered, partly because of their original histological structure when examined with a microscope, their black-blueish colour when subjected to cathodoluminescence, and the generally good preservation potential for enameloid when not recrystallized (e.g. Kohn and Cerling, 2002). The distinct range in values between *Asteracanthus* and Pycnodontiformes enameloid, both when compared to one another and to dentine-bearing samples within the same group, further supports preservation of original values. Also, the fact that an *Asteracanthus* enameloid value measured on a tooth is lower than its dentine counterpart from the same tooth shows that the enameloid did not experience intense alteration, unlike the dentine that clearly recrystallized. Entirely altered specimens would give a similar value, whatever the tissue analysed. The same can be inferred from the isotopic difference between *Asteracanthus* and Pycnodontiformes enameloid values, which would be expected to result in similar values if they would have experienced the same diagenetic alteration (see Fischer et al., 2012). Because of these rea-
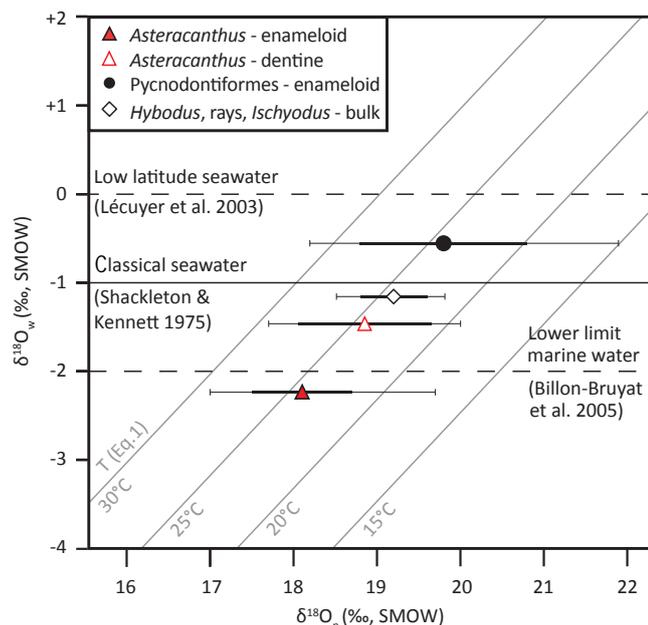
Figure 4. Graphic representation of the $\delta^{18}O_p$ values (average, standard deviation, end members) measured for Porrentruy in this study and their corresponding water temperature using Eq. (1). Comparable water temperatures for all taxa require different $\delta^{18}O_w$ values, which relate to salinity. Bulk and dentine values might have suffered diagenesis. Note the strong difference between $\delta^{18}O_w$ of Pycnodontiformes and *Asteracanthus* enameloid values (i.e. distinct palaeoenvironments) when similar ecological T is assumed. The wide value range of Pycnodontiformes indicates a tolerance to salinity fluctuations occurring within the platform, and possibly a living area broader than the shallow-marine platform. No attempt to define the final $\delta^{18}O_w$ values or water temperatures is made here.

sons, the significant differences in $\delta^{18}O_p$ values of *Asteracanthus* and Pycnodontiformes enameloid from Porrentruy (Student's t test, $t_{(38)} = 6.36$, $p < 0.01$) are interpreted as reflecting actual differences in the living conditions rather than in the alteration process (Fig. 4).

Water temperatures calculated with Eq. (1) from enameloid $\delta^{18}O_p$ of Pycnodontiformes and *Asteracanthus* differ by 7.4 °C (1.6 ‰). The two taxa are found in the same deposits and such a temperature difference is not plausible neither laterally, nor vertically, given that the water depth did not exceed a few tens of metres in the study area (Waite et al., 2013). Most of our Pycnodontiformes $\delta^{18}O_p$ values (18.2 to 21.9 ‰) indicate marine conditions, since they are comparable with the isotopic composition measured on several marine vertebrate taxa from the Late Jurassic of western Europe (18.5 to 22.8 ‰) (see Billon-Bruyat et al., 2005; Dromart et al., 2003; Lécuyer et al., 2003). Those values are consistent with the marine conditions indicated by the associated fauna of Porrentruy. When used in Eq. (1), the Pycnodontiformes $\delta^{18}O_p$ values give a mean temperature range that is also consistent with the palaeogeographical settings of the study site

(23.9 ± 4.4 °C, $n = 13$). However, the range in values is quite wide (see Fig. 4) and can be interpreted as a tolerance to salinity fluctuations for this taxon, since some of those bony fish are known to be euryhaline and are probably poor environmental indicators (Kocsis et al., 2009; Poyato-Ariza, 2005). Semi-confined lagoons induced by local depth differences on the platform and subjected to higher evaporation rates during the dry season would have been characterized by a higher salinity and thus higher isotopic composition, potentially recorded by Pycnodontiformes. For the lowest value (18.2 ‰), an influence of a slightly reduced salinity cannot be excluded. On the other hand, the highest values can also be interpreted as reflecting a deeper, cooler environment around the platform. The good state of preservation of Pycnodontiformes remains and the presence of several mandibles and tooth palates suggest that the material was not transported over long distances.

The preservation of the fine ornamentation of *Asteracanthus* teeth also suggests that they lived in the vicinity, even if the isotopic composition of *Asteracanthus* is significantly different from that of Pycnodontiformes. Also, the associated record of several large *Asteracanthus* fin spines in marly deposits of the Lower *Virgula* Marls (lagoonal deposits indicating a low-energy context) (see Waite et al., 2013) argues against long distances of sediment transport for those relatively large fossils (up to 26.5 cm long), supporting an autochthonous character of this genus. Moreover, the preservation of the root in several *Asteracanthus* teeth – an indication of post-mortem embedding rather than tooth loss in hybodonts (Underwood and Cumbaa, 2010) – also precludes transport. Yet, temperatures obtained with *Asteracanthus* enameloid samples using the Eq. (1) are higher (average 31.3 ± 2.9 °C, $n = 27$). This could imply a habitat closer to the sea surface but would then also suggest a possible influence of more evaporative conditions on the oxygen isotope composition of the water with $\delta^{18}O_w$ values higher than the global average used above (i.e. 1 ‰). For example, 0 ‰ as proposed by Lécuyer et al. (2003) for low-latitude marginal seas with high evaporation rates. However, higher $\delta^{18}O$ values of water would also result in higher temperatures calculated with an average of 35.8 °C and a maximum reaching 41.0 °C, which are considered unrealistic. A more consistent explanation is to consider *Asteracanthus* as living in a freshwater-influenced environment, i.e. an environment with a lower $\delta^{18}O_w$ value (Fig. 4).

5.2 Shark nurseries in reduced salinity environments for *Asteracanthus*?

Assessing the tooth replacement rate of an extinct shark is difficult, and studies of such rates are scarce (e.g. Botella et al., 2009). However, *Asteracanthus* possesses a crushing dentition composed of a rather small amount of large teeth (see figure in Rees and Underwood, 2008, p. 136) organized in a relatively low number of files and rows (*sensu*

Cappetta, 2012); hence, a relatively slow replacement rate is likely, compared to other sharks with numerous slender, cuspidated teeth adapted to clutch and tear their prey. This implies that the $\delta^{18}O_p$ values of *Asteracanthus* potentially reflect an average of the surrounding water parameters over a relatively longer growing period. The lower $\delta^{18}O_p$ values of *Asteracanthus*, compared to typical Late Jurassic marine compositions (see data from marine vertebrates of other studies in Sect. 5.1), corresponds either to a constant brackish living environment or to a marine environment with regular excursions into fresh- or brackish waters (or vice-versa). As *Asteracanthus* remains were not re-sedimented nor transported over long distances, it can be proposed that they partly inhabited the marine realm, as indicated by the associated fauna, but not continuously. Lateral salinity changes are readily caused by rainy winters coupled with an irregular morphology of the platform, creating marked depth differences and lagoons (Waite et al., 2013) where the proportion of meteoric water could have been important. However, excursions into more distant brackish and/or freshwater realms can also be considered. Extant elasmobranchs that occupy different environmental niches during relatively long period of their lives (not necessarily with salinity variations) can do so for different reasons: seasonal environmental changes, reproduction, and development in a distinct environment during the first ontogenetic stages (White and Sommerville, 2010).
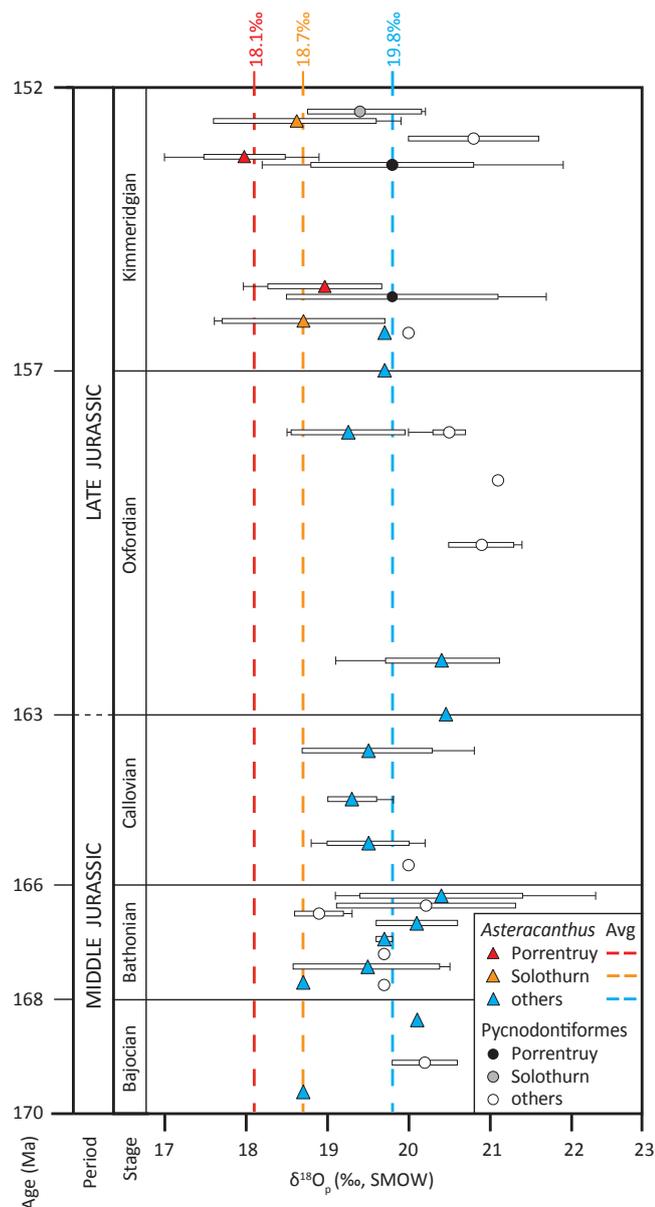
More than 130 *Asteracanthus* teeth were found in the Porrentruy excavation sites. Only four of them appeared to be clearly undersized (< 1 cm) (Fig. 3). As illustrated in Rees and Underwood (2008, p. 136), the size difference between lingual-most and labial-most teeth of any file is quite small in *Asteracanthus medius*. Even if a stronger heterodonty cannot be excluded for other species of the genus, it seems more likely that the clearly undersized dental material belonged to juvenile individuals. The record of hundreds of submillimetric fish remains such as dermal denticles resulting from sieving of hundreds of kilograms of sediments exclude a taphonomic bias linked to the size of the teeth. *Asteracanthus* juveniles could have spent the first period of their life in estuaries, rivers or lagoons, sheltered from predators such as crocodilians or the bony fish *Caturus*. Extant euryhaline bull shark females (*Carcharhinus leucas*) and their juveniles are known to have a similar behaviour (Jenson, 1976; Pillans et al., 2005), as is the case for some small hybodont sharks (Fischer et al., 2011; Klug et al., 2010). The location of this environment with reduced salinity remains open, especially since some sharks are known to migrate across very long distances, e.g. the blacktip shark (Castro, 1996). Regarding the fish faunal composition of Porrentruy, salinity fluctuations within the study area cannot be excluded. Two of the most abundant bony fish taxa recorded – Pycnodontiformes and "*Lepidotes*" – are known to tolerate salinity fluctuations (Amiot et al. 2010; Kocsis et al., 2009; Poyato-Ariza, 2005). Additionally, several chondrichthyan taxa recorded are potential indicators of reduced salinity: the chimaeroid genus *Ischyodus* was reported in Jurassic freshwater deposits of Russia (Popov and Shapovalov, 2007) and can therefore not be considered as strictly marine. The modern shark *Palaeoscyllium*, relatively scarce but present in our fossil assemblage, is the oldest modern shark known to tolerate freshwater, so far only in the Cretaceous though (Sweetman and Underwood, 2006). Finally, and as mentioned above, hybodonts and rays are in some cases also linked to reduced salinity conditions (Duffin and Thies, 1997; Thies, 1995). Salinity fluctuations (from pliohaline to brachyhaline) are supported by different ostracods assemblages in the study site (Schudack et al., 2013), yet they overwhelmingly indicate brachyhaline conditions in our sample sections.

In Fig. 5, the oxygen isotopic compositions of Pycnodontiformes and *Asteracanthus* enameloid samples measured in this study are shown for the Porrentruy and Solothurn localities and compared to previously published data from others – mostly older – Swiss, French, and British Jurassic localities (Billon-Bruyat et al., 2005; Dromart et al., 2003; Lécuyer et al., 2003). Generally, the Porrentruy *Asteracanthus* $\delta^{18}O_p$ values – especially in the Late Kimmeridgian – are lower than in other studies, while Pycnodontiformes values are comparable. The material from Solothurn (Kimmeridgian) – a locality with similar palaeoenvironment but under Tethyan influence only – shows some affinities with the Porrentruy material, for instance with unusually low oxygen isotope values for several *Asteracanthus*. The Porrentruy *Asteracanthus* $\delta^{18}O_p$ values tend to get lower in the Upper Kimmeridgian but this trend must be considered with caution due to the relatively small amount of Lower Kimmeridgian samples.

This global comparison suggests that the low $\delta^{18}O_p$ values measured for *Asteracanthus* here are likely linked to the age of the deposits. Interestingly, a tolerance of *Asteracanthus* to salinity variations has briefly been mentioned by Kriwet (2000), based on its presence in the younger deposits of the Purbeck and Wealden group in southern England (Woodward, 1895). *Asteracanthus* remains from freshwater deposits are also recorded in the Upper Cretaceous of Sudan (Buffetaut et al., 1990). The present data indicate an adaptation to a wider salinity range through time and in the Kimmeridgian already, maybe in response to the spectacular diversification of modern sharks in the marine realms of Western Europe at the end of the Jurassic (Cuny and Benton, 1999). Also, the shallow-water platform of NW Switzerland may have somehow represented a shelter for the hybodonts, still dominating the shark fauna around Porrentruy. The high sea-level in the Kimmeridgian (Hardenbol et al., 1998) could have opened new niches in shallow-water environments that was influenced by freshwater run-offs. These new living places could have provided shelter and nursery ground for *Asteracanthus*.

This is the first isotopic evidence of a euryhaline ecology for the large, durophagous shark *Asteracanthus*, classically considered as marine (Agassiz, 1843; Rees and Underwood, 2006, 2008).

2. Comparisons with geochemical data of older European Jurassic localities confirm the unusual character of the *Asteracanthus* isotopic compositions measured in the material from this study. This new freshwater-influenced isotopic composition of *Asteracanthus* is likely linked to a change in its ecology through geologic time, as suggested by similar results obtained with Kimmeridgian material from Solothurn. The Kimmeridgian transgression (i.e. opening of new shallow-water niches) (see Fig. 2) and probably competing stress from quickly diversifying neoselachians could have played an important role in the adaptation to brackish and freshwater realms.

3. A predominantly marine ecology is proposed for *Asteracanthus*, combined with regular excursions into freshwater and/or brackish environments, possibly for reproduction purposes considering the rarity of juvenile material in the marine, depositional environment.

The Supplement related to this article is available online at doi:10.5194/bg-12-6945-2015-supplement.

Figure 5. Comparison of $\delta^{18}O_p$ values (average, standard deviation, end members) of Pycnodontiformes and *Asteracanthus* enameloid samples from Porrentruy, Solothurn and other European localities through time. The stratigraphical position is approximate and corresponds to Early, Middle, Late divisions of each stage. The approximate geographical positions of previously studied localities (Dromart et al., 2003; Lécuyer et al., 2003; Billon-Bruyat et al., 2005) are shown in Fig. 1. Detailed localities and stratigraphic positions are available in the Supplement.

6 Concluding remarks

1. Most of the $\delta^{18}O_p$ values of enameloid measured in the hybodont shark *Asteracanthus* are too low to reflect fully marine conditions.

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