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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 mineralised 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 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 as 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 ~~primitive 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 paleoenvironmental settings (e.g. lagoonal, open marine, reduced salinity) (Duffin and Thies, 1997; Müller, 2011; Underwood, 2002). Their teeth are predominantly composed of fluor-apatite, 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 mineralise 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 paleoenvironmental 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 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 Transjurane 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 paleoclimate 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 paleoecology 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 ~~so-called “primitive sharks” or hybodonts~~ (order Hybodontiformes), modern sharks ~~(superorder Selachimorpha~~) and rays (suborder Rhinobatoidei). Chimaeras (superorder Holocephali, order Chimaeriformes) 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 (*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 mineralised part (enamel s.l., i.e. enamel and enameloid) was isolated from Pycnodontiformes and *Asteracanthus* teeth (Fig. 3). From eleven of the *Asteracanthus* teeth, dentine was 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 enamel and dentine. The visibly most unaltered and dentine-free teeth were selected.

From the Porrentruy material, 38 samples of *Asteracanthus* teeth (27 enamel 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, enamel of 9 *Asteracanthus* and 3 Pycnodontiformes teeth were added for comparison. Altogether, a total of 77 analyses were made.

The sample powders were pre-treated following the procedure of Koch et al. (1997), and the PO_4^{3-} ion of the apatite was separated and precipitated as silver-phosphate (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 standards (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 Finnigan 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. The overall analytical error is 0.3 ‰, however individual samples often reproduced better. For the NBS–120c an average value of 21.3 ± 0.3 ‰ ($n = 6$) was obtained.

The oxygen isotopic composition of unaltered fish teeth is function of both, water temperature and isotopic composition of ambient water during tooth growth (Kolodny et al., 1983; Lécuyer et al., 2013; Longinelli and Nuti, 1973). Here below is the phosphate fractionation equation of Lécuyer et al. (2013) used for calculating the temperature of sea water:

$$T(°C) = 117.4(\pm 9.5) - 4.50(\pm 0.43) \times \left(\delta^{18}O_{PO_4} - \delta^{18}O_{H_2O}\right). \tag{1}$$

For marine fauna, the global, average seawater isotopic composition can be used as an approximation that is assumed to be equal to −1 ‰ for Late Jurassic seawater (e.g. Shackleton and Kennet, 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) enamel 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 ‰, $n = 13$). Dentine values of *Asteracanthus* average 18.9 ± 0.8 ‰ (17.7–20.0 ‰, $n = 11$), indicating a statistically significant difference to the equivalent enamel samples collected on the same teeth (student 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 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) and crocodilians (Thalattosuchia) are common ~~(Schaefer, 2012~~).

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 conditions still favourable to hybodonts in Porrentruy, unlike in neighbouring localities from southern Germany (Nusplingen, Solnhofen) or France (Cerin), where hybodonts are

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scarce or absent. However, our chondrichthyan assemblage is similar to that in northern Germany (e.g. in Oker) (Duffin and Thies, 1997; Thies, 1995), also dominated by hybodonts and rays and associated to 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 non-renewable 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, the few modern sharks of our assemblage (~~Heterodontiformes,~~ Squatiniformes and Scyliorhinidae) are all thought to have had a benthic lifestyle, 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 enamel – and regarding that the dentine samples of *Asteracanthus* tend to similar values, all these specimens could have been affected by alteration during diagenesis.

In contrast, the isotopic compositions of Pycnodontiformes and *Asteracanthus* enamel samples are considered not to have been altered, because of their distinct range in values, their original histological structure when examined with a microscope and the generally good preservation potential for enamel/enameloid when not recrystallised (e.g. Kohn and Cerling, 2002). The significant differences in $\delta^{18}O_p$ values of *Asteracanthus* and Pycnodontiformes enamel from Porrentruy (Student *t* test, $t_{(38)} = 6.36$, $p < 0.01$) hence indicate different living environments (Fig. 4).

Water temperatures calculated with Eq. (1) from enamel $\delta^{18}O_p$ 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 meters in the study area (Waite et al., 2013). Most of the Pycnodontiformes $\delta^{18}O_p$ values are compatible with the marine conditions indicated by the associated fauna and the resulting average sea surface temperature is also consistent (23.9 ± 4.4 °C, $n = 13$). 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. For the lowest Pycnodontiformes values however, an influence of reduced salinity cannot be excluded since some of those bony fish are known to be euryhaline (Kocsis et al., 2009; Poyato-Ariza, 2005).

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. Moreover, the record of *Asteracanthus* fin spines and several teeth still preserved with their root (see Fig. 3) – an indication of post-mortem embedding rather than tooth loss in hybodonts (Underwood and Cumbaa, 2010) – also precludes transport. Yet, temperatures obtained with *Asteracanthus* enamel 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, such a change towards higher $\delta^{18}O$ values of water would also raise the temperature calculated to an unrealistic average of 35.8 °C, with a maximum reaching 41.0 °C. 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 impossible. However, *Asteracanthus* possesses a crushing dentition composed of a rather small amount of large teeth (see Rees and Underwood, 2008); 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 period. The isotopically lower signature of *Asteracanthus*, compared to a classical marine signal, 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/freshwater realms can also be considered.

While more than 130 middle-sized to large *Asteracanthus* teeth were found in the Porrentruy excavation sites, only 4 very small-scaled (< 1 cm) and badly preserved teeth were discovered among hundreds of kilograms of sediment sieved and picked, which suggests a different living environment during the juvenile stage, and excursions of adult individuals for reproduction purposes. The record of hundreds of submillimetric fish remains such as dermal denticles 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

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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). Middle-sized teeth potentially represent young individuals that had already colonised the marine realm. *Asteracanthus* individuals that have reached a considerable size were then a less easy prey and also able to feed on the large ammonites and bivalves living in the marine realm of the platform. 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). Several chondrichthyan taxa recorded in Porrentruy 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).

In Fig. 5, the oxygen isotopic compositions of Pycnodontiformes and *Asteracanthus* enamel 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). ~~All data given in this Figure are available in the Supplement~~. 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 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 cautiously due to the relatively small amount of Lower Kimmeridgian samples.

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This global comparison suggests that the especially 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 ~~for more than 150 years~~ (Agassiz, 1843; Rees and Underwood, 2006, 2008).

6 Concluding remarks

1. The $\delta^{18}O_p$ values of enamel measured in the hybodont shark *Asteracanthus* are too low to reflect fully marine conditions.
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) 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/brackish environments for reproduction purposes, and a brackish to freshwater habitat during early ontogenetic life stages.

The Supplement related to this article is available online at doi:10.5194/bgd-12-1-2015-supplement.

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References

Agassiz, L. J. R.: Recherches sur les poissons fossiles, Volume 5, Imprimerie de Petipierre, Neuchâtel, 1843.

Anquetin, J., Püntener, C., and Billon-Bruyat, J.-P.: A taxonomic review of the Late Jurassic eucryptodiran turtles from the Jura Mountains (Switzerland and France), PeerJ, 2, e369, doi:10.7717/peerj.369, 2014.

Billon-Bruyat, J.-P., Lécuyer, C., Martineau, F., and Mazin, J.-M.: Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles, and crocodilians, Palaeogeogr. Palaeocl., 216, 359–375, doi:10.1016/j.palaeo.2004.11.011, 2005.

Buffetaut, E., Bussert, R., and Brinkman, W.: A new nonmarine vertebrate fauna in the Upper Cretaceous of northern Sudan, Berliner Geowissenschaftliche Abhandlungen, Freie Universität Berlin, Berlin, A120, 183–202, 1990.

Cappetta, H.: Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth, edited by: Schultze, H.-P., Handbook of Paleoichthyology, Volume 3E, Verlag Dr. Friedrich Pfeil, Munich, 2012.

Castro, J. I.: Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States, B. Mar. Sci., 59, 508–522, 1996.

Colombié, C. and Rameil, N.: Tethyan-to-boreal correlation in the Kimmeridgian using high-resolution sequence stratigraphy (Vocontian Basin, Swiss Jura, Boulonnais, Dorset), Int. J. Earth Sci., 96, 567–591, doi:10.1007/s00531-006-0117-3, 2007.

Comment, G., Ayer, J., and Becker, D.: Deux nouveaux membres lithostratigraphiques de la Formation de Reuchenette (Kimméridgien, Ajoie, Jura suisse) – Nouvelles données géologiques et paléontologiques acquises dans le cadre de la construction de l'autoroute A16 (Transjurane), Swiss Bull. für Angew. Geol., 16, 3–24, 2011.

Cuny, G. and Benton, M. J.: Early radiation of the neoselachian sharks in western Europe, Geobios, 32, 193–204, 1999.

Dromart, G., Garcia, J.-P., Gaumet, F., Picard, S., Rousseau, M., Atrops, F., Lécuyer, C., and Sheppard, S. M. F.: Perturbation of the carbon cycle at the Middle/Late Jurassic transition: geological and geochemical evidence, Am. J. Sci., 303, 667–707, 2003.

Duffin, C. J. and Thies, D.: Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany, Geol. Palaeontol., 31, 235–256, 1997.

Fischer, J., Voigt, S., Schneider, J. W., Buchwitz, M., and Voigt, S.: A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries, J. Vertebr. Paleontol., 31, 937–953, 2011.

Hardenbol, J., Thierry, J., Farley, M. B., Jacquin, T., de Graciansky, P.-C., and Vail, P. R.: Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins: mesozoic-Cenozoic Sequence, Stratigr. Eur. Basins SEPM Spec. Publ., 60, 3–13 and 763–781, 1998.

Jank, M., Meyer, C., and Wetzel, A.: Late Oxfordian to Late Kimmeridgian carbonate deposits of NW Switzerland (Swiss Jura): stratigraphical and palaeogeographical implications in the transition area between the Paris Basin and the Tethys, Sediment. Geol., 186, 237–263, doi:10.1016/j.sedgeo.2005.08.008, 2006.

Jenson, N. H.: Reproduction of the Bull Shark, *Carcharhinus leucas*, in the Lake Nicaragua-Rio San Juan System, Investig. Ichthyofauna Nicar. Lakes, 40, 539–559, 1976.

Klug, S., Tütken, T., Wings, O., Pfretzschner, H., and Martin, T.: A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China, Palaeobiodiversity and Palaeoenvironments, 90, 241–257, doi:10.1007/s12549-010-0032-2, 2010.

Koch, P. L., Tuross, N., and Fogel, M. L.: The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite, J. Archaeol. Sci., 24, 417–429, 1997.

Kocsis, L.: Geochemical compositions of marine fossils as proxies for reconstructing ancient environmental conditions, Chimia, 65, 787–791, 2011.

Kocsis, L., Vennemann, T. W., and Fontignie, D.: Migration of sharks into freshwater systems during the Miocene and implications for Alpine paleoelevation, Geology, 35, 451–454, doi:10.1130/G23404A.1, 2007.

Kocsis, L., Ösi, A., Vennemann, T., Trueman, C. N., and Palmer, M. R.: Geochemical study of vertebrate fossils from the Upper Cretaceous (Santonian) Csehbánya Formation (Hungary): evidence for a freshwater habitat of mosasaurs and pycnodont fish, Palaeogeogr. Palaeocl., 280, 532–542, doi:10.1016/j.palaeo.2009.07.009, 2009.

Kohn, M. J. and Cerling, T. E.: Stable Isotope Compositions of Biological Apatite, in: Phosphate: Geochemical, Geobiological, and Materials Importance, Mineralogy and Geochemistry, Volume 48, Mineralogical Society of America Reviews, 4, 455–488, 2002.

Kolodny, Y., Luz, B., and Navon, O.: Oxygen isotope variations in phosphate of biogenic apatites: fish bone apatite – rechecking the rules of the game, Earth Planet. Sc. Lett., 64, 398–404, 1983.

Kriwet, J.: The fish fauna from the Guimarota mine, in: Guimarota – A Jurassic Ecosystem, edited by: Martin, T. and Krebs, B., Verlag Dr. Friedrich Pfeil, Munich, 41–50, 2000.

Kriwet, J. and Klug, S.: Diversity and biogeography patterns of Late Jurassic neoselachians (Chondrichthyes: Elasmobranchii), Geol. Soc. London, Spec. Publ., 295, 55–70, doi:10.1144/SP295.5, 2008.

Lécuyer, C., Picard, S., Garcia, J.-P., Sheppard, S. M. F., Grandjean, P., and Dromart, G.: Thermal evolution of Tethyan surface waters during the Middle-Late Jurassic: evidence from δ^{18}O values of marine fish teeth, Paleoceanography, 18, 16, doi:10.1029/2002PA000863, 2003.

Lécuyer, C., Amiot, R., Touzeau, A., and Trotter, J.: Calibration of the phosphate δ^{18}O thermometer with carbonate–water oxygen isotope fractionation equations, Chem. Geol., 347, 217–226, doi:10.1016/j.chemgeo.2013.03.008, 2013.

Longinelli, A. and Nuti, S.: Oxygen isotope measurements of phosphate from fish teeth and bones, Earth Planet. Sc. Lett., 20, 337–340, 1973.

Marty, D.: Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology, GeoFocus, 21, 278 pp., 2008.

Marty, D. and Billon-Bruyat, J.-P.: Field-trip to the excavations in the Late Jurassic along the future Transjurane highway near Porrentruy (Canton Jura, NW Switzerland): dinosaur tracks, marine vertebrates and invertebrates, in: 5th International Symposium on Lithographic Limestone and Plattenkalk, Switzerland, 17–22 August, 94–129, 2009.

Marty, D., Ayer, J., Becker, D., Berger, J.-P., Billon-Bruyat, J.-P., Braillard, L., Hug, W. A., and Meyer, C.: Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW Switzerland): overview and measures for their protection and valorisation, Bull. für Angew. Geol., 12, 75–89, 2007.

Müller, M. K.: The fish fauna of the Late Jurassic Solothurn Turtle Limestone (NW Switzerland), Swiss. J. Geosci., 104, 133–146, doi:10.1007/s00015-011-0061-5, 2011.

O'Neil, J. R., Roe, L. J., Reinhard, E., and Blake, R. E.: A rapid and precise method of oxygen isotope analysis of biogenic phosphate, Israel. J. Earth Sci., 43, 203–212, 1994.

Philippe, M., Billon-Bruyat, J.-P., Garcia-Ramos, J. C., Bocat, L., Gomez, B., and Piñuela, L.: New occurrences of the wood *Protocupressinoxylon purbeckensis* Francis: implications for terrestrial biomes in southwestern Europe at the Jurassic/Cretaceous boundary, Palaeontology, 53, 201–214, doi:10.1111/j.1475-4983.2009.00926.x, 2010.

Pillans, R. D., Good, J. P., Anderson, W. G., Hazon, N., and Franklin, C. E.: Freshwater to seawater acclimation of juvenile bull sharks (*Carcharhinus leucas*): plasma osmolytes and Na^+/K^+-ATPase activity in gill, rectal gland, kidney and intestine, J. Comp. Physiol. B, 175, 37–44, doi:10.1007/s00360-004-0460-2, 2005.

Popov, E. V. and Shapovalov, K. M.: New finds of chimaeroid fishes (Holocephali, Chimaeroidei) from the Jurassic of European Russia, in Modern Russian Paleontology: classic and newest methods, vol. C, edited by: Rozanov, A. Y., Paleontological Institute, Russian Academy of Sciences, Moscow, 25–44, 2007.

Poyato-Ariza, F. J.: Pycnodont fishes: morphologic variation, ecomorphologic plasticity, and a new interpretation of their evolutionary history, Bull. Kitakyushu Museum Nat. Hist. Hum. Hist., A3, 169–184, 2005.

Püntener, C., Billon-Bruyat, J.-P., Bocat, L., Berger, J.-P., and Joyce, W. G.: Taxonomy and phylogeny of the turtle *Tropidemys langii* Rütimeyer, 1873, based on new specimens from the Kimmeridgian of the Swiss Jura Mountains, J. Vertebr. Paleontol., 34, 353–374, doi:10.1080/02724634.2013.804412, 2014.

Rees, J. and Underwood, C. J.: Hybodont sharks from the Middle Jurassic of the Inner Hebrides, Scotland, T. Roy. Soc. Edin.-Earth, 96, 351–363, 2006.

Rees, J. and Underwood, C. J.: Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic), Palaeontology, 51, 117–147, doi:10.1111/j.1475-4983.2007.00737.x, 2008.

Schaefer, K.: Variabilité de la morphologie dentaire des crocodiliens marins (Thalattosuchia) du Kimméridgien d'Ajoie (Jura, Suisse), MS thesis, University of Fribourg, Switzerland, 111 pp., 2012.

Shackleton, N. and Kennet, J. P.: Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279, and 281, Initial Rep. Deep Sea, 29, 743–756, 1975.

Stahl, B. J.: Chondrichthyes III, Holocephali, edited by: Schultze, H.-P., Handbook of Paleoichthyology, Volume E, Verlag Dr. Friedrich Pfeil, Munich, 1999.

Sweetman, S. C. and Underwood, C. J.: A Neoselachian shark from the non-marine Wessex Formation (Wealden Group: Early Cretaceous, Barremian) of the Isle of Wight, southern England, Palaeontology, 49, 457–465, 2006.

Thies, D.: Placoid scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of northern Germany, J. Vertebr. Paleontol., 15, 463–481, 1995.

Underwood, C. J.: Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, Palaeontology, 45, 297–325, 2002.

Underwood, C. J.: Environmental controls on the distribution of neoselachian sharks and rays within the British Bathonian (Middle Jurassic), Palaeogeogr. Palaeocl., 203, 107–126, doi:10.1016/S0031-0182(03)00663-1, 2004.

Underwood, C. J. and Cumbaa, S. L.: Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada, Palaeontology, 53, 903–944, doi:10.1111/j.1475-4983.2010.00969.x, 2010.

Underwood, C. J. and Rees, J.: Selachian faunas from the earliest Cretaceous ~~purbeck~~ groups of Dorset, Southern England, Spec. Pap. Palaeontol., 68, 107–19, 2002.

Underwood, C. J. and Ward, D. J.: Neoselachian sharks and rays from the British Bathonian (Middle Jurassic), Palaeontology, 47, 447–501, 2004.

Vennemann, T., Hegner, E., Cliff, G., and Benz, G. W.: Isotopic composition of recent shark teeth as a proxy for environmental conditions, Geochim. Cosmochim. Ac., 65, 1583–1599, 2001.

Vennemann, T. W., Fricke, H. C., Blake, R. E., O'Neil, J. R., and Colman, A.: Oxygen isotope analyses of phosphates: a comparison of techniques for analysis of Ag_3PO_4, Chem. Geol., 185, 321–336, 2002.

Waite, R., Marty, D., Strasser, A., and Wetzel, A.: The lost paleosols: masked evidence for emergence and soil formation on the Kimmeridgian Jura platform (NW Switzerland), Palaeogeogr. Palaeocl., 376, 73–90, 2013.

Woodward, A. S.: Catalogue of the fossil fishes in the British Museum (Natural History), British Museum (Natural History), Dept. of Geology, London, 1889–1901.

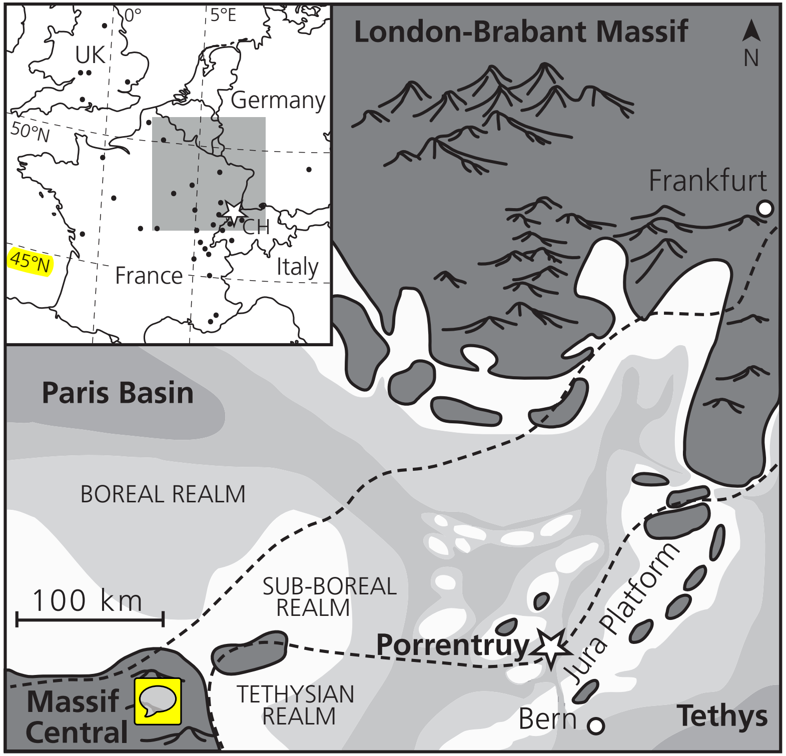

Figure 1. Geographical position of Porrentruy (☆) and other European sites (•) of previously published studies and providing geochemical data compared in Fig. 5. Paleogeographical map of the shaded square area (Late Kimmeridgian, modified from Comment et al., 2011). CH = Switzerland, paleolatitude of Porrentruy = ∼30° N. Emerged land is outlined, darker grey corresponds to deeper water.

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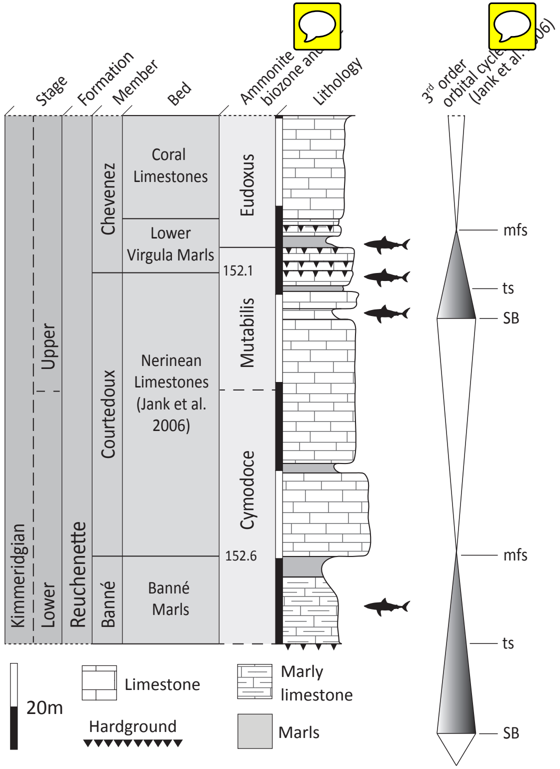

Figure 2. Simplified stratigraphic profile of the Porrentruy area with third order orbital cycle and section yielding the studied chondrichthyan material. Numbers indicate geological age in millions of years. SB = sequence boundary, ts = transgressive surface, mfs = maximum flooding surface.

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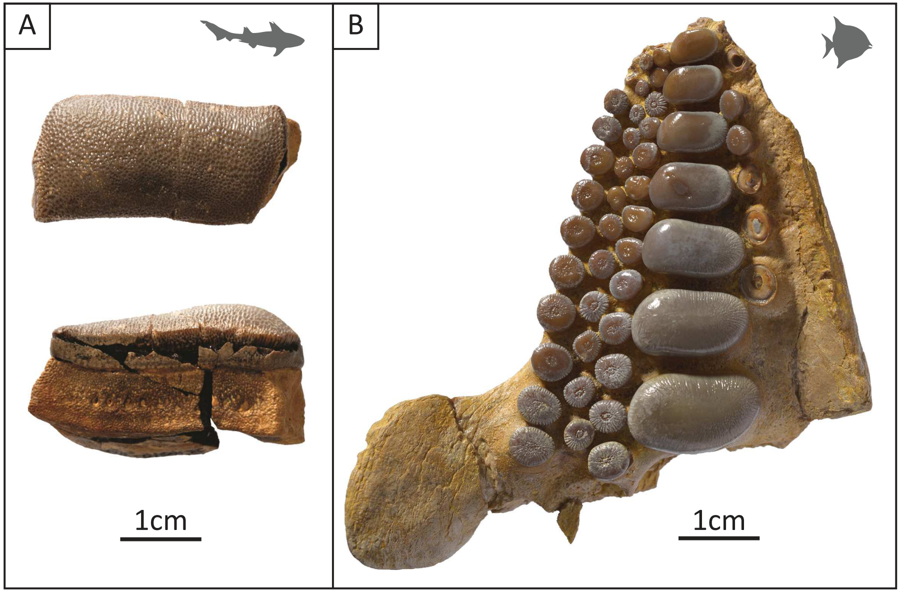

Figure 3. Fossil material from the study site. **(a)** Tooth of *Asteracanthus* in occlusal (top) and lateral view, with root preserved (specimen SCR010-303). **(b)** Left prearticular bone of Pycnodontiformes with teeth (specimen SCR010-1204). Photographs by PAL A16.

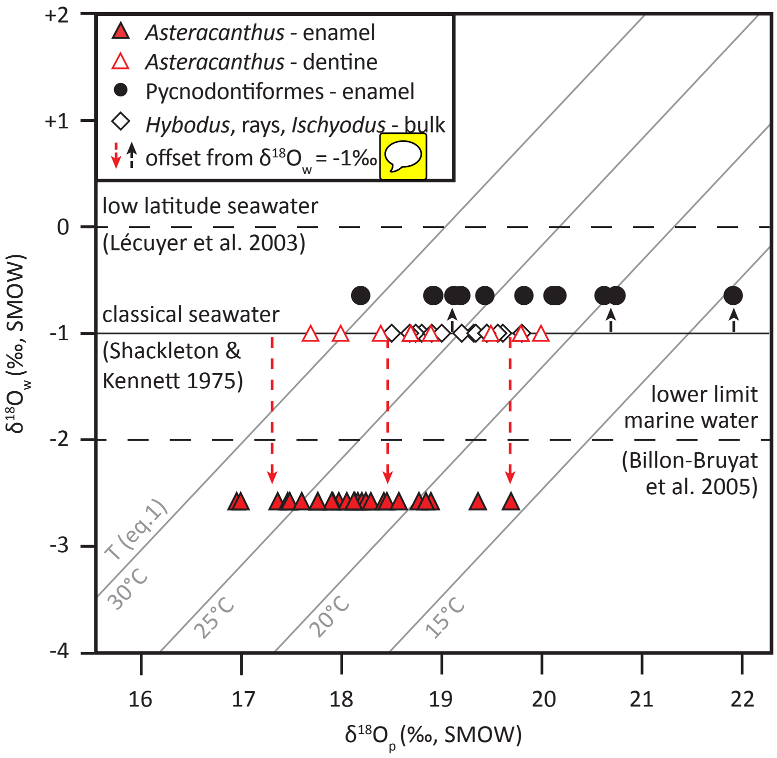

Figure 4. $\delta^{18}O_p$ values of Porrentruy fish samples and related water temperature (T) resulting from Eq. (1). *Hybodus*, rays, *Ischyodus* as well as most *Asteracanthus* dentine samples are considered diagenetically altered. Arrows show effect of varying $\delta^{18}O_w$ in Eq. (1) from classical seawater value (−1 ‰). Realistic and consistent temperatures for *Asteracanthus* and Pycnodontiformes imply the influence of respectively distinct paleoenvironments.

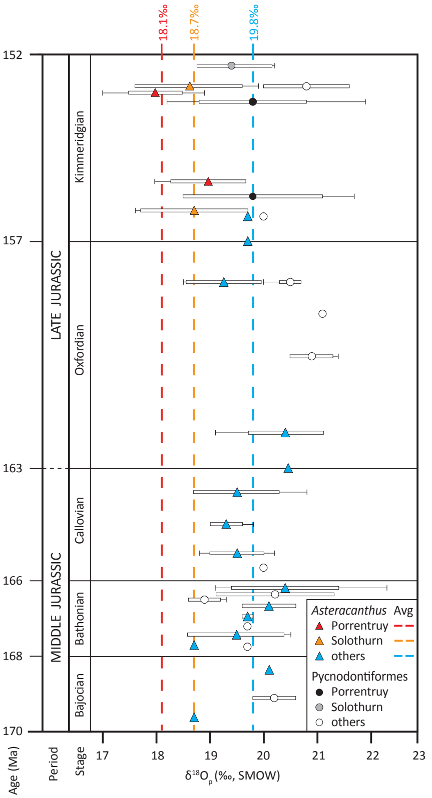

Figure 5. Comparison of $\delta^{18}O_p$ values (average, standard deviation, end members) of Pycnodontiformes and *Asteracanthus* enamel samples from Porrentruy, Solothurn and other European localities through time. The approximate geographical position of previously studied localities (Dromart et al.,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