Author's response

Answer to comment bdg-12-C5631-2015 by referee Jan Fischer

Page 3, line 19

1) Referee comment:
"Primitive" sharks, compared with modern neoselachians, would be the Devonian Cladoselache or the symmoriid Stethacanthus. Hybodonts, the extinct sister group of the neoselachians, and especially the Late Jurassic species were advanced and already highly derived fishes of the extensive chondrichthyan steam group, from where the modern crown group (sharks and rays) derived.

2) Author's response:
Accepted.

3) Changes in the text:
~~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).~~
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).

Page 4, line 16

1) Referee Comment:
According to Ziegler 1990, during the Kimmeridgian, the Massif Central wasnt formed, but this land mass would be the Amorican Massif? Is this correct or already outdated?

Ziegler, P. A. (1990): Geological Atlas of Western and Central Europe. Shell International Petroleum Maatschappij, The Hague: 239 p.

2) Author's response:
In the works of Hug (2003) and Thierry et al. (2010), both terms, Armorican and Central Massifs, are used in the context of the Early Kimmeridgian already. However, the Central Massif mentioned in those studies and in our manuscript is not the equivalent to the extant Massif Central. Gely et al. (2014) use the "Central platform" to avoid any confusion. Since Massif Central is an expression commonly used in the literature, we will

leave it as it is in our manuscript. Also, it allows a direct comparison with other works of the PAL A16 team on the Porrentruy region.

Gély, Jean-Pierre, F. Hanot, Francis Amédro, Françoise Bergerat et al. (2014). Le Bassin Parisien - Un Nouveau Regard Sur La Géologie. Bulletin D'information Des Géologues Du Bassin de Paris, Mémoire hors-série Vol. 9.

Hug, W. A. 2003: Sequenzielle Faziesentwicklung der Karbonatplattform des Schweizer Jura im Späten Oxford und frühesten Kimmeridge. Geofocus 7, Fribourg, 1-155

Thierry, J. et al. (44 co-auhors) 2000: Map 10: Early Kimmeridgian (146-144 Ma). In: Dercourt, J., Gaetani, M., Vrielvynck, B., Barrier, E., Biju- Duval, B., Brunet, M. F., Cadet, J. P., Crasquin, S. & Sandulescu, M. (eds.), Atlas Peri-Tethys, Paris, palaeogeographical map

3) Changes in the text:

None.

Page 5, lines 6-9

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1) Referee Comment:

- What taxa have been found on genus level besides *Asterhacanthus*, *hybodus* and *Ischyodus*?
- hybodont sharks, the extinct sister group of modern sharks - Maisey 2004

Maisey, J. G., Naylor, J. P. & Ward, D. J. (2004): Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. - In: Arratia, G. & Tintori, A. (eds): Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity. Proceeding of the international meeting Serpiano, 2001. Verlag Dr. Friedrich Pfeil, München, p. 17-56.

- subchohort Neoselachii or subdevision Selachii of the Sublass Elasmobranchii of the class Chondrichthyes.

Confusing, I know. A superorder of the Selachii would be Squalomorphii or Galeomorphii (Cappetta 2012). Since you mention Heterodontiformes, Squatiniformes and Scyliorhinidae (Carcharhiniformes) (p. 8) taxa from both superorders are contained.

Cappetta, H. (2012): Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth. - In: Schultze, H.-P. (ed): Handbook of Paleoichthyology 3E. Verlag Dr. Friedrich Pfeil, München: 512 p.

2) Author's response:

We agree that it needs more precision (a detailed publication on the fauna will follow).

3) Changes in the text:

~~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.~~

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,** order Chimaeriformes**: *Ischyodus***) are also present.

Added reference :

Maisey, J. G., Naylor, J. P. & Ward, D. J.: Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. - In: Arratia, G. & Tintori, A. (eds): Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity. Proceeding of the international meeting Serpiano, 2001. Verlag Dr. Friedrich Pfeil, München, p. 17-56, 2004.

Page 5, line 22

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1) Referee Comment:

I would recommend using enameloid in the whole text instead of enamel since it describes the outer hypermineralized tissue of shark teeth as well as fish teeth that is distinct in its structure to mammal enamel. And enamleoid is the used term in scientific publications.

Enax, J., Prymak, O., Raabe, D. & Epple, M. (2012): Structure, composition, and mechanical properties of shark teeth. Journal of Structural Biology 178 (3): p. 290-299.

Vennemann, T. W., Hegner, E., Cliff, G. & Benz, G. W. (2001): Isotopic composition of recent shark teeth as a proxy for environmental conditions. Geochimica et Cosmochimica Acta 65 (10): p. 1583-1599.

2) Author's response:

Accepted. Changed in the commented sentence and throughout the whole text, including figures. See comment Page 21, figure 3 for the new figure. We chose another adult *Asteracanthus* tooth than the previously figured one. The new one is better comparable to the juvenile specimen.

3) Changes in the text:

~~The best mineralised part (enamel *s.l., i.e.* enamel and enameloid) was isolated from Pycnodontiformes and *Asteracanthus* teeth (Fig. 3).~~

The best mineralized part **of the teeth, the enameloid,** was isolated in Pycnodontiformes and *Asteracanthus* (Fig. 3).

Page 6, lines 1-2

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1) Referee Comment:

What were the criteria to decide whats unaltered and whats not?

2) Author's response:

Here we provide some more detail. Please see response to comment on Page 8, lines 21-25 for a more detailed discussion on the preservation, based on the results.

3) Changes in the text:

~~The visibly most unaltered and dentine-free teeth were selected~~

Due to its very small size, only the outer aspect of this material was considered to select visibly best-preserved specimens, *i.e.* not worn-out teeth and/or with ornamentation well defined. After manual removing of the largest part possible of the root, the most dentine-free teeth were selected.

Page 6, line 8

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1) Referee Comment:

How much material of enameloid or bulk sample was needed for a single sample?

2) Author's response:

The minimum quantity of powder sampled was 2mg.

3) Changes in the text:

~~The sample powders were pre-treated following the procedure of Koch et al. (1997),and the PO43- ion of the apatite was separated and precipitated as silver-phosphate (e.g. Kocsis, 2011; O'Neil et al., 1994).~~

The sample powders **(at least 2mg per sample)** 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).

Page 6, line 17

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1) Referee Comment:

explain in brackets

Vienna Standard mean Ocean Water

2) Author's response:

Accepted

3) Changes in the text:

~~The data are expressed in permil and reported as $\delta^{18}O_p$ on the VSMOW scale.~~

The data are expressed in permil and reported as $\delta^{18}O_p$ on the VSMOW scale **(Vienna Standard Mean Ocean Water)**.

Page 6, line 18

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1) Referee Comment:

Were the data normalized to the NBS-120c value?

2) Author's response:

The data were not corrected to NBS-120c. It was only used for cross-checking preparation of the samples. As no accepted and real matrix match standard exist for bioapatite, the slightly lower NBS-120c (compare to other reported values) is thought to be related to heterogeneity in this reference material. Additionally, NBS120c is a sedimentary phosphorite therefore it could respond differently to pretreatments and also to dissolution compared to pure enamel. When very extreme values are obtained the samples are always re-prepared and re-run.

3) Changes in the text:

~~For the NBS-120c an average value of 21.3_0.3‰ (n = 6) was obtained.~~

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), still no correction was applied here as the small offset is thought to be due to heterogeneity in the sedimentary phosphorite and its different response to pretreatments than enameloid.

Added reference:

Halas, S., Skrzypek, G., Meier-Augenstein, W., Pelc, A., Kemp, H.F.: Inter-laboratory calibration of new silver orthophosphate comparison materials for the stable oxygen isotope analysis of phosphates. Rapid Commun. Mass Spectrom. 25, 579–584, 2011.

Page 6, lines 20-28

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1) Referee Comment:

- d18Oh20 or d18Ow?

See Fig. 4 figure caption as well as Supplement Table and Legend.

- (d18Ow)
- for the ice-free

2) Author's response:

The text was modified accordingly to make it more consistent. Thank you.

3) Changes in the text:

~~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:~~

~~$T\ (°C) = 117.4(\pm9.5) - 4.50(\pm0.43) \times (\delta^{18}O_{PO4} - \delta^{18}O_{H2O})$ (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).~~

The oxygen isotopic composition of unaltered fish teeth ($\boldsymbol{\delta^{18}O_p}$) is function of both, water temperature (T) and isotopic composition of ambient water ($\boldsymbol{\delta^{18}O_w}$) during tooth growth (Kolodny et al., 1983; Lécuyer et al., 2013; Longinelli and Nuti, 1973). Here below is the phosphate fractionation equation of Lécuyer et al. (2013) used for calculating the temperature of sea water:

$$T\ (°C) = 117.4(\pm9.5) - 4.50(\pm0.43) \times (\delta^{18}O_{\mathbf{P}} - \delta^{18}O_{\mathbf{w}}) \qquad (1)$$

For marine fauna, the global, average seawater isotopic composition ($\boldsymbol{\delta^{18}O_w}$) 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 Kennet**t**, 1975).

Reference corrected :

Shackleton, N. and Kennet**t**, 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.

Page 7, line 10

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1) Referee Comment:

What does it mean?

2) Author's response:

The statistics of Student's t-test shows a significant difference between enamel and dentine, a difference already observed by several authors (Lécuyer et al., 2003; Sharp et al., 2000; Pucéat et al., 2003). That is a further argument for the better preservation of enamel compared to dentine and for the focus on enamel samples in the interpretation. However, since this is the Results section, these precisions will be given further in the text.

3) Changes in the text:

~~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).~~

The average value of 18.9±0.8‰ (17.7–20.0‰, n=11) in the *Asteracanthus'* dentine is significantly different to the equivalent enameloid samples collected on the same teeth demonstrated by Student's t-test: t(20) = 2.98, p < 0.01.

References added :

Pucéat, E., Lécuyer, C., Sheppard, S. M. F., Dromart, G., Reboulet, S. and Grandjean, P.: Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels, Paleoceanography, 18(2), 1-12, doi:10.1029/2002PA000823, 2003.

Sharp, Z. D., Atudorei, V. and Furrer, H.: The effect of Diagensis on oxygen isotope ratios of biogenic phosphates, Am. J. Sci., 3000, 222–237, 2000.

Page 7, line 19

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1) Referee Comment:

(Schaefer, 2012)

2) Author's response:

Accepted, more consistent with the rest of the sentence.

3) Changes in the text:

~~Among vertebrates, coastal marine turtles (Plesiochelyidae) (Anquetin et al., 2014; Püntener et al., 2014)~~
~~and crocodilians (Thalattosuchia) are common (Schaefer, 2012).~~

Among vertebrates, coastal marine turtles (Plesiochelyidae) (Anquetin et al., 2014; Püntener et al., 2014)
and crocodilians (Thalattosuchia) (Schaefer, 2012) are common.

Page 8, lines 2-3

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1) Referee Comment:

- references for that fact?
- So far nothing has been said about conditions of reduced salinity in Porrentruy. Anticipating of the interpretation.

2) Author's response:

- A paper on the chondrichthyan fauna is in preparation. The genera now listed above (in response to your comment on Page 5, lines 6-9) are comparable to the references proposed (Duffin and Thies, 1997; Thies, 1995).

- Accepted. Here, the "also" is confusing and can be understood as both "also dominated by hybodonts", and "also associated to conditions of reduced salinity". The authors did not mean to inform on the salinity of Porrentruy at this point of the manuscript.

3) Changes in the text:

~~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).~~

Our chondrichthyan assemblage **(see section 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 to conditions of reduced salinity (Underwood and Rees, 2002; Underwood and Ward, 2004; Underwood, 2002, 2004).

Page 8, line 9-12

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1) Referee Comment:

- "Heterodontiformes" is crossed out

- That kind of durophagous lifestyle can be also assumed for *Asteracanthus* with its clutching-crushing-grinding-dentition.

Cappetta, H. (2012): Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth. - In: Schultze, H.-P. (eds): Handbook of Paleoichthyology 3E. Verlag Dr. Friedrich Pfeil, München: 512 p.

Cuny, G. (2012): Freshwater hybodont sharks in Early Cretaceous ecosystems : A review. - In: Godefroit, P. (eds): Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems. Indiana University Press, Bloomington, p. 518-529.

- references for the lifestyles of these sharks?

2) Author's response:

- According to Cappetta (2012), Heterodontiformes are part of the Neoselachii and should not be crossed out. Here we added Neoselachii to make clearer what we mean about "modern sharks", which can be confusing.
- We agree about the durophagous diet for *Asteracanthus*, though a benthic lifestyle is more disputable. The possibility for the most grown-up individuals to feed on ammonites cannot be discarded, regarding their dentition (ammonites are abundant in the study area). In his book "Les requins sont-ils des fossiles vivants ? – L'évolution des poissons cartilagineux" (EDP Sciences, 2002), Gilles Cuny briefly mentions a possible relation between the large size reached by ammonites and *Asteracanthus*. Based on the quite stable isotopic composition of *Asteracanthus* teeth coming from deposits of different depths, Lécuyer et al. (2003, see references) consider *Asteracanthus* as a surface dweller.

A benthic lifestyle is more reasonable for the modern shark taxa we list: *Pseudorhina* and *Protospinax* show a dorso-ventral flattening; extant relatives of our *Heterodontus* and *Palaeoscyllium* (e.g. *Heterodontus francisci* and *Scyliorhinus stellaris*) live close to the sea floor. A benthic lifestyle is proposed for those taxa in the references we cite.

3) Changes in the text:

~~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.~~

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.

Reference added:

Cappetta, H.: Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth. - In: Schultze, H.-P. (eds): Handbook of Paleoichthyology 3E. Verlag Dr. Friedrich Pfeil, München: 512 p., 2012.

Page 8, line 21-25

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1) Referee Comment:

- What kind of distinct range is this between *Astercanthus* dentine (17.7-20 permil) and *Asteracanthus* enameloid (17.0-19.7 permil)? What points to alteration in the first one? The wider range?
- You examined cathodoluminescence on the material or how do you decided whats altered and whats not? What means original and how do you detect it?
- The stability of enameloid has been repeatedly questioned: e.g.:

Kohn, M. J., Schoeninger, M. J. & Barker, W. W. (1999): Altered states: Effects of diagenesis on fossil tooth chemistry. Geochimica et Cosmochimica Acta 63 (18): p. 2737-2747.

Sharp, Z. D., Atudorei, V. & Furrer, H. (2000): The effect of diagenesis on oxygen isotope ratios of biogenic phosphates. American Journal of Science 300: p. 222-237.

Zazzo, A., Lécuyer, C. & Mariotti, A. (2004): Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions. Geochimica et Cosmochimica Acta 68 (1): p. 1-12.

2) Author's response:

Here, apart from general aspect of the fossil material (well-defined ornamentation, absence of sign of transportation), microscopic observation of thin sections and CL analyses (revealing non-luminescence) were performed. As there is no way to be completely sure of the pristine quality of a fossil shark tooth, we also infer the good preservation of enamel samples using their isotopic value range. "Distinct range in value" refers here to the difference between *Asteracanthus* enamel and Pycnodontiformes enamel values only.

However, here is more detail:

- Since all samples analyzed in this work come from the same deposits (always several taxa analyzed in a same bed), one would expect a uniform isotopic signature in all samples if the material was diagenetically altered.

- *Asteracanthus* and Pycnodontiformes enamel value ranges are distinct from each other, *Asteracanthus* ones being in average lower. This difference is most probably due to different original isotopic composition and not to diagenesis.
There is another way to explain those taxon-related differences in the isotopic value, but it seems very unlikely: teeth from one taxon could have been deposited in an environment different to the study environment, suffered different alteration, then been reworked and redeposited in the study area, together with authochthonous material from the other taxon. Preliminary trace element study (i.e., rare earth element distribution) did not support mixed-reworked fauna.

- *Asteracanthus* and Pycnodontiformes enamel values are also distinct from the ones of dentine-bearing samples of other taxa (*i.e*. bulk samples of *Hybodus* and rays, dentine of *Ischyodus*).

- *Asteracanthus* dentine isotopic values are all higher than their enamel counterpart measured on the same tooth, except one that is slightly below (sample BSY008-579). As a less resistant, more porous tissue, the dentine seemingly suffered alteration to some extent. The *Asteracanthus* dentine values *tend* to values similar to dentine-bearing samples of other taxa and this is also why dentine-bearing samples in general are ruled out from the final interpretation, since they are more likely to be diagenetically altered than enamel samples.

- About the stability of enameloid, Zazzo et al. (2004) showed that even under organic conditions (bacterium mediated – which may change the PO_4 and $\delta\ ^{18}O$ too) enamel retains the original isotopic composition.

3) Changes in the text:
~~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 dfferences 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).~~

In contrast, 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 non-luminescent character when subjected to cathodoluminescence**, and the generally good preservation potential for enameloid (*e.g.* Kohn and Cerling, 2002). **Still, the distinct range in values of *Asteracanthus* and Pycnodontiformes enameloid, both when compared to one another and to dentine-bearing samples, is the best indicator of their good preservation. Indeed, *Asteracanthus* enameloid values measured on a tooth always differ from their dentine counterpart from the same specimen – the dentine being higher, except in one case. This shows that the**

enameloid did not suffer the same level of alteration that the dentine underwent. 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 undergone the same diagenetic alteration (see Fischer et al., 2012). Because of these reasons, the significant differences in $\delta^{18}O_p$ values of *Asteracanthus* and Pycnodontiformes enameloid from Porrentruy (Student 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). We will focus on those values for the rest of the discussion.**

Reference added :

Fischer, J., Voigt, S., Franz, M., Schneider, J. W., Joachimski, M. M., Tichomirowa, M., Götze, J. & Furrer, H. (2012): Palaeoenvironments of the late Triassic Rhaetian Sea: Implications from oxygen and strontium isotopes of hybodont shark teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 353-355: p. 60-72.

Page 9, line 7-9

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1) Referee Comment:

What are the Late Jurassic comparative marine values for a "classical marine signal" based on what and who determined them? References?

2) Author's response:

We base on the papers we use as comparison isotopic compositions. Those papers are about Jurassic marine vertebrates from Western Europe. You can refer to Fig. 5 to look at the value ranges from those comparison studies. This is now clarified in the text.

3) Changes in the text:

~~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).~~

Most of our Pycnodontiformes $\delta^{18}O_p$ values (18.2-21.9‰) indicate marine conditions**, since they are comparable with the isotopic composition measured on several marine vertebrate taxa from the Late Jurassic of western Europe (18.5-22.8‰) (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 the Eq. (1), the Pycnodontiformes $\delta^{18}O_p$ values result in a mean temperature range that is consistent considering the paleogeographical settings of the study site (23.9±4.4 °C, n=13).**

Page 9, line 18

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1) Referee Comment:

Why do hybodont fin spines preclude post mortem transport?

2) Author's response:

You are right, the presence of fin spines alone does not directly preclude transport. However, because of their size, fin spines are unlikely to be transported on large distances in our context of shallow and low-energy platform (as indicated by the sediment type where most shark remains are found, the marls). We agree this needs some precision.

3) Changes in the text:

~~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.~~
Also, the associated record of several large *Asteracanthus* fin spines in the Lower Virgula Marls (a lagoonal facies indicating a low-energy context) (see Waite et al., 2013) points out the absence of transport over long distances of those relatively large objects (up to 26.5 cm long) and supports hereby the autochthonous character of this genus. Moreover, the preservation of the root in several *Asteracanthus* teeth (see Fig. 3) – an indication of post-mortem embedding rather than tooth loss in hybodonts (Underwood and Cumbaa, 2010) – also precludes transport.

Page 9, lines 20-21

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1) Referee Comment:

For your values an extant analogon - euryhaline bull sharks generally occupy brackish inshore and riverine environments with temperatures of 26–32 °C

Carlson, J. K., Ribera, M. M., Conrath, C. L., Heupel, M. R. & Burgess, G. H. (2010): Habitat use and movement patterns of bull sharks Carcharhinus leucas determined using pop-up satellite archival tags. Journal of Fish Biology 77 (3): p. 661-675.

Fischer, J., Voigt, S., Franz, M., Schneider, J. W., Joachimski, M. M., Tichomirowa, M., Götze, J. & Furrer, H. (2012): Palaeoenvironments of the late Triassic Rhaetian Sea: Implications from oxygen and strontium isotopes of hybodont shark teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 353-355: p. 60-72.

2) Author's response:

Thank you for this very valuable information.

3) Changes in the text:

None directly at the place of the comment. The reference of Fischer et al. (2012) was added in the diagenesis part, see Comment on Page 8, lines 21-25.

Page 10, line 1

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1) Referee Comment:
Makes sense - Extant relatives with comparable ecological niches such as heterodontid sharks dwell in warm-temperate waters around 20 °C

White, W. T. & Sommerville, E. (2010): Elasmobranchs of Tropical Marine Ecosystems. - In: Carrier, J. C.et al. (eds): Sharks and their relatives II - Biodiversity, adaptive Physiology, and Conservation. CRC Press, London New York, p. 160-200.

2) Author's response:
Another valuable data, thank you.

3) Changes in the text:
Sentence added:
Extant elasmobranchs that occupy different environments 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 distinct environment in first ontogenetic stages (White and Sommerville, 2010).

Reference added:
White, W. T. and Sommerville, E.: Elasmobranchs of Tropical Marine Ecosystems, in Sharks and their relatives II - Biodiversity, adaptive Physiology, and Conservation, edited by J. C. Carrier, J. A. Musick, and M. R. Heithaus., pp. 160-200, CRC Press, London New York, 2010.

Page 10, line 4

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1) Referee Comment:
I agree but there are still other opinions:

Botella, H., Valenzuela-Ríos, J. I. & Martínez-Pérez, C. (2009): Tooth replacement rates in early chondrichthyans: a qualitative approach. Lethaia 42 (3): p. 365-376.

2) Author's response:
Accepted. Changed for a more moderate declaration

3) Changes in the text:

~~Assessing the tooth replacement rate of an extinct shark is impossible.~~

Assessing the tooth replacement rate of an extinct shark is **difficult**, and studies in respect are scarce (e.g. Botella et al., 2009).

Reference added :

Botella, H., Valenzuela-Ríos, J. I. and Martínez-Perez, C.: Tooth replacement rates in early chondrichthyans: A qualitative approach, Lethaia, 42(3), 365–376, doi:10.1111/j.1502-3931.2009.00152.x, 2009.

Page 10, line 5

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1) Referee Comment:

... of rather few files of large teeth?

file according to Cappetta 2012 (p. 10) for a series of teeth perpendicular to the jaw edge

Cappetta, H. (2012): Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth. - In: Schultze, H.-P. (eds): Handbook of Paleoichthyology 3E. Verlag Dr. Friedrich Pfeil, München: 512 p.

2) Author's response:

Both the files and lines are quite limited in *Asteracanthus*, compared to other sharks, e.g. with tearing-type dentition (see picture on p.136 in Rees & Underwood (2008): Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). Palaeontology, 51).

3) Changes in the text:

~~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.~~

However, *Asteracanthus* possesses a crushing dentition composed of a rather small amount of large teeth (see 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.

Page 10, lines 10-11

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1) Referee Comment:

Please define it in 5.1 before for the Late Jurassic marine realm

2) Author's response:

Se response to comment on Page 9, lines 7-9

3) Changes in the text:

~~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).~~

The isotopically lower signature of *Asteracanthus*, compared to a classical Late Jurassic marine signal **(see data from marine vertebrates of other studies in section 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).

Page 10, lines 20-21

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1) Referee Comment:

- What means middle sizes or large?
- If I understand it correctly, the determination of juvenile teeth is singly based on its size?

Why are these teeth not the extreme lateral teeth of the dentition that are distinctly reduced as shown in Cappetta 2012 and Rees and Underwood 2008?

Are there any morphological traits or hints for ontogenetic heterodonty, that allow such assignment? I know that it is very difficult to identify but your assignment need a little bit more substantiated.

Cappetta, H. (2012): Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth. - In: Schultze, H.-P. (eds): Handbook of Paleoichthyology 3E. Verlag Dr. Friedrich Pfeil, München: 512 p.

Fischer, J., Voigt, S., Schneider, J. W., Buchwitz, M. & Voigt, S. (2011): A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries. Journal of Vertebrate Paleontology 31 (5): p. 937-953.

Rees, J. & Underwood, C. J. (2008): Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). Palaeontology 51 (1): p. 117-147.

2) Author's response:

We agree this needs more precision. Again compared to the picture on p.136 in Rees & Underwood (2008) (Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). Palaeontology, 51), the "small-scaled teeth" we mention are clearly undersized. Furthermore, the size difference between this small material and the other, larger teeth is much greater than the size difference between lingual-most and labial-most teeth in the figure of Rees & Underwood (2008).

A photograph of this small-sized material has been added in Figure 3 for a direct comparison with the normal adult size and we propose to moderate our assumptions in the text.

3) Changes in the text:

~~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.~~

More than 130 *Asteracanthus* teeth were found in the Porrentruy excavation sites. Only 4 of them appeared to be clearly undersized (< 1 cm) **(Figure 3). As illustrated in Rees & 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. Their proportionally limited number suggests a different living environment during the juvenile stage. Therefore, excursions of adult individuals for reproduction purposes can be considered.** 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.

Page 11, lines 3-4

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1) Referee Comment:

The same problem.

The dentition of *Astercanthus* is formed by small posterior teeth, followed by the large, up to 6 cm large lateral brick-like teeth and midde sized anterior ones in front.

I guess distinction of different morphotypes of a single dentition and different ontogenetic stages just works with the morphology of the teeth. If all teeth have more or less the same shape this might point to different sizes of the ancient shark. If the size difference is accompanied by different morphology (see Fig. 3 in Rees and Underwood 2008) different teeth of a heterodont dentition seems to be more realistic.

2) Author's response:

See comment above. Here, we propose to take out the assumptions made on “medium-scaled teeth” which represent an intermediate size, more difficult to define.

3) Changes in the text:

~~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.~~

Page 11, line 20

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1) Referee Comment:

It is already written in the figure caption

2) Author's response:

Accepted.

3) Changes in the text:

~~All data given in this Figure are available in the Supplement.~~

Page 12, line 17

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1) Referee Comment:

Not necessary since you already cite Kriwet 2000 above

2) Author's response:

Accepted.

3) Changes in the text:

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).

Page 12, line 20

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1) Referee Comment:

Most of the d18Op values....

Not all of them exceeding the tolerance limit for modern fishes of 38-40C as you even show in Fig. 4

2) Author's response:

You are right. Considering the excursions into lower salinity that we propose, all intermediates between the highest isotopic composition reflecting "normal marine" conditions and the lowest one representing a lower salinity are expectable.

3) Changes in the text:

Rewriting the sentence:

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

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

Page 18, line 4

---

1) Referee Comment:
Purbeck

2) Author’s response:
Accepted.

3) Changes in the text:
~~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 Rees, J.: Selachian faunas from the earliest Cretaceous **P**urbeck groups of Dorset, Southern England, Spec. Pap. Palaeontol., 68, 107–19, 2002.

Page 19, figure 1

1) Referee Comment:
- According to Ziegler 1990, during the Kimmeridgian, the Massif Central wasnt formed, but this land mass would be the Amorican Massif? Is this correct or already outdated?

Ziegler, P. A. (1990): Geological Atlas of Western and Central Europe. Shell International Petroleum Maatschappij, The Hague: 239 p.
- How could the paleoaltitude of Porrentry at about ~30°N when in the small map is far above 45°N?

2) Author’s response:
About the Central Massif, see answer to the comment on Page 4, line 16.
The small square on the upper left represents a present geographical map, with the shaded area indicating the sample sites of other studies. This is not a paleogeographical map. As such, the latitudes on this part of the picture are also present latitudes. The large picture represents the paleogeographical setting.
We agree this can be misunderstood and changed the legend to make it clearer:

3) Changes in the text:
~~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.~~

Figure 1. Paleogeographical map of the study site and surroundings (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.
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**.

Page 20, figure 2

1) Referee Comment:

- The orbital cycles are not mentioned or discussed in the text. Thus, this part of the figure iseems to be unnecessary.
- Is there a reference for the used ammonite biozone availabe?

2) Author's response:

- The orbital cycles highlight the transgression of the Upper Kimmeridgian. The transgression is mentionned in the abstract in the 2nd point of the Concluding remarks. We added the reference to the figure at that point.
- Reference for the ammonite zone added in the figure (Comment et al. 2011)

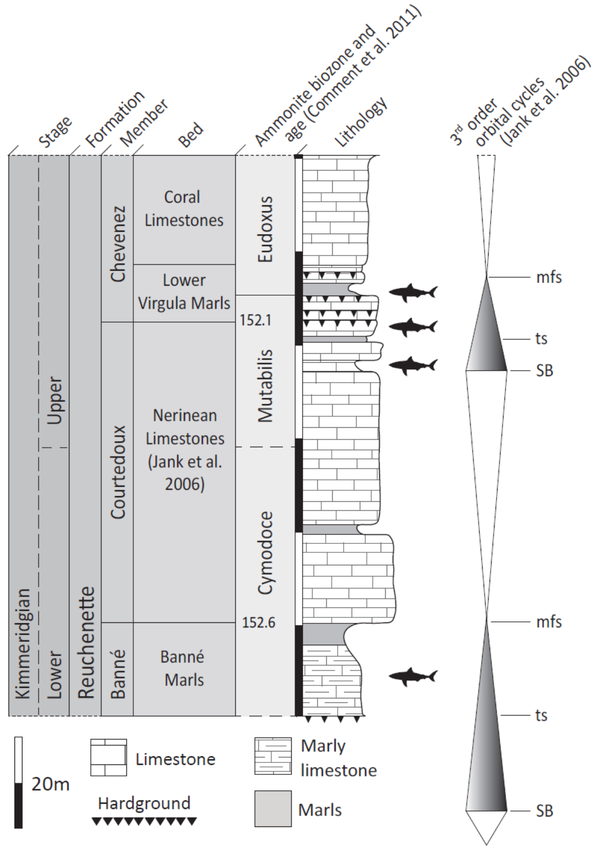
3) Changes in the text:

On Page 13, lines 1-4:

~~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.~~

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.

Figure change :



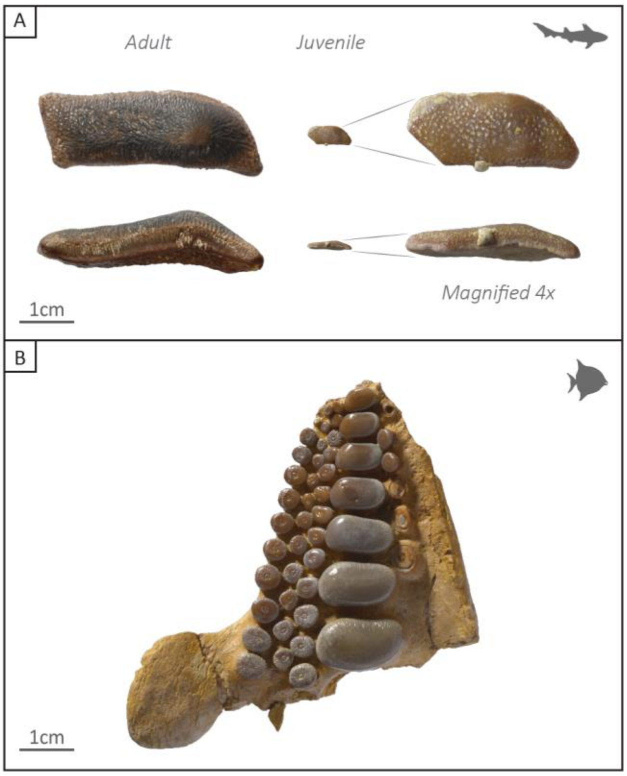
Page 21, figure 3

1) Referee Comment:
... of Porrentury

2) Author's response:
Accepted.

3) Changes in the text:
~~Figure 3. Fossil material from the study site.~~
Figure 3. Fossil material from the study site **of Porrentruy.**

Figure change :



Page 22, figure 4

1) Referee Comment:

- The offset is based on what exactly? it appears arbitrary.
- Realistic based on what? Who decides whats realistic values? References or data? So, the offset appears to be arbitrarily

2) Author's response:

- This figure is a graphic representation of the Eq. 1. You are right, the offset is arbitrary, since no attempt is made of defining the water temperature. That's what we meant with "Arrows show **effect** of varying $\delta^{18}O_w$". The water temperature resulting from Eq. 1 is only used to guide the interpretation, in our case to highlight the fact that the lowest *Asteracanthus* data points require lower delta18Ow, because of the very high water temperatures they otherwise indicate. If we consider that *Asteracanthus* migrates from marine to less marine waters, all the intermediate are expected.
- We meant "realistic" referring to the maximum temperatures obtained for *Asteracanthus* if you keep the data points at the classical seawater value of -1 per mil. We discuss this point in the paragraph starting on line 5, page 9. Such high water

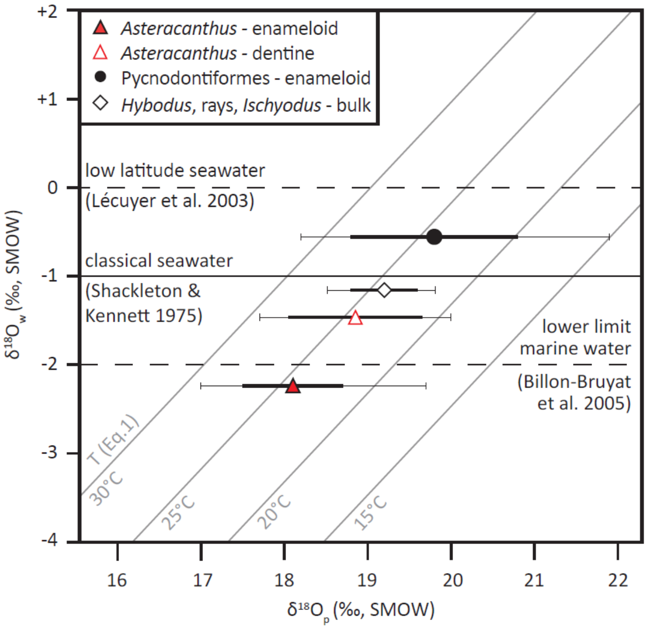
temperatures would require a higher $\delta^{18}O_w$ (because of higher evaporation rates) that would in turn rise even more the water temperature.
We agree the legend needs to be reformulated.

3) Changes in the text:

~~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* enameloid 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 supplementary material.

Figure change :



Answer to comment bgd-12-C6417-2015 by referee Romain Amiot

The authors thank the referee Romain Amiot for his comments. Since no point-by-point comment was provided, we present the comments of the referee in blue and our response in black.

"One major point, however, needs to be properly discussed before this manuscript could be recommended for publication in BGD: the assessment of original isotopic preservation. This is really the key parameter that may allow to confidently interpret anomalous values in terms of original ecologies or environment, and should constitute a first paragraph in the discussion. In particular, comparison between enamel and dentin should be more discussed and maybe presented in a graph, and comparison between expected ecologies of each fish groups with measured values may hint to preservation or not of primary isotope compositions."

We hope that the details added following the revision of Fischer provide enough precision. See response to comment on Page 8, lines 21-25.

"It would be also more convenient for the reader if, in the data table, enamel and dentin samples of the same individuals are grouped."

We agree and changed the table.

"The second point that intrigues me is the value range for pycnodontiformes, somewhat larger than that of *Asteracanthus* samples. If we consider that *Asteracanthus* migrated to brackish or freshwater environments, it would explain indeed the low values in some samples as well as the large range in δ18Op values. Then what is the meaning of such a large range in Pycnodontiformes? Could it be related to peculiar ecologies? Could it be related to more fluctuating climatic or environmental conditions during the deposition of the considered sedimentary layer?"

About the lowest value of Pycnodontiformes, we wrote in section 5.1 "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)." As visible in the Figure 5, the value range for Pycnodontiformes is broad in deposits from both, the Lower and Upper Kimmeridgian, and in the different stratigraphic intervals (see details in table 1), which could point to salinity fluctuations and a tolerance to those for this taxa. In general, Pycnodontiformes values indicate a higher salinity than *Asteracanthus* values. Since we wrote in 5.2. that "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.", semiconfined lagoon could also have created pools of higher salinity when subjected to evaporation in the dry season. There, some Pycnodontiformes could have recorded a higher isotopic composition. For the highest values that point out a relatively low water temperature, a deeper, colder environment (*i.e.* away from the platform) can be considered. In the manuscript, we already mentioned the possibility of the presence of salinity fluctuation in the study area. We propose to enhance this part.

Changes in the text:
Section 5.1.
When used in the eq. (1), the Pycnodontiformes $\delta^{18}O_p$ values result in a mean temperature range that is consistent considering the paleogeographical settings of the study site (23.9±4.4 °C, n=13). **Still, the value range 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 bad 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 characterised 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. The highest values are 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.

Section 5.2.
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.**

Figure 4. – caption
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 the 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 δ^{18}O$_w$ values or water temperatures is made here.

"Related to this point, Figure 4 shows that Pycnodontiformes of Porrentruy and Solothurn are not synchronous with *Asteracanthus* values of the same locality. Values should be put on the same level or it must be notified in the caption that for an easier reading, values have been slightly shifted."

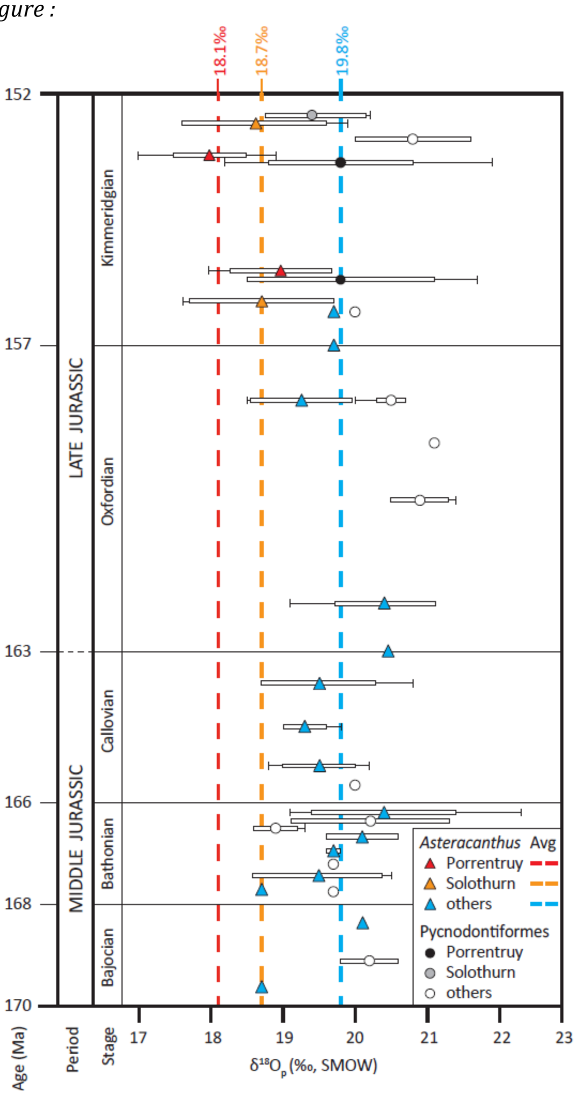
Author's response:

When the referee writes about Figure 4, we assume that he wanted to say Figure 5. In that figure, we shifted a bit the values that would otherwise superpose and make the graph unreadable. We agree that we can group better the data points of each study site. For more precision about the Porrentruy and Solothurn samples relative positions, please refer to the ammonite zones in the supplementary material. As for the stratigraphical position of the data points from other studies, the precision is sometimes limited ("Early-Middle Bathonian" for example).

Changes in the text:

Figure 5. Comparison of δ^{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 position**s** of previously studied localities (Dromart et al., 2003, Lécuyer et al., 2003, Billon-Bruyat et al., 2005) is shown in Fig. 1. Detailed localities **and stratigraphic positions** are available in the supplementary material.

Changes in the figure :



List of all relevant changes

- Affiliation n° 3 in the authors list changed following a restructuration of the institute.
- Material and Methods : list of the material with more detail on the taxa present. Precision on analytical methods.
- Discussion (5.1.) : more detailed argumentation on the good preservation of enameloid samples, more detail on the ecology
- Discussion (5.2.) : argumentation on the juvenile character of *Asteracanthus* smallest teeth
- Figure 2 (stratigraphic profile) changed according to an *in prep* revision study of the local stratigraphy. New stratigraphic units were recently published in a figure of Püntener et al. 2015 (reference added).
- Figure 3 : addition of a juvenile *Asteracanthus* tooth. Change of the adult material for another tooth better comparable with the juvenile specimen.
- Figure 4 changed to make it more readable
- Figure 5 changed to make it more readable
- Supplementary material : stratigraphic units changed in respect with the changes of Figure 2. Reorganisation of dentine/enameloid samples.

Marked, compared manuscript

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 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 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~~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 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 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 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~~hybodont sharks~~” or hybodonts~~ – the extinct sister group of modern sharks (Maisey et al., 2004) (order Hybodontiformes~~), modern sharks (superorder Selachimorpha~~: "*Hybodus*", *Planohybodus*, *Asteracanthus*) –, the modern sharks (subcohort Neoselachii, order Carcharhiniformes: *Palaeoscyllium*, *Corysodon*; order Heterodontiformes: *Heterodontus*, *Paracestracion*; order Protospinaciformes: *Protospinax*; order Squatiniformes: *Pseudorhina*) and rays (~~suborder Rhinobatoidei).~~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 mineralised part ~~(enamel *s.l.*, *i.e.* enamel and~~of the teeth, the enameloid~~)~~, was isolated ~~from~~in Pycnodontiformes and *Asteracanthus* ~~teeth~~ (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.

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For the very small material (1-5 mm) – as in rays and *Hybodus* – several isolated teeth were analysed together as bulk samples of ~~enamel~~enameloid and dentine. ~~The~~Due to the small size, only the outer aspect of this material was sampled as it was visibly the best preserved, *i.e.* not 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 ~~unaltered and~~ dentine-free teeth were ~~selected.~~ used for analysis.

From the Porrentruy material, 38 samples of *Asteracanthus* teeth (27 ~~enamel~~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, ~~enamel~~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 2mg per sample) 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 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 ~~isotopic~~isotope composition of unaltered fish teeth ($\delta^{18}O_p$) is 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 equation of Lécuyer et al. (2013) used for calculating the temperature of sea water:

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$$T\,(^\circ C) = 117.4\,(\pm 9.5) - 4.50\,(\pm 0.43) * (\cancel{\delta^{18}O_{PO4} - \delta^{18}O_{H2O}}\,\delta^{18}O_{p} - \delta^{18}O_{w}). \tag{1}$$

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 ~~Kennet~~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) ~~enamel~~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). ~~Dentine values of *Asteracanthus*~~The average value of 18.9 ±0.8 ‰ (17.7–20.0 ‰, n=11~~), indicating a statistically significant difference to~~) in the *Asteracanthus*' dentine is significantly different from the equivalent ~~enamel samples collected on~~enameloid sampled from the same teeth ~~(student~~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 the data are available and detailed in the supplementary material.

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; Püntener et al., 2015) and crocodilians (Thalattosuchia) ~~are common~~ (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,

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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 scarce or absent. ~~However, our~~Our chondrichthyan assemblage (see section 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~~ and~~. There, the fauna is 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, most of the few modern sharks (Neoselachii) of our assemblage (~~Heterodontiformes, Squatiniformes and Scyliorhinidae~~*i.e. Heterodontus, Palaeoscyllium, Protospinax, Pseudorhina*) are ~~all~~ 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.

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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~~enameloid – and ~~regarding~~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.

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

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Water temperatures calculated with eq. (1) from ~~enamel~~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 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).~~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 the eq. (1), the Pycnodontiformes $\delta^{18}O_p$ values give a mean temperature range that is also consistent with the paleogeographical 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 characterised 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. ~~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).~~

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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)~~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* ~~enamel~~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, ~~such a change towards~~ higher $\delta^{18}O$ values of water would also ~~raise the temperature~~result in higher temperatures calculated ~~to~~with an ~~unrealistic~~ average of 35.8 °C~~, with~~ and a maximum reaching 41.0~~°C~~ °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).

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

Assessing the tooth replacement rate of an extinct shark is ~~impossible.~~difficult, and studies of such rates are scarce (*e.g.* Botella et al., 2009). However, *Asteracanthus* possesses a crushing

Mis en forme : Ne pas ajuster l'espace entre le texte latin et asiatique, Ne pas ajuster l'espace entre le texte et les nombres asiatiques, Taquets de tabulation : Pas à 0,99 cm + 1,75 cm + 3,5 cm + 16 cm dentition composed of a rather small amount of large teeth (see figure in Rees and Underwood, 2008, p.136) organised 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 ~~isotopically~~ lower ~~signature~~$\delta^{18}O_p$ values of *Asteracanthus*, compared to ~~a classical~~typical Late Jurassic marine ~~signal,~~compositions (see data from marine vertebrates of other studies in section 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/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 distinct environment during the first ontogenetic stages (White and Sommerville, 2010).

~~While more~~More than 130 ~~middle-sized to large~~ *Asteracanthus*, teeth were found in the Porrentruy excavation sites~~, only 4 very small-sealed (< 1cm)~~. Only 4 of them appeared to be clearly undersized (< 1 cm) (Figure 3). As illustrated in Rees & Underwood (2008, p.136), the size difference between lingual-most and ~~badly preserved~~labial-most teeth ~~were discovered among hundreds of kilograms of sediment sieved and picked, which suggests a different living environment during the~~ 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 ~~stage, and excursions of adult~~ individuals~~ for reproduction purposes.~~. 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*

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

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~~Most of the $\delta^{18}O_p$ values of ~~enamel~~enameloid 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) (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/brackish environments, possibly for reproduction purposes~~, and a brackish to freshwater habitat during early ontogenetic life stages~~ considering the rarity of juvenile material in the marine, depositional environment.

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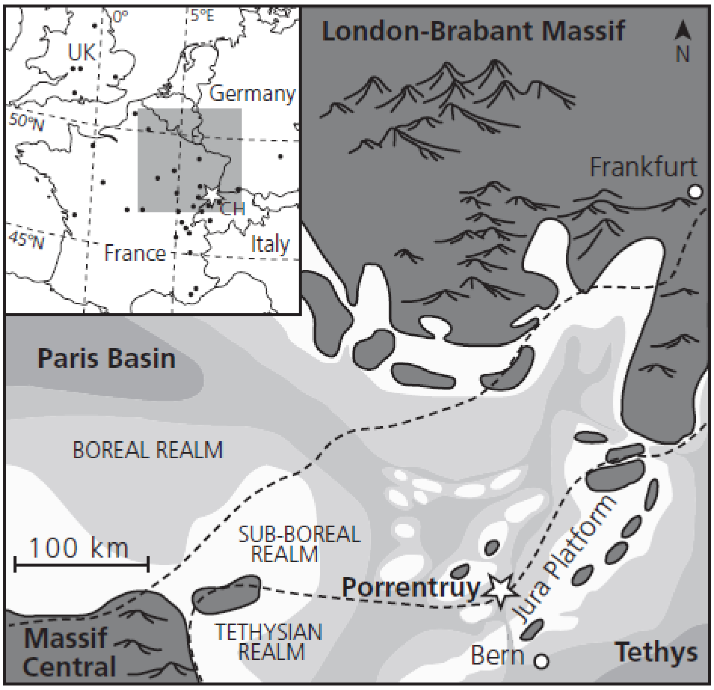
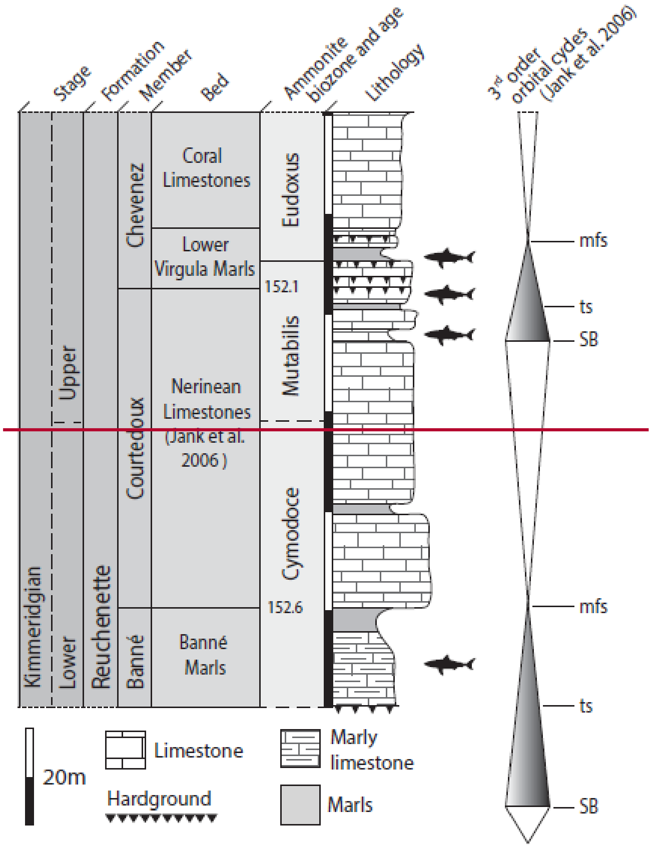


Figure 1. ~~Geographical position of Porrentruy (☆) and other European sites (•) of previously published studies and providing geochemical data compared in Fig. 5.~~ Paleogeographical map of the ~~shaded square area~~study site and surroundings (Late Kimmeridgian, modified from Comment et al~~.~~., 2011).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


Stage
Formation
Member
Bed
Ammonite biozone and age
Lithology
3rd order orbital cycles (Jank et al. 2006)
Kimmeridgian
Upper
Lower
Reuchenette
Chevenez
Courtedoux
Banné
Coral Limestones
Lower Virgula Marls
Nerinean Limestones (Jank et al. 2006)
Banné Marls
Eudoxus
Mutabilis
Cymodoce
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152.6
mfs
ts
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mfs
ts
SB
20m
Limestone
Hardground
Marly limestone
Marls

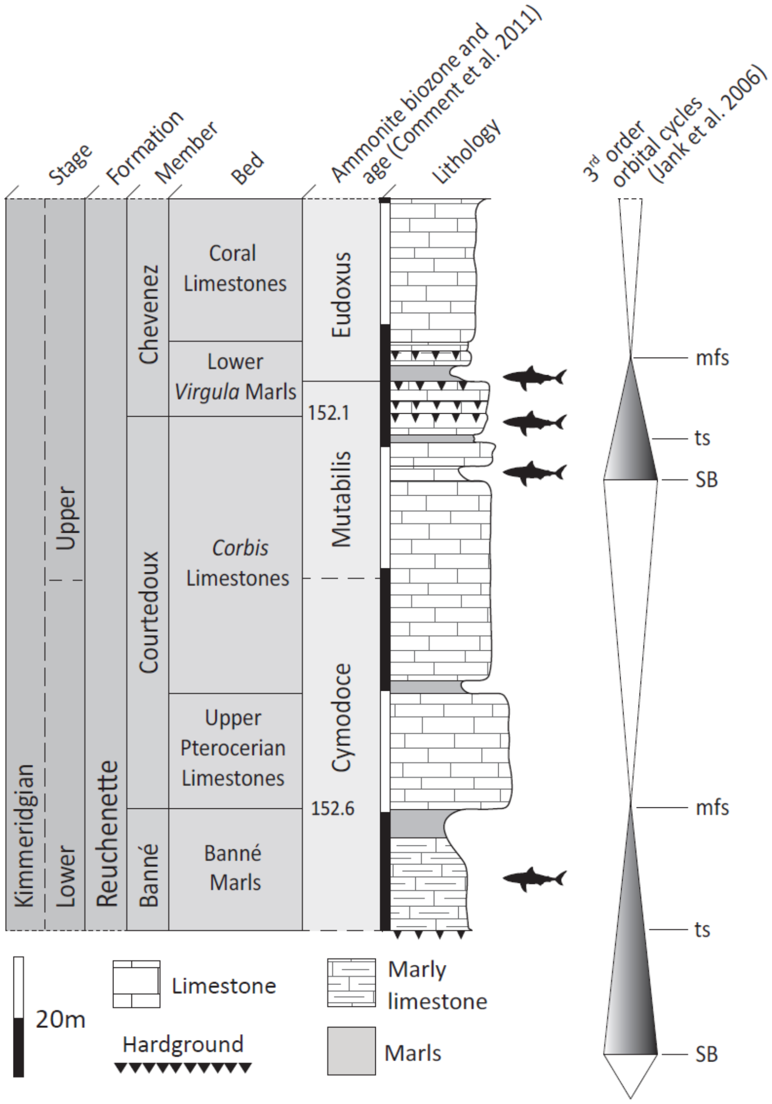
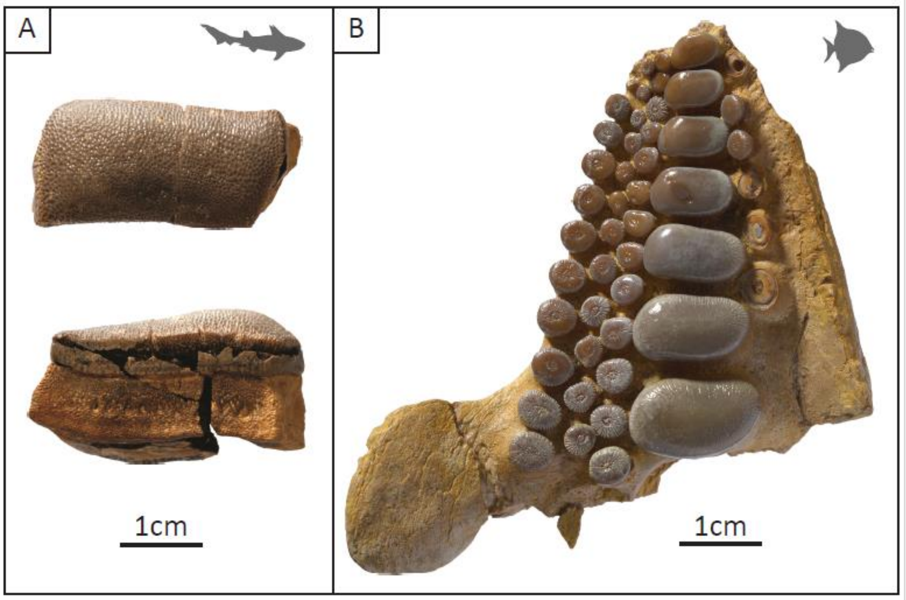


Figure 2. Simplified stratigraphic profile of the Porrentruy area with third order orbital cycle and section yielding the studied chondrichthyan material. Numbers indicate geological age in millions of years. SB = sequence boundary, ts = transgressive surface, mfs = maximum flooding surface.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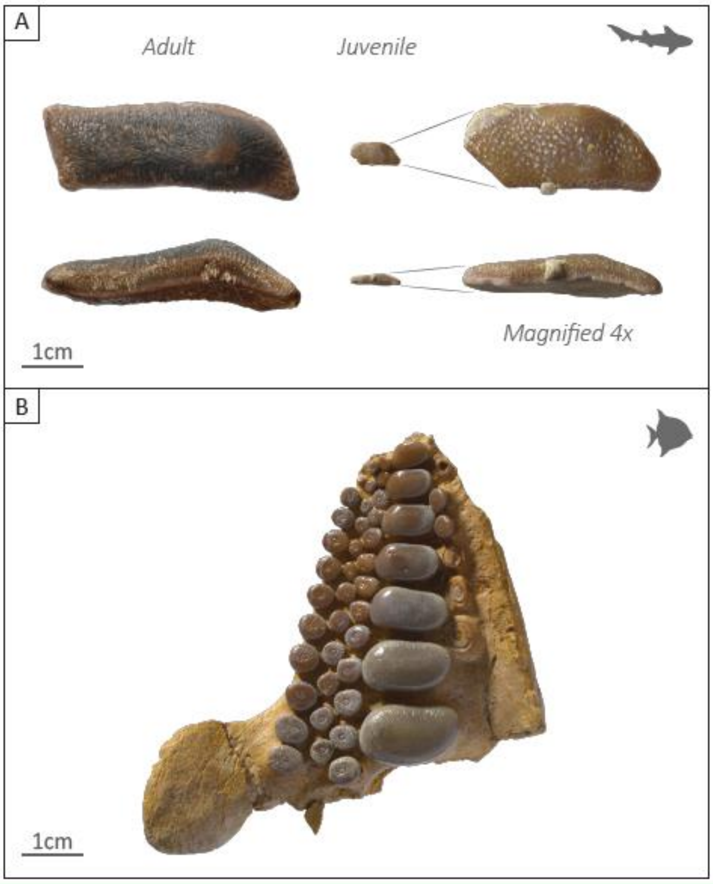
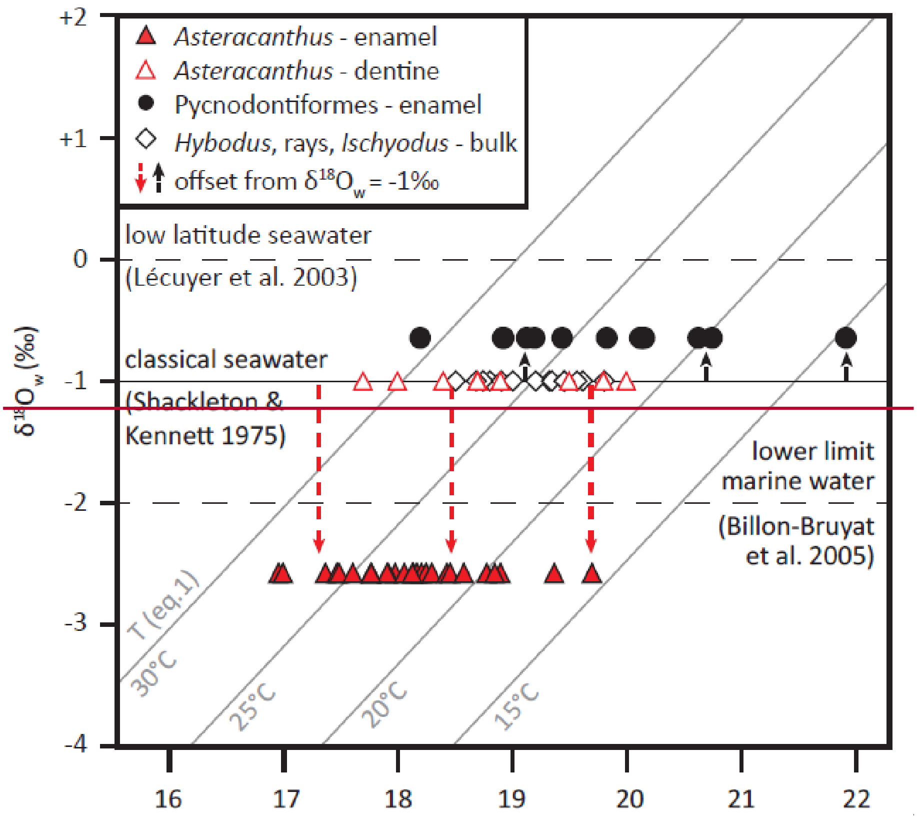
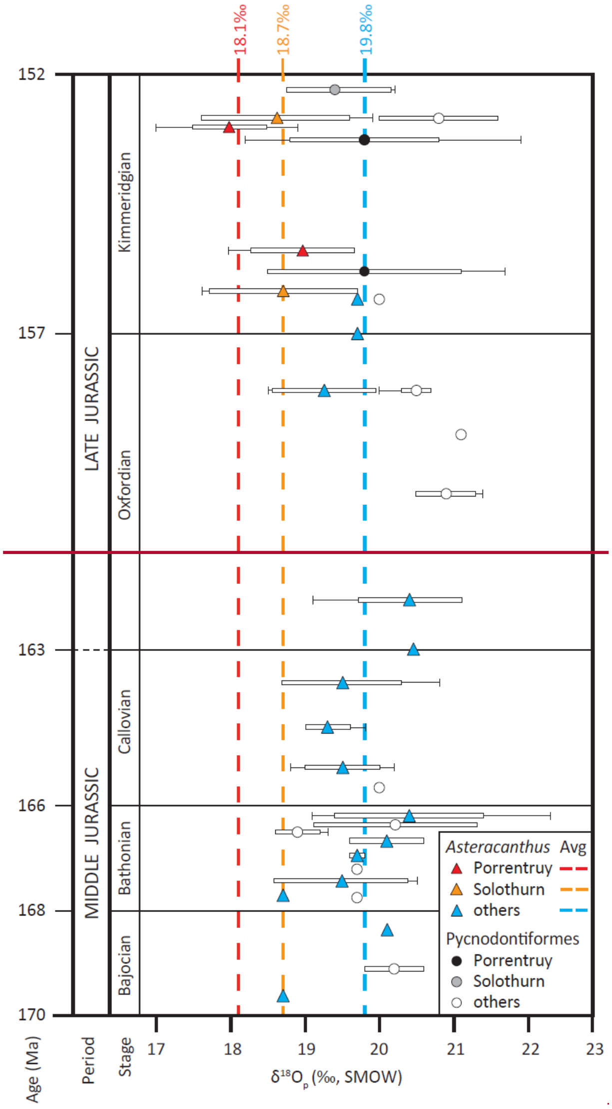


Figure 3. Fossil material from the study site~~.~~ of Porrentruy. A: ~~Tooth~~ Teeth of *Asteracanthus* ~~in occlusal.~~. *Left*: adult specimen (SCR010-1125). *Right*: juvenile specimen (SCR004-221) to scale and magnified. Occlusal (top) and lateral ~~view, with root preserved (specimen SCR010-303).~~(bottom) views. 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.~~

1


18.1‰
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152
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163
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168
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LATE JURASSIC
MIDDLE JURASSIC
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Age (Ma)
Period
Stage
17
18
19
20
21
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Pycnodontiformes
Porrentruy
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others

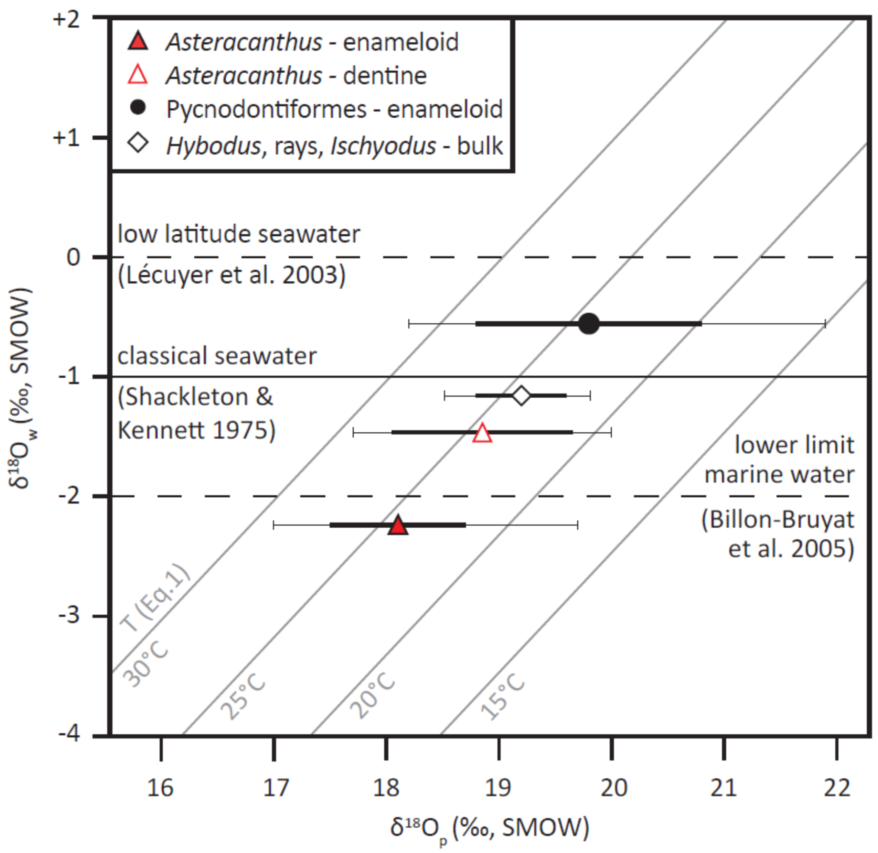

Figure 4. Graphic representation of the $\delta^{18}O_p$ values (average, standard deviation, end members) measured for Porrentruy in this study and their corresponding water temperature using the eq. (1). Comparable water temperatures for all taxa require different $\delta^{18}O_w$ values, which relate 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.

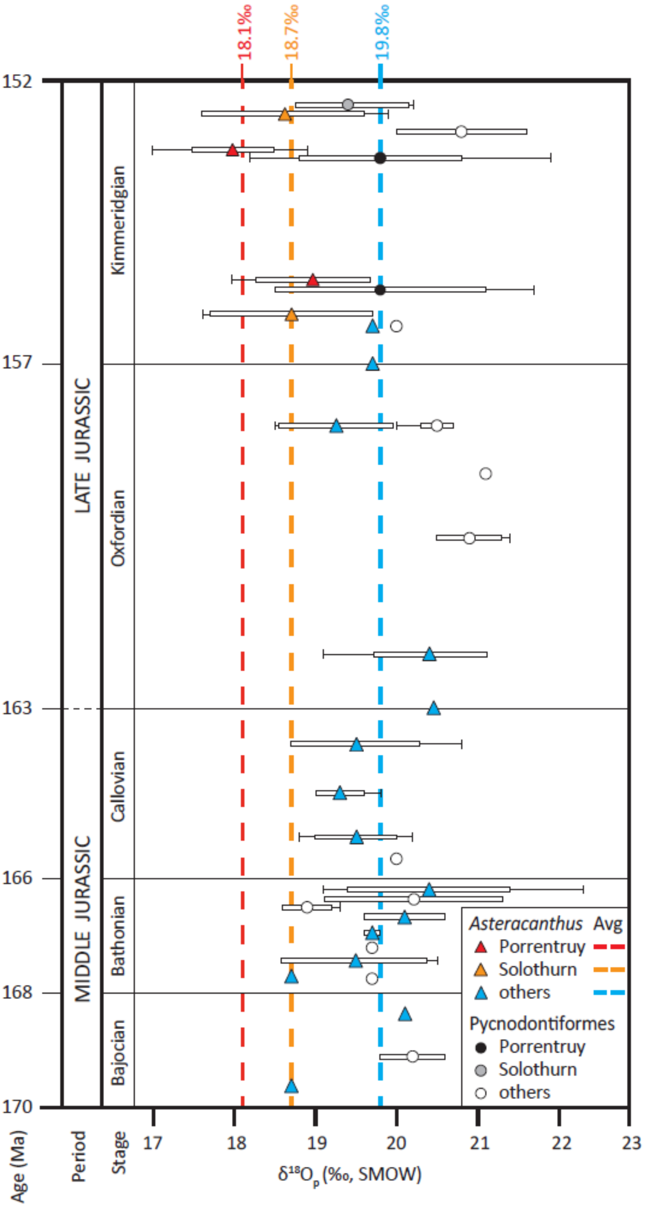

Figure 5. Comparison of $\delta^{18}O_p$ values (average, standard deviation, end members) of Pycnodontiformes and *Asteracanthus* ~~enamel~~enameloid samples from Porrentruy, Solothurn and other European localities through time. The stratigraphical position is approximate and corresponds to Early, Middle, Late divisions of each stage. The approximate geographical

~~position~~positions of previously studied localities (Dromart et al~~.~~., 2003~~,~~; Lécuyer et al~~.~~., 2003~~,~~; Billon-Bruyat et al~~.~~., 2005) ~~is~~are shown in Fig. 1. Detailed localities and stratigraphic positions are available in the supplementary material.