

Paleoclimate and ecology of Cretaceous continental ecosystems of Japan inferred from the stable oxygen and carbon isotope compositions of vertebrate bioapatite

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- Paleoclimate and ecology of Cretaceous continental ecosystems of Japan inferred from the
- 2 stable oxygen and carbon isotope compositions of vertebrate bioapatite

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Abstract

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We investigated the environmental conditions that prevailed in continental ecosystems recorded in sedimentary deposits of Japan during the Cretaceous through the analysis of oxygen and carbon isotope compositions of phosphate ($\delta^{18}O_p$) and apatite-bound carbonate ($\delta^{18}O_c$ and $\delta^{13}C_c$) of vertebrate teeth and bones. Local surface water $\delta^{18}O_w$ values were calculated using known phosphate-water isotope fractionation equations. Anomalously low $\delta^{18}O_w$ values of local waters strongly suggest a significant contribution of high-altitude precipitation from nearby mountains to local surface waters. Mean air temperatures were estimated using a global meteoric water $\delta^{18}O_{mw}$ value – Mean Annual Air Temperature relationship, and compared to surface water temperatures estimated from fish apatite $\delta^{18}O_p$ values. Local mean annual precipitations (MAP) were estimated using the known relationship existing between MAP and C_3 plant $\delta^{13}C_p$ value, the latter being calculated using apatite-diet ¹³C-enrichment applied to plant-eating sauropod and ornithopod dinosaur δ¹³C_c values. Reconstructed environmental conditions suggest that climate changed from cool temperate to warm temperate, being relatively cold and dry during the Late Hauterivian and Barremian to warmer and seasonally more humid during the Aptian and Albian, and even warmer during the Cenomanian-Coniacian. Proposed thermal evolution during the Early Cretaceous is compatible with the absence of thermophilic taxa such as crocodylomorphs before the Aptian in the fossil record of Japan.

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Keywords: Vertebrates; Cretaceous; Japan; stable isotopes; paleoenvironment, paleoecology

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1 Introduction

During the Cretaceous, Southwest Japan was located at mid latitude in the eastern margin of the Asian continent (Hisada et al., 2008; Lee, 2008; Maruyama et al., 1997; Nakama et al., 2010). Cretaceous continental deposits of Japan have yielded rich vertebrate assemblages, the most documented one being the Tetori Biota that flourished during the Early Cretaceous (see Sano and

Yabe (2017) for a review). Some faunal assemblages of the Tetori Biota have attracted much attention as they were almost coeval with the Jehol Biota of Northeastern China that yielded numerous feathered dinosaurs (Zhou et al., 2003; Zhou and Wang, 2017). Despite being located within the same latitudinal belt and distant of about a thousand kilometers during the Cretaceous, these two biotas shared only very few faunal and floral elements with each other, as well as with other contemporaneous faunas of East Asia (Fernandez et al., 2009; Sano and Yabe, 2017). Differences in paleoclimatic and paleogeographic conditions have been proposed to explain the strong provincialism that characterizes East Asian faunas during the Early Cretaceous, such as a strong latitudinal thermal gradient (Amiot et al., 2011) or differences in humidity and amount of precipitations (Amiot et al., 2015) linked to regional paleotopography (Liu et al., 2015) and marine influence (Matsukawa et al., 1993). The associated phytocenoses suggest that the biogeographical partitioning was induced by a longitudinal gradient of continentality (Oh et al., 2011). Another peculiar aspect of the temporal evolution of the Tetori Biota is the change from choristoderan occurrences without crocodilyforms in the Okurodani and Kuwajima formations to crocodilyform occurrence without choristoderes in the Kitadani Formation, suggesting climatic change from cool to hot (Matsumoto et al., 2015). This change is also documented by the vegetation that changed from the Oguchi Flora flourishing in temperate and moderate humid conditions (Yabe et al., 2003) to the Kitadani Flora containing elements reflecting warmer and possibly drier climatic conditions (Yabe and Shibata, 2011). Interestingly, these climatic changes inferred from both vertebrate and flora compositions have not been recognized in the Jehol Biota that remained somewhat stable up to the deposition of the Aptian-Albian Fuxin and Shahai formations (Amiot et al., 2011, 2010; Sano and Yabe, 2017). Stable oxygen and carbon isotope compositions of apatite vertebrate constitute valuable proxies to explore the differences in environmental conditions between The Jehol and Tetori biotas. Indeed, the oxygen isotope compositions of apatite phosphate ($\delta^{18}O_p$) and carbonate ($\delta^{18}O_c$)

from vertebrate bones, teeth and fish scales depend on the $\delta^{18}O_{bw}$ value of the animal body water as

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well as on its body temperature (Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984). The $\delta^{18}O_{bw}$ value is linked to the $\delta^{18}O_{w}$ value of ingested water and to the animal ecology and physiology. For most continental vertebrates, the main source of ingested water is drinking surface waters or plant water, the ultimate source of which is meteoric water (D'Angela and Longinelli, 1990; Kohn, 1996; Langlois et al., 2003; Luz et al., 1984). By using phosphate-water isotope fractionation equations established for extant species, it is possible to estimate the $\delta^{18}O_w$ values of ingested water by a vertebrate from its apatite phosphate $\delta^{18}O_p$ value (Amiot et al., 2017, 2007; Barrick et al., 1999; Lécuyer et al., 2013). These equations have been successfully applied to Mesozoic faunas that include dinosaurs, crocodilians, turtles and freshwater fishes (Amiot et al., 2011, 2009, 2004; Barrick et al., 1999; Domingo et al., 2015; Suarez et al., 2012). In turn, the $\delta^{18}O_{mw}$ value of meteoric waters depends on climate parameters such as air temperature, humidity and amount of precipitation (Dansgaard, 1964; Fricke and O'Neil, 1999; Gat, 1996; Grafenstein et al., 1996). Vertebrates thus record in their phosphatic tissues the climatic conditions of their living environment. However, the $\delta^{18}O_w$ value of surface waters can significantly differ from that of precipitations due to local processes such as evaporation, mixing with ground waters or with river drainage catchments having different water oxygen isotope compositions. Such processes complicate the interpretations in terms of climatic reconstructions. It is also worth noting that ecological specificities such as plant-water use among herbivorous communities also affect the $\delta^{18}O_{\text{\tiny p}}$ value of vertebrates. Indeed, large differences in $\delta^{18}O_{\text{\tiny p}}$ values have been observed between coexisting herbivorous mammals that drink surface waters and those that only rely on water in plants, usually enriched in ¹⁸O by several per mil relative to surface waters (Kohn et al., 1996). Carbon isotope compositions of apatite ($\delta^{13}C_c$) from air-breathing vertebrates primarily reflect animal diets, with a ¹³C-enrichment relative to ¹²C that varies depending on the animal digestive physiology (Passey et al., 2005). The δ^{13} C_c value of plant-eating vertebrates thus records the δ^{13} C value of the plant tissues they have ingested, mainly leaves. In turn, plants have carbon isotope compositions mainly controlled by their photosynthetic pathway (see Ehleringer and

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Monson (1993) for a review). The C₃ pathway is the most common one, occurring in all trees, most shrubs and herbs, and grasses in regions with a cool growing season. Today, C₃ plants have a mean δ^{13} C value of -27% (range from -35% to -22%), reflecting both the δ^{13} C value of atmospheric carbon dioxide and local environmental conditions. C₄ photosynthesis operates in grasses from regions with a warm growing season, and in some sedges and dicots. Finally, crassulacean acid metabolism (CAM) occurs in succulent plants. Because C₄ and CAM plants were most likely absent in Early Cretaceous ecosystems as they only appeared in abundance during the Cenozoic, they will not be discussed any further. Abiotic factors such as variations in light intensity, water and osmotic stress, local temperature and pCO₂, influence the carbon isotopic compositions of C₃ plants by affecting leaf stomatal conductance, which in turn constrains the magnitude of CO₂ diffusion through plant epidermis. All these parameters results in variations in the δ^{13} C values of C₃ plants (Ehleringer and Monson, 1993). A significant relationship has been established between the δ^{13} C values of modern terrestrial C₃ plants and the mean annual precipitations (MAP; (Diefendorf et al., 2010; Kohn, 2010). The carbon isotope compositions of local plants ingested by the herbivorous vertebrates can be retrieved from the δ¹³C_c value of their apatite carbonate. Consequently, the combined use of the apatite-diet carbon heavy isotope enrichment ($\Delta^{13}C_{ap-diet}$) of those plant-eating vertebrates and the MAP- δ^{13} C_{C3 plant} relationship allow the amount of precipitation to be estimated if the Δ^{13} C_{ap-diet} can be determined with a satisfactory level of confidence. Tejada-Lara et al. (2018) have shown that the Δ^{13} C_{ap-diet} is mainly controlled by the body mass of the animal and its digestive system. At the first-order, $\Delta^{13}C_{ap-diet}$ increases with body mass and the highest documented values for extant mammals reach about 15% (e.g. elephants). In agreement with this relationship, apatite-diet ¹³C-enrichments of about 18‰ have been estimated for two ornithischian dinosaurs, the ceratopsians and hadrosaurs (Fricke et al., 2008; Fricke and Pearson, 2008), and of about 15-16‰ for one saurischian group, the sauropods (Domingo et al., 2015; Tütken, 2011). For example, such relationships have been successfully applied to plant-eating dinosaurs (Amiot et al., 2015).

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In this study, vertebrate apatites recovered from four Early and one early Late Cretaceous localities have been analyzed for their oxygen and carbon isotope compositions of phosphate ($\delta^{18}O_p$) and apatite-bound carbonate ($\delta^{18}O_c$ and $\delta^{13}C_c$). Local climatic conditions were inferred from stable isotopes and discussed in the light of the biogeographical context of East Asian faunas and Floras and their dynamics during the Cretaceous.

2 Material and methods

2.1 Sample identification and origin

Fifty-three samples of tooth and bone from dinosaurs, crocodylomorphs, turtles, tritylodonts and scales from bony fish have been collected from five Early to Late Cretaceous localities in Japan (**Fig. 1, 2**) and analyzed for their oxygen and carbon isotope compositions of apatite phosphate and structural carbonate.

Indeterminate iguanodontid teeth (Hasegawa et al., 1995), turtle shell bone (Evans et al., 1998) and lepisosteid scales come from the Okurodani Formation cropping out at a locality near the village of Shokawa, Gifu Prefecture. It consists of a matrix of dark gray silty-sandstone deposited as part of an extensive floodplain characterized by a network of stagnant pools or "ox-bow" lakes, rich in organic matter and choked with silts (Evans et al., 1998). The depositional age of the Okurodani Formation is still controversial, being either considered as Barremian-Aptian according to tuffaceous mudstone zircons U-Pb age of 117.5±0.7 (2 SE) Ma determined by Kusuhashi et al. (2006), and of 129.2±0.4 (95% CI) Ma (Nagata et al., 2019), or as Late Hauterivian or younger according to Sano and Yabe (2017).

Teeth of an indeterminate styracosternan iguanodontian (Barrett and Ohashi, 2016), teeth of the tritylodont *Montirictus kuwajimaensis* (Matsuoka et al., 2016), shell bones of Trionychoid turtles (Hirayama, 2000) and scales attributed to the freshwater fish genus *Sinamia* (Yabumoto, 2005) have been recovered from the "Kuwajima Kaseki-kabe" site. It constitutes an outcrop of the

Lower Cretaceous Kuwajima Formation of the Tetori Group, in Shiramine District, Hakusan City, Ishikawa Prefecture, central Japan. This outcrop of the uppermost part of the Kuwajima Formation consists of alternating fine- to coarse-grained arkoses, fine-grained sandstones, and mudstones, which are interpreted as channel and interchannel deposits of braided rivers (Isaji et al., 2005). The depositional age of the Kuwajima Formation remains ambiguous, the most recent papers considering it either between the Barremian and Aptian (Matsuoka et al., 2016), or within the Hauterivian – Barremian interval (Barrett and Ohashi, 2016). It must be noted that Matsumoto et al. (2006) and Nagata et al. (2019) reported tuffaceous mudstone zircons U-Pb age of 130.7 \pm 0.8 (2 SE) Ma and of 129.1±1.5 (95% CI) Ma for the base of the Kuwajima Formation, respectively, and Sakai et al. (2019) reported from tuff beds zircons U-Pb age of 121.2±1.1 (95% CI) Ma from the Akaiwa Fm that is thought to conformably overlie the Kuwajima Fm. This would better fit with a Barremian to Aptian age for the Kuwajima Formation. Teeth of indeterminate theropods, titanosauriform sauropods (Azuma and Shibata, 2010), iguanodontians (Kobayashi and Azuma, 2003) and goniopholidid crocodylomorphs (Azuma, 2003), as well as turtle shell bones and ganoid fish scales (Azuma, 2003), come from the Kitadani Formation at Kitadani Dinosaur Quarry on the Sugiyama River in the northern part of the city of Katsuyama, Fukui, Japan. The fossil layers consist of alternating beds of mudstone and mediumgrained sandstone, likely deposited by ancient meandering rivers (Azuma, 2003; Legrand et al., 2013), and this part of the formation is considered as early Aptian in age based on molluscan, ostracod and charophyte biostratigraphy (Cao, 1996; Isaji, 1993; Kozai et al., 2002; Kubota, 2005), as well as on geological correlation with coeval strata (Sano, 2015; Sano and Yabe, 2017). Indeterminate theropod, titanosauriform, iguanodontian and ornithopod teeth have been collected from the Ohyamashimo Formation of Sasayama Group at the locality of Kamitaki near Tamba City, Hyogo (Saegusa et al., 2010; Saegusa and Ikeda, 2014; Saegusa and Tomida, 2011). The Ohyamashimo Formation (Hayashi et al., 2017) is mainly composed of conglomerate, sandstone, and mudstone intercalating several tuff beds, it is considered as early Albian in age based

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on U–Pb dating of tuff beds zircons providing an age of 112.1±0.4 Ma (95% CI) (Kusuhashi et al., 2013).

A neosuchian crocodyliform tooth (Ikegami, 2003) as well as adocid and anosteirin turtle shell bones (Hirayama, 1998) come from the "Upper Formation" of the Mifune Group near Mifune (locality named Kumamoto). The "Upper Formation" is characterised by red mudstone, greyish green sandstone and more than a dozen tuff beds indicating a floodplain deposit that includes calcareous nodules and a palaeosol structure interpreted as reflecting semi-arid subtropical to warm-temperate climatic conditions (Lee et al., 2003). Dating the Mifune Group is still problematic.

Ammonites and bivalves date the "Lower Formation" of the Mifune Group as Cenomanian (Tamura, 1979; Tamura and Matsumura, 1974), and the Mifune Group if covered by the Lower Santonian Gankaizan Formation. Fission-track dating has been tentatively performed on tuff beds zircons from both the "Lower Formation" providing two ages of 93.1±4.4 Ma and 89.8±4.0 Ma and the "Upper Formation" providing two ages of 83.6±3.1Ma and 82.1±11.1 Ma, which would range the Mifune Group between the Turonian and the Campanian (Ikegami et al., 2007). Because of the large uncertainties associated with FT dating and the incongruence of these results with the age of the overlying Gankaizan Formation, an age between the Cenomanian and Coniacian is considered for the "Upper Formation" (Ikegami, 2016).

2.2 Analytical technique

3.2.10xygen isotope analysis of biogenic apatite phosphate samples

Apatite powders have been treated following the wet chemistry protocol described by Crowson et al. (1991) and slightly modified by Lécuyer et al. (1993). This protocol consists in the isolation of phosphate (PO₄³⁻) from apatite as silver phosphate (Ag₃PO₄) crystals using acid dissolution and anion-exchange resin. For each sample, 20-30 mg of enamel powder was dissolved in 2 mL of 2 M HF. The CaF₂ residue was separated by centrifugation and the solution was neutralized by adding 2.2 mL of 2 M KOH. AmberliteTM anion-exchange resin beads were added to

the solution to isolate the PO₄³⁻ ions. After 24 h, the solution was removed, the resin was rinsed and eluted with 6 mL of 0.5 M NH₄NO₃. After 4 h, 0.5 mL of NH₄OH and 15 mL of an ammonia solution of AgNO₃ were added and the solutions were placed in a thermostatic bath at 70 °C for 7 h allowing the precipitation of Ag₃PO₄ crystals. Oxygen isotope compositions of silver phosphate crystals were measured using a high temperature elemental analyzer equipped with "purge and trap" technology interfaced in continuous flow mode to an isotopic ratio mass spectrometer (Fourel et al., 2011) at the Laboratoire de Géologie de Lyon (UMR 5276, Université Claude Bernard Lyon 1). For each sample, 5 aliquots of 300 µg of Ag₃PO₄ were mixed with 300 µg of pure graphite powder loaded in silver foil capsules. Pyrolysis was performed at 1450 °C with a glassy carbon reactor using a varioPYROcubeTM Elemental Analyzer interfaced in Continuous Flow mode with an Isoprime™ Isotopic Ratio Mass Spectrometer. Measurements have been calibrated against silver phosphate precipitated from the NBS120c (natural Miocene phosphorite from Florida), as well as with the NBS127 (Barium sulfate precipitated using seawater from Monterey Bay, California, USA). The value of NBS120c was fixed at 21.7% (V-SMOW; Vienna Standard Mean Ocean Water) accordingly to Lécuyer et al. (1993), and that of NBS127 set at the value of 9.3% V-SMOW (Hut, 1987) for correction of instrumental mass fractionation during CO isotopic analysis. Silver phosphate precipitated from standard NBS120c along with the silver phosphate samples derived from fossil bioapatites was repeatedly analyzed ($\delta^{18}O_p = 21.75 \pm 0.35\%$, n = 13) to ensure that no isotopic fractionation occurred during the wet chemistry. Data are reported as δ^{18} O values vs. V-SMOW (in % δ units; 1% = 1mUr).

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2.2.2 Oxygen and carbon isotope analysis of biogenic apatite carbonate samples

In order to remove potential organic contaminant as well as secondarily precipitated calcite, about 10 mg of apatite powder was pre-treated using the protocol of Koch et al. (1997). Powders were washed with a 2% NaOCl solution to remove organic matter, then rinsed five times with double deionized water and air-dried at 40 °C for 24 hours. 0.1 M acetic acid was then added and

left for 24 hours, after which the powder was again rinsed five times with double deionized water and air-dried at 40 °C for 24 hours. For both treatments, the powder/solution ratio was kept constant at 0.04 g mL⁻¹. Stable isotope ratios were determined using a Gasbench II system connected online in continuous flow mode to a MAT253 isotope ratio mass spectrometer (Thermo Fisher Scientific-Germany) at the Lab for Environmental Isotope Geochemistry of the Institute of Geology and Geophysics (Chinese Academy of Sciences, China). For each sample, two aliquots of 2 mg of pretreated apatite were reacted with 5 drops of supersaturated orthophosphoric acid at 72 °C for one hour under a He atmosphere. The CO_2 produced during the reaction was then transferred to the ConfloIII interface and analyzed by cycles of 10 measurements from each aliquot with the mass spectrometer. The measured oxygen isotopic compositions were normalized relative to the NBS-19 marble calibrated material (Hut, 1987) and have a reproducibility better than $\pm 0.2\%$. Isotopic compositions are quoted in the standard δ notation relative to V-SMOW for oxygen and V-PDB (Vienna Pee Dee Belemnite) for carbon.

3 Results

For the whole vertebrate dataset, oxygen isotope compositions of phosphate range from 9.1% to 14.9% V-SMOW, from 10.9% to 17.5% V-SMOW for apatite-bound carbonates and and carbon isotope compositions range from -12.1% to +2.8% V-PDB for carbon (**Table 1; Fig. 3**).

Local surface waters have been calculated by applying to dinosaur $\delta^{18}O_p$ values the phosphate-water isotope fractionation equation determined for extant birds, their nearest living relatives (Amiot et al., 2017):

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$$\delta^{18}O_w = 1.119 \pm 0.040 \ \delta^{18}O_p - 24.222 \pm 0.644, (\sigma_{est} = 0.45)$$
 (1),

Where σ_{est} corresponds to the mean standard error for the estimated parameter ($\delta^{18}O_w$). The

264 phosphate-water fractionation equation of extant crocodilians has been applied to crocodylomorphs

265 (Amiot et al., 2007):

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$$\delta^{18}O_{w} = 0.823 \pm 0.062 \ \delta^{18}O_{p} - 19.129 \pm 1.076, \ (\sigma_{est} = 1.13)$$
 (2),

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269 to turtles the phosphate-water fractionation equation of their extant living (Barrick et al. (1999),

270 updated in Pouech et al. (2014)):

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$$\delta^{18}O_w = 0.994 \pm 0.046 \ \delta^{18}O_p - 21.197 \pm 0.755, (\sigma_{est} = 0.89)$$
 (3),

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and to tritylodonts the phosphate-water fractionation equation of extant plant-eating mammals

275 considered as their closest living relatives has been used (Amiot et al., 2004):

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$$\delta^{18}O_{\text{w}} = 1.113 \pm 0.003 \ \delta^{18}O_{\text{p}} - 26.441 \pm 0.051, \ (\sigma_{\text{est}} = 0.28)$$
 (4).

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Calculated local water $\delta^{18}O_w$ value and associated uncertainties (2 σ) range from -13.3±1%

280 to -11.1±1.8% V-SMOW for the Shokawa locality, from -12.8±0.6% to -8.2±1.8% for the

281 Kuwajima Kaseki-kabe locality, from -11.3±1.0% to -7.8±2.2% for the Kitadani Dinosaur Quarry,

282 from $-12.3\pm1.0\%$ to $-8.4\pm1.0\%$ for the Kamitaki locality, and from $-7.6\pm1.8\%$ to $-6.4\pm1.8\%$ for the

Early Late Cretaceous locality of Kumamoto (**Table 2, Fig. 4**). Using the global MAT-δ¹⁸O_w

284 relationship proposed by Lécuyer (2014):

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$$\delta^{18}O_{w} = 0.481 \pm 0.02 \text{ T}(^{\circ}C) - 14.254 \pm 0.261$$
 (5),

Mean Air Temperatures (MAT) and associated uncertainties (2 σ) derived from these $\delta^{18}O_w$ values respectively range from 2±2°C to 7±4°C, from 3±2°C to 13±4°C, from 6±2°C to 13±4°C and from 4±2°C to 12±2°C, and from 14±4°C to 16±4°C (**Fig. 5; Table 2**). For the three localities of Shokawa, Kuwajima Kaseki-Kabe and Kitadani Dinosaur Quarry (**Fig. 5; Table 2**), surface water temperatures derived from fish $\delta^{18}O_p$ values have been calculated using local water $\delta^{18}O_w$ values estimated from dinosaurs, crocodylomorphs and turtles $\delta^{18}O_p$ values and the phosphate-water temperature scale established for extant fish (Lécuyer et al., 2013):

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$$T(^{\circ}C) = 117.4 \pm 9.5 - 4.50 \pm 0.43 \ (\delta^{18}O_p - \delta^{18}O_w)$$
 (6).

Calculated water temperatures are globally higher than mean air temperatures, ranging from $17\pm8^{\circ}\text{C}$ to $27\pm8^{\circ}\text{C}$ for the Shokawa locality, from $3\pm5^{\circ}\text{C}$ to $27\pm8^{\circ}\text{C}$ for the Kuwajima Kaseki-Kabe locality, and from $11\pm8^{\circ}\text{C}$ to $36\pm10^{\circ}\text{C}$ for the Kitadani Dinosaur Quarry (**Table 2; Fig. 5**). It must be noted that the large ranges of calculated temperatures using fish $\delta^{18}\text{O}_p$ values do not reflects real temperature variability, as fish $\delta^{18}\text{O}_p$ variability is quite low, but variability in calculated water $\delta^{18}\text{O}_w$ values from other vertebrates.

Carbon isotope compositions of local plants ingested by sauropod and ornithischian dinosaurs has been estimated from their $\delta^{13}C_c$ values and the apatite-diet ^{13}C -enrichment determined by Tütken (2011), Fricke and Pearson (2008) and Fricke et al. (2008). In turn, Mean Annual Precipitation (MAP) has been estimated using the MAP- $\Delta^{13}C_{C3 \text{ plant}}$ relationship established for gymnosperms by Diefendorf et al. (2010), modified in Amiot et al. (2015):

310 Log (MAP) =
$$0.0802\pm0.0102 * \Delta^{13}C_{C3 plant} + 1.3726\pm0.1875$$
 (7),

with MAP in mm, $\Delta^{13}C_{C3 \text{ plant}} = (\delta^{13}C_{atm} - \delta^{13}C_{plant}) / (1 + 10^{-3} * \delta^{13}C_{plant})$ and atmospheric CO₂ $\delta^{13}C_{atm}$ values calculated by Barral et al. (2017) for the studied Cretaceous time periods. Estimated MAPs

and associated uncertainties (2σ) range from 497±17 mm to 560±50mm, from 397±12 mm to 542±40 mm, from 782±35mm to 1162±78 mm and from 717±27 mm to 1235±72 mm for the localities of Shokawa, Kuwajima Kaseki-kabe, Kitadani Dinosaur Quarry, Kamitaki and Kumamoto, respectively (**Table 2; Fig. 5**).

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4 Discussion

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4.1 Primary preservation of the stable carbon and oxygen isotope compositions Biotic and abiotic processes leading to the decomposition, burial and fossilization of living organisms may alter the original isotopic composition of bioapatite through processes of secondary precipitation, ion adsorption or dissolution-recrystallization of bioapatite (Blake et al., 1997; Kolodny et al., 1996; Lécuyer et al., 2003; Trueman et al., 2003; Zazzo et al., 2004b, 2004a). Therefore, pristine preservation of the isotopic records needs to be assessed before discussing the ecological and climatic significance of the oxygen and carbon isotope compositions of fossil vertebrate apatites. Although no method can definitely demonstrate whether the original isotopic compositions have been kept, several ways to assess the preservation state of the isotopic record have been considered (Fricke et al., 1998; Iacumin et al., 1996; Kolodny et al., 1996; Lécuyer et al., 2003; Pucéat et al., 2004; Tütken et al., 2008; Zazzo et al., 2004b). Both phosphate and carbonate in apatite have δ^{18} O values reflecting that of the animal's body water, but with a different mineralwater ¹⁸O enrichment. Consequently, a positive linear correlation between the $\delta^{18}O_p$ and the $\delta^{18}O_c$ values with a slope close to unity has been observed on extant vertebrates (Bryant et al., 1996; Chenery et al., 2012; Iacumin et al., 1996; Lécuyer et al., 2010) and used as a test for primary preservation of fossil vertebrate apatites (Amiot et al., 2015; Tütken et al., 2008; Zazzo et al., 2004b). Due to the limited range of apatite δ^{18} O values within each Japanese locality, no significant correlation between phosphate and carbonate can be observed. However, a comparison of the distribution of $\delta^{18}O_p$ and $\delta^{18}O_c$ pairs with those of other East Asian Early Cretaceous vertebrates

reveals similar isotopic ranges (**Fig. 6**), suggesting at least a partial preservation of the oxygen isotope compositions.

A strong case in favor of the preservation of the isotope compositions is the distribution within each locality of the $\delta^{13}C$ and $\delta^{18}O$ values of co-existing vertebrates showing significant differences between taxa (**Fig. 3**). Such a pattern would be a result of differences in ecology, digestive physiology, water strategies and thermophysiologies between taxa rather than diagenetic processes that would have more randomly distributed the values. However, the narrow range in $\delta^{13}C$ values observed between taxa of the Kamitaki and Shokawa localities may point to some diagenetic alteration of the carbon isotope composition that would reflect the $\delta^{13}C$ value of the diagenetic carbon source. Therefore, $\delta^{13}C$ values from these two localities must be considered with caution. Another clue to primary isotopic preservation is that the carbon isotope compositions of plant diet estimated from plant-eating dinosaurs fall within a range typical of C_3 plants considering the relatively high $\delta^{13}C_{\text{atm}}$ value of atmospheric CO_2 that was, according to Barral et al. (2017), about 3% higher than the present-day value of about -8% (**Table 2**). It is noteworthy that sample SH20 has a $\delta^{13}C_c$ value anomalously high pointing to a possible diagenetic alteration. This value is treated as an outlier and not considered for subsequent interpretations (**Fig. 3**).

Finally, the weight percentage of carbonate in analysed fossil apatites, which ranges from 1% to 7%, lies within the expected biological range of modern vertebrate apatites (Brudevold and Soremark, 1967; Rink and Schwarcz, 1995; Tarnowski et al., 2002; Vennemann et al., 2001).

From all these lines of evidence, we consider that vertebrate apatites have kept most of their original isotopic compositions, allowing them to be interpreted in terms of paleoclimate and paleoecology.

4.2 Environmental conditions recorded in Cretaceous deposits of Southwest Japan and adjacent areas

Fossil plant and vertebrate records within the Tetori Biota hint at a climatic change between the Barremian Kuwajima Formation and the Early Aptian Kitadani Formation. According to differences in floristic composition and physiognomy between the Oguchi flora (found in the Okurodani and Kuwajima formations) and Kitadani flora, a change to warmer and possibly drver climate has been proposed (Yabe et al., 2003). In contrast with its lower part (Okurodani and Kuwajima formations) which only features the boreal fossil wood genus *Xenoxylon*, the upper part of the Tetori group (Kitadani Formation) yielded beside *Xenoxylon* two more genera, *Brachyoxylon* and Podocarpoxylon (Terada and Yabe, 2011; Yamazaki et al., 1990), which thrived under warmer climates (Philippe et al., 2017). A similar switch from *Xenoxylon*-exclusive or dominated fossil wood floras to warmer wood floras with Agathoxylon and Brachyoxylon is also reported in Southern Korea at the Barremian to Aptian transition (Philippe et al., 2011). Warmer conditions have also been suggested from the occurrence of crocodylomorphs in the Kitadani Formation, whereas they were absent from the underlying Kuwajima and Okurodani formations (Amiot et al., 2011; Matsumoto et al., 2015). Amiot et al. (2011) used a generic phosphate-water oxygen isotope relationship (Amiot et al., 2004) to infer average local meteoric water δ^{18} O value from the average δ¹⁸O_p value of continental vertebrates. Cool temperate climatic conditions with MAT of 10±4°C recorded at mid latitudes in East Asia were thus inferred from the oxygen isotope compositions of vertebrates from the Late Barremian Yixian Formation of the Jehol Biota as well as from the Kuwajima Formation. In our study, we have applied available phosphate-water oxygen isotope fractionation equations determined for extant vertebrates (birds, mammals, crocodilians and turtles) to their Cretaceous relatives (dinosaurs, tritylodonts, crocodylomorphs and turtles, Fig. 4) and estimated mean air temperature ranges and surface water temperatures using freshwater fish $\delta^{18}O_p$ values (Table 2, Fig. 6). Air temperature increase is observed from the Hauterivian to the early Late Cretaceous, however, temperature values comprised between 4°C and 13°C for the Aptian Kitadani Formation and Albian Ohyamashimo Formation seem too low to be considered as realistic estimates. Indeed, the occurrence of crocodylomorphs with a minimum mean living temperature

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requirement of 14.2°C (Markwick, 1998) indicates that mean air temperatures are largely underestimated. During the Mesozoic, intense tectonic activity linked to the subduction of the Izanagi plate led terranes constituting Japanese Islands to form a segment of the Mesozoic subduction-related orogen that grew along East Asian margin at least since the Jurassic time (Charvet, 2013; Isozaki et al., 2010). The proximity of these high mountain ranges most probably supplied the river systems with high-altitude waters, which seasonally fed lakes and ponds of the sedimentary basin with low δ^{18} O waters. These waters characterized by elevated temporal variations of δ^{18} O_w values would ultimately be ingested by the vertebrate fauna that would in turn show highly variable δ^{18} O values between and within coexisting taxa (Suarez et al., 2014) as observed in the present dataset (Fig. 4). A study of the lithofacies assemblages of the Sasayama Group also concluded that they were deposited in an inter-montane basin (Hayashi et al., 2017). According to the conglomerate facies analysis of the Sasayama Group, Hayashi et al. interpreted that only the distal part of the alluvial fan was preserved. Such preservation suggests that mountains surrounding the basin were high and distant, and that the basin may have been far larger than the present distribution of the Sasayama Group seems to indicate. Alternatively, mountains may have been low and close to the center of the basin, and the alluvial fan was of small size (Hayashi et al., 2017). It is noteworthy that the first hypothesis better fits with measured oxygen isotope compositions. The regional topography may therefore explain why air temperatures inferred from the $\delta^{18}O_n$ of vertebrates are underestimated because of this isotopic altitude effect. Of peculiar interest is the case of fish that recorded *in situ* temperatures of their aquatic living environment characterized by the same low $\delta^{18}O_{mw}$ of water ingested by terrestrial vertebrates. Using equation (6), fish $\delta^{18}O_p$ values allowed us to calculate surface water temperatures that were much higher than those inferred from the global $\delta^{18}O_{mw}$ – MAT relationship (**Fig. 5**). This result, however, needs to be tempered considering that the optimal growth period of freshwater fish such as lepisosteids occurs during the warm season (Love, 2004). If the climatic regime was characterized by a marked seasonality in air temperatures, such calculated temperatures might not represent MAAT but those of the warm

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season only. Because during the warm season meteoric water $\delta^{18}O_w$ values are higher than during winter, the most accurate water temperatures recorded by the fish $\delta^{18}O_p$ values should be those of the high part of temperature ranges. However, the available dataset does not allow to better constrain calculated water temperatures.

Carbon isotope compositions of local vegetation ingested by plant-eating dinosaurs range from about -21‰ to -26‰ V-PDB. They are comparable to the range of organic matter δ^{13} C values measured from the contemporaneous sediments of the Tateyama section located nearby the localities of Kuwajima Kaseki-Kabe, Kitadani Dinosaur Quarry and Shokawa localities (Hasegawa and Hibino, 2006). Carbon isotope composition of local plants remained constant during the deposition of the Okurodani and Kuwajima formations but shifted by about -3‰ between the Barremian and Early Aptian and remained stable during the deposition of the Kitadani and Ohyamashimo formations (**Table 2**). Applying the MAP- Δ^{13} C_{C3 plant} relationship to these values, reconstructed MAP changed from about 500±100 mm during the deposition of the Okurodani and Kuwajima formations to about 1500±300 mm during the deposition of the Kitadani Formation and the Ohyamashimo Formation (**Fig. 5**).

According to both δ^{18} O and δ^{13} C values of vertebrate apatites, climate became warmer and wetter around the period of the Barremian-Aptian boundary. This result is only partially in agreement with paleobotanical and palynological studies that inferred warmer but also possibly drier conditions during the deposition of the Kitadani Formation (Terada and Yabe, 2011; Yabe and Shibata, 2011). Legrand et al. (2013) proposed an alternative scenario with humid and warm-temperate climatic conditions with locally dry environments. This apparent contradiction is also documented by the co-occurrence of three fossil wood genera within the Kitadani Formation. Whereas *Xenoxylon*, which was a water-demanding tree (Oh et al., 2015; Philippe et al., 2009; Philippe and Thévenard, 1996) is common and exclusive in the underlying Itoshiro subgroup of the Tetori Group, the Kitadani Formation of the Akaiwa subgroup yielded two more wood genera, *Brachyoxylon* and *Podocarpoxylon* (Terada and Yabe, 2011; Yamazaki et al., 1990). The two latter

both suggest a tropophilous climate with a marked dry season and are only rarely associated to Xenoxylon (Oh et al., 2015), possibly only in environments where beside riparian forests existed drier settings. A similar mixture of *Xenoxylon* and more thermophilous element was reported from the coeval Nakdong Formation in South Korea (Jeong et al., 2014). A paleobotanical study of the Sawada Formation of the Sasayama Group documented a flora related to those of the Ryoseki-type usually recorded in the Outer Zone of Japan, with an abundance of xerophytic microphyllous taxa such as Brachyphyllum spp. and Pseudofrenelopsis sp. (Yamada et al., 2018). These floristic components, together with the overall rarity of fern remains, would indicate the prevalence of a seasonaly arid tropophilous climate. The wood genus *Brachyoxylon* was also reported from the Sawada Formation (Terada, 2012), similarly suggesting a subtropical tropophilous climate (Philippe et al., 2017). This interpretation is supported by sedimentary facies observed at the locality of Kamitaki as well as in the Ohyamashimo Formation cropping out at Sasayama city (Hayashi et al., 2017). Mudstone shows features seen in vertisols such as a strong development of slickensides and high smectite content (Saegusa et al., 2010), suggesting that high amount of precipitation occurred during the rainy season, as well as the occurrence of strong shrinkage of clay rich soil indicating a intense dry seasons. The possible intense dry season is also supported by the presence of caliche in other mudstone layers in Kamitaki (Saegusa et al., 2010). Vertebrates from the Ohyamashimo Formation of the Sasayama Group have low apatite carbonate $\delta^{13}C_c$ values that reflect large amounts of annual precipitation compatible with the existence of a "wet and dry" tropophilous climate.

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Compared with the Jehol Biota, estimated MATs from the Kuwajima Fm., Kitadani Fm. and the Ohyamashimo Fm. are similar to those estimated for the Late Barremian Yixian, and the Aptian-Albian Fuxin formations (Amiot et al., 2011). As discussed above, MAT estimated from $\delta^{18}O_p$ values of Cretaceous vertebrates of Japan might be underestimated due to the contribution of high-altitude meteoric waters, whereas in Northeastern China, the persistent absence of crocodylomorphs suggests that low air temperatures still prevailed. Mean Annual Precipitation values estimated from

both Yixian and Kuwajima formations are within a similar range of 500-600 mm, but significant differences in MAP are observed with Aptian-Albian Fuxin Formation being drier (about 500 mm) than the Aptian Kitadani Formation and Albian Sasayama Group (about 1000 mm).

According to a study based on the reconstruction of spatio-temporal changes in the latitudinal distribution of desert deposits and the prevailing surface-wind patterns recorded in the Asian interior, a humid zone should have existed at mid latitudes during the mid-Cretaceous, as documented by the coal-bearing deposits observed in the Gobi basin of Mongolia (Hasegawa et al., 2012). This would be compatible with the amount of precipitations calculated from the Aptian Kitadani and Albian Sasayama vertebrate δ^{13} C values, but not with the drier environments inferred from the Fuxin vertebrates (Amiot et al., 2015). Far-East Asia fossil wood record for the Cretaceous is consistent with the hypothesis that regional paleogeography might explain this peculiar climate pattern (Oh et al., 2011). Indeed, Northeastern China was then bordered on the southeast by the Su-Lu mountain range, locally producing a "rain shadow" that limited air moisture from the Pacific Ocean to enter from the East inlandward. Such topography may have contributed to constitute continental-like climatic conditions with a thermal seasonality enough contrasted to be unsuitable for the presence of crocodylomorphs. Further ecological and environmental studies might elucidate the apparent contradiction between isotopic and paleobotanical data from the Aptian Kitadani and Albian Sasayama fossil assemblages, and help to better understand the mosaic environments that seem to have characterized East Asia during the Cretaceous.

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5 Conclusion

Oxygen and carbon isotope compositions of Early and early-Late Cretaceous continental vertebrate apatites recovered from five Japanese localities have been analysed. Using existing phosphate-water oxygen isotope fractionation equations, the $\delta^{18}O_w$ values of local environmental waters ingested by studied vertebrates were calculated as well as local surface temperatures based on modern MAT- $\delta^{18}O_w$ relationships. Using published apatite-diet ^{13}C -enrichment estimated for

sauropod and ornithopod dinosaurs, the $\delta^{13}C$ values of consumed local plants have been calculated and converted into Mean Annual Precipitation based on the existing MAP- $\delta^{13}C_{C3\,plant}$ relationship. The following results are underlined:

a significant contribution of ¹⁸O-depleted waters from high altitude to local surface waters support the inter-montane origin of some early Cretaceous continental basins in Central Japan.

Regional climate may have changed from cool to warm temperate, being relatively cold and dry during the Late Hauterivian and Barremian to warmer and seasonally more humid during the Aptian and Albian, and even warmer during the Cenomanian-Coniacian.

The peculiar paleogeographic and climatic characteristics of Central Japan during the Cretaceous may at least partly account for the observed faunal and floral differences with the neighboring Cretaceous continental deposits of northeastern China.

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Figure captions 515 Figure 1: Geographic location of the studied localities. 1: Shokawa; 2: Kuwajima Kaseki-Kabe; 3: 516 517 Kitadani Dinosaur Quarry; 4: Kamitaki, Tamba City; 5: Kumamoto. 518 519 Figure 2: Stratigraphy of the 5 Cretaceous units in the Japanese Islands bearing the studied 520 localities sampled for vertebrate remains and their tentative correlation (see text for detail). 521 522 **Figure 3:** Oxygen isotope compositions of vertebrate apatite phosphate ($\delta^{18}O_p$) reported against the 523 carbon isotope compositions of structural carbonate ($\delta^{13}C_c$) for the five studied Cretaceous 524 localities. Numbers in brackets refer to the locality described in Figure 1. Sample SH20 having an anomalously high $\delta^{13}C_c$ value is treated as an outlier and not used for subsequent MAP calculations. 525 526 **Figure 4:** Taxon-averaged drinking water $\delta^{18}O_w$ value and associated standard deviation (horizontal 527 528 bars) estimated for each studied locality. 529 530 Figure 5: Temporal variations of surface temperature and amount of precipitation ranges estimated from vertebrate apatite $\delta^{18}O_p$ and $\delta^{13}C_c$ values. Numbers refer to the localities described in Figure 1. 531 532 Published indicators of qualitative environmental conditions described in the text are figured as 533 symbols. 534 **Figure 6:** Oxygen isotope compositions of carbonate ($\delta^{18}O_c$) of all analyzed vertebrates plotted 535 against their corresponding oxygen isotope compositions of phosphate ($\delta^{18}O_p$), and compared to the 536 published $\delta^{18}O_p$ - $\delta^{18}O_c$ pairs for Early Cretaceous East Asian localities (Amiot et al., 2015). Dashed 537 line with a slope of unity is drawn for reference. 538 539

Table captions

Table 1: Oxygen and carbon isotope compositions of apatite phosphate and carbonate from vertebrates reported along with the weight percent of apatite-bound carbonate, sample number, apatite material, identification, provenance and geological age.

Table 2: Left side: For each locality, surface water $\delta^{18}O$ range estimated from vertebrate $\delta^{18}O_p$ values using phosphate-water isotopic fractionation equations (1 to 4; see text) are reported along with Mean Air Temperature (MAT) range calculated from equation (5), and surface water temperatures calculated using equation (6). Right side: Plant $\delta^{13}C$ range estimated from the $\delta^{13}C_c$ values of plant-eating dinosaurs using their known apatite-diet ^{13}C -enrichment factor, are reported along with the corresponding $\delta^{13}C_{atm}$ value of atmospheric CO_2 from Barral et al. (2017), the plant carbon discrimination (see text) and the calculated Mean Annual Precipitation using equation (7).