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

3

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32 **Abstract**

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

50

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

52

53 **1 Introduction**

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

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

82 Indeed, the oxygen isotope compositions of apatite phosphate ($\delta^{18}\text{O}_p$) and carbonate ($\delta^{18}\text{O}_c$)
83 from vertebrate bones, teeth and fish scales depend on the $\delta^{18}\text{O}_{\text{bw}}$ value of the animal body water as

84 well as on its body temperature (Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984). The
85 $\delta^{18}\text{O}_{\text{bw}}$ value is linked to the $\delta^{18}\text{O}_{\text{w}}$ value of ingested water and to the animal ecology and
86 physiology. For most continental vertebrates, the main source of ingested water is drinking surface
87 waters or plant water, the ultimate source of which is meteoric water (D'Angela and Longinelli,
88 1990; Kohn, 1996; Langlois et al., 2003; Luz et al., 1984). By using phosphate-water isotope
89 fractionation equations established for extant species, it is possible to estimate the $\delta^{18}\text{O}_{\text{w}}$ values of
90 ingested water by a vertebrate from its apatite phosphate $\delta^{18}\text{O}_{\text{p}}$ value (Amiot et al., 2017, 2007;
91 Barrick et al., 1999; Lécuyer et al., 2013). These equations have been successfully applied to
92 Mesozoic faunas that include dinosaurs, crocodylians, turtles and freshwater fishes (Amiot et al.,
93 2011, 2009, 2004; Barrick et al., 1999; Domingo et al., 2015; Suarez et al., 2012). In turn, the
94 $\delta^{18}\text{O}_{\text{mw}}$ value of meteoric waters depends on climate parameters such as air temperature, humidity
95 and amount of precipitation (Dansgaard, 1964; Fricke and O'Neil, 1999; Gat, 1996; Grafenstein et
96 al., 1996). Vertebrates thus record in their phosphatic tissues the climatic conditions of their living
97 environment. However, the $\delta^{18}\text{O}_{\text{w}}$ value of surface waters can significantly differ from that of
98 precipitations due to local processes such as evaporation, mixing with ground waters or with river
99 drainage catchments having different water oxygen isotope compositions. Such processes
100 complicate the interpretations in terms of climatic reconstructions. It is also worth noting that
101 ecological specificities such as plant-water use among herbivorous communities also affect the
102 $\delta^{18}\text{O}_{\text{p}}$ value of vertebrates. Indeed, large differences in $\delta^{18}\text{O}_{\text{p}}$ values have been observed between
103 coexisting herbivorous mammals that drink surface waters and those that only rely on water in
104 plants, usually enriched in ^{18}O by several per mil relative to surface waters (Kohn et al., 1996).

105 Carbon isotope compositions of apatite ($\delta^{13}\text{C}_{\text{c}}$) from air-breathing vertebrates primarily
106 reflect animal diets, with a ^{13}C -enrichment relative to ^{12}C that varies depending on the animal
107 digestive physiology (Passey et al., 2005). The $\delta^{13}\text{C}_{\text{c}}$ value of plant-eating vertebrates thus records
108 the $\delta^{13}\text{C}$ value of the plant tissues they have ingested, mainly leaves. In turn, plants have carbon
109 isotope compositions mainly controlled by their photosynthetic pathway (see Ehleringer and

110 Monson (1993) for a review). The C₃ pathway is the most common one, occurring in all trees, most
111 shrubs and herbs, and grasses in regions with a cool growing season. Today, C₃ plants have a mean
112 δ¹³C value of -27‰ (range from -35‰ to -22‰), reflecting both the δ¹³C value of atmospheric
113 carbon dioxide and local environmental conditions. C₄ photosynthesis operates in grasses from
114 regions with a warm growing season, and in some sedges and dicots. Finally, crassulacean acid
115 metabolism (CAM) occurs in succulent plants. Because C₄ and CAM plants were most likely absent
116 in Early Cretaceous ecosystems as they only appeared in abundance during the Cenozoic, they will
117 not be discussed any further. Abiotic factors such as variations in light intensity, water and osmotic
118 stress, local temperature and pCO₂, influence the carbon isotopic compositions of C₃ plants by
119 affecting leaf stomatal conductance, which in turn constrains the magnitude of CO₂ diffusion
120 through plant epidermis. All these parameters results in variations in the δ¹³C values of C₃ plants
121 (Ehleringer and Monson, 1993). A significant relationship has been established between the δ¹³C
122 values of modern terrestrial C₃ plants and the mean annual precipitations (MAP; (Diefendorf et al.,
123 2010; Kohn, 2010). The carbon isotope compositions of local plants ingested by the herbivorous
124 vertebrates can be retrieved from the δ¹³C_c value of their apatite carbonate. Consequently, the
125 combined use of the apatite-diet carbon **heavy** isotope enrichment (Δ¹³C_{ap-diet}) of those plant-eating
126 vertebrates and the MAP-δ¹³C_{C3 plant} relationship allow the amount of precipitation to be estimated if
127 the Δ¹³C_{ap-diet} can be determined with a satisfactory level of confidence. Tejada-Lara et al. (2018)
128 have shown that the Δ¹³C_{ap-diet} is mainly controlled by the body mass of the animal and its digestive
129 system. At the first-order, Δ¹³C_{ap-diet} increases with body mass and the highest documented values for
130 extant mammals reach about 15‰ (e.g. elephants). In agreement with this relationship, apatite-diet
131 ¹³C-enrichments of about 18‰ have been estimated for two ornithischian dinosaurs, the
132 ceratopsians and hadrosaurs (Fricke et al., 2008; Fricke and Pearson, 2008), and of about 15-16‰
133 for one saurischian group, the sauropods (Domingo et al., 2015; Tütken, 2011). For example, such
134 relationships have been successfully applied to plant-eating dinosaurs (Amiot et al., 2015).

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

140

141 **2 Material and methods**

142

143 **2.1 Sample identification and origin**

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

148 Indeterminate iguanodontid teeth (Hasegawa et al., 1995), turtle shell bone (Evans et al.,
149 1998) and lepisosteid scales come from the Okurodani Formation cropping out at a locality near the
150 village of Shokawa, Gifu Prefecture. It consists of a matrix of dark gray silty-sandstone deposited as
151 part of an extensive floodplain characterized by a network of stagnant pools or “ox-bow” lakes, rich
152 in organic matter and choked with silts (Evans et al., 1998). The depositional age of the Okurodani
153 Formation is still controversial, being either considered as Barremian-Aptian according to
154 tuffaceous mudstone zircons U-Pb age of 117.5 ± 0.7 (2 SE) Ma determined by Kusuhashi et al.
155 (2006), and of 129.2 ± 0.4 (95% CI) Ma (Nagata et al., 2019), or as Late Hauterivian or younger
156 according to Sano and Yabe (2017).

157 Teeth of an indeterminate styracosternan iguanodontian (Barrett and Ohashi, 2016), teeth of
158 the tritylodont *Montirictus kuwajimaensis* (Matsuoka et al., 2016), shell bones of Trionychoid
159 turtles (Hirayama, 2000) and scales attributed to the freshwater fish genus *Sinamia* (Yabumoto,
160 2005) have been recovered from the “Kuwajima Kaseki-kabe” site. It constitutes an outcrop of the

161 Lower Cretaceous Kuwajima Formation of the Tetori Group, in Shiramine District, Hakusan City,
162 Ishikawa Prefecture, central Japan. This outcrop of the uppermost part of the Kuwajima Formation
163 consists of alternating fine- to coarse-grained arkoses, fine-grained sandstones, and mudstones,
164 which are interpreted as channel and interchannel deposits of braided rivers (Isaji et al., 2005). The
165 depositional age of the Kuwajima Formation remains ambiguous, the most recent papers
166 considering it either between the Barremian and Aptian (Matsuoka et al., 2016), or within the
167 Hauterivian – Barremian interval (Barrett and Ohashi, 2016). It must be noted that Matsumoto et al.
168 (2006) and Nagata et al. (2019) reported tuffaceous mudstone zircons U-Pb age of 130.7 ± 0.8 (2
169 SE) Ma and of 129.1 ± 1.5 (95% CI) Ma for the base of the Kuwajima Formation, respectively, and
170 Sakai et al. (2019) reported from tuff beds zircons U-Pb age of 121.2 ± 1.1 (95% CI) Ma from the
171 Akaiwa Fm that is thought to conformably overlie the Kuwajima Fm. This would better fit with a
172 Barremian to Aptian age for the Kuwajima Formation.

173 Teeth of indeterminate theropods, titanosauriform sauropods (Azuma and Shibata, 2010),
174 iguanodontians (Kobayashi and Azuma, 2003) and goniopholidid crocodylomorphs (Azuma, 2003),
175 as well as turtle shell bones and ganoid fish scales (Azuma, 2003), come from the Kitadani
176 Formation at Kitadani Dinosaur Quarry on the Sugiyama River in the northern part of the city of
177 Katsuyama, Fukui, Japan. The fossil layers consist of alternating beds of mudstone and medium-
178 grained sandstone, likely deposited by ancient meandering rivers (Azuma, 2003; Legrand et al.,
179 2013), and this part of the formation is considered as early Aptian in age based on molluscan,
180 ostracod and charophyte biostratigraphy (Cao, 1996; Isaji, 1993; Kozai et al., 2002; Kubota, 2005),
181 as well as on geological correlation with coeval strata (Sano, 2015; Sano and Yabe, 2017).

182 Indeterminate theropod, titanosauriform, iguanodontian and ornithopod teeth have been
183 collected from the Ohyamashimo Formation of Sasayama Group at the locality of Kamitaki near
184 Tamba City, Hyogo (Saegusa et al., 2010; Saegusa and Ikeda, 2014; Saegusa and Tomida, 2011).
185 The Ohyamashimo Formation (Hayashi et al., 2017) is mainly composed of conglomerate,
186 sandstone, and mudstone intercalating several tuff beds, it is considered as early Albian in age based

187 on U–Pb dating of tuff beds zircons providing an age of 112.1 ± 0.4 Ma (95% CI) (Kusuhashi et al.,
188 2013).

189 A neosuchian crocodyliform tooth (Ikegami, 2003) as well as adocid and anosteirin turtle
190 shell bones (Hirayama, 1998) come from the “Upper Formation” of the Mifune Group near Mifune
191 (locality named Kumamoto). The “Upper Formation” is characterised by red mudstone, greyish
192 green sandstone and more than a dozen tuff beds indicating a floodplain deposit that includes
193 calcareous nodules and a palaeosol structure interpreted as reflecting semi-arid subtropical to warm-
194 temperate climatic conditions (Lee et al., 2003). Dating the Mifune Group is still problematic.
195 Ammonites and bivalves date the “Lower Formation” of the Mifune Group as Cenomanian
196 (Tamura, 1979; Tamura and Matsumura, 1974), and the Mifune Group is covered by the Lower
197 Santonian Gankaizan Formation. Fission-track dating has been tentatively performed on tuff beds
198 zircons from both the “Lower Formation” providing two ages of 93.1 ± 4.4 Ma and 89.8 ± 4.0 Ma and
199 the “Upper Formation” providing two ages of 83.6 ± 3.1 Ma and 82.1 ± 11.1 Ma, which would range
200 the Mifune Group between the Turonian and the Campanian (Ikegami et al., 2007). Because of the
201 large uncertainties associated with FT dating and the incongruence of these results with the age of
202 the overlying Gankaizan Formation, an age between the Cenomanian and Coniacian is considered
203 for the “Upper Formation” (Ikegami, 2016).

204

205 **2.2 Analytical technique**

206 **3.2.1 Oxygen isotope analysis of biogenic apatite phosphate samples**

207 Apatite powders have been treated following the wet chemistry protocol described by
208 Crowson et al. (1991) and slightly modified by Lécuyer et al. (1993). This protocol consists in the
209 isolation of phosphate (PO_4^{3-}) from apatite as silver phosphate (Ag_3PO_4) crystals using acid
210 dissolution and anion-exchange resin. For each sample, 20–30 mg of enamel powder was dissolved
211 in 2 mL of 2 M HF. The CaF_2 residue was separated by centrifugation and the solution was
212 neutralized by adding 2.2 mL of 2 M KOH. Amberlite™ anion-exchange resin beads were added to

213 the solution to isolate the PO_4^{3-} ions. After 24 h, the solution was removed, the resin was rinsed and
214 eluted with 6 mL of 0.5 M NH_4NO_3 . After 4 h, 0.5 mL of NH_4OH and 15 mL of an ammonia
215 solution of AgNO_3 were added and the solutions were placed in a thermostatic bath at 70 °C for 7 h
216 allowing the precipitation of Ag_3PO_4 crystals. Oxygen isotope compositions of silver phosphate
217 crystals were measured using a high temperature elemental analyzer equipped with “purge and trap”
218 technology interfaced in continuous flow mode to an isotopic ratio mass spectrometer (Fourel et al.,
219 2011) at the Laboratoire de Géologie de Lyon (UMR 5276, Université Claude Bernard Lyon 1). For
220 each sample, 5 aliquots of 300 μg of Ag_3PO_4 were mixed with 300 μg of pure graphite powder
221 loaded in silver foil capsules. Pyrolysis was performed at 1450 °C with a glassy carbon reactor
222 using a varioPYROcube™ Elemental Analyzer interfaced in Continuous Flow mode with an
223 Isoprime™ Isotopic Ratio Mass Spectrometer. Measurements have been calibrated against silver
224 phosphate precipitated from the NBS120c (natural Miocene phosphorite from Florida), as well as
225 with the NBS127 (Barium sulfate precipitated using seawater from Monterey Bay, California,
226 USA). The value of NBS120c was fixed at 21.7‰ (V-SMOW; Vienna Standard Mean Ocean Water)
227 accordingly to Lécuyer et al. (1993), and that of NBS127 set at the value of 9.3‰ V-SMOW (Hut,
228 1987) for correction of instrumental mass fractionation during CO isotopic analysis. Silver
229 phosphate precipitated from standard NBS120c along with the silver phosphate samples derived
230 from fossil bioapatites was repeatedly analyzed ($\delta^{18}\text{O}_p = 21.75 \pm 0.35\text{‰}$, $n = 13$) to ensure that no
231 isotopic fractionation occurred during the wet chemistry. Data are reported as $\delta^{18}\text{O}$ values vs. V-
232 SMOW (in ‰ δ units; 1‰ = 1mUr).

233

234 **2.2.2 Oxygen and carbon isotope analysis of biogenic apatite carbonate samples**

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

239 left for 24 hours, after which the powder was again rinsed five times with double deionized water
240 and air-dried at 40 °C for 24 hours. For both treatments, the powder/solution ratio was kept constant
241 at 0.04 g mL⁻¹. Stable isotope ratios were determined using a Gasbench II system connected online
242 in continuous flow mode to a MAT253 isotope ratio mass spectrometer (Thermo Fisher Scientific-
243 Germany) at the Lab for Environmental Isotope Geochemistry of the Institute of Geology and
244 Geophysics (Chinese Academy of Sciences, China). For each sample, two aliquots of 2 mg of pre-
245 treated apatite were reacted with 5 drops of supersaturated orthophosphoric acid at 72 °C for one
246 hour under a He atmosphere. The CO₂ produced during the reaction was then transferred to the
247 ConFloIII interface and analyzed by cycles of 10 measurements from each aliquot with the mass
248 spectrometer. The measured oxygen isotopic compositions were normalized relative to the NBS-19
249 marble calibrated material (Hut, 1987) and have a reproducibility better than ±0.2‰. Isotopic
250 compositions are quoted in the standard δ notation relative to V-SMOW for oxygen and V-PDB
251 (Vienna Pee Dee Belemnite) for carbon.

252

253 **3 Results**

254 For the whole vertebrate dataset, oxygen isotope compositions of phosphate range from
255 9.1‰ to 14.9‰ V-SMOW, from 10.9‰ to 17.5‰ V-SMOW for apatite-bound carbonates and
256 carbon isotope compositions range from -12.1‰ to +2.8‰ V-PDB for carbon (**Table 1; Fig. 3**).

257 Local surface waters have been calculated by applying to dinosaur δ¹⁸O_p values the
258 phosphate-water isotope fractionation equation determined for extant birds, their nearest living
259 relatives (Amiot et al., 2017):

260

$$261 \delta^{18}\text{O}_w = 1.119 \pm 0.040 \delta^{18}\text{O}_p - 24.222 \pm 0.644, (\sigma_{\text{est}} = 0.45) \quad (1),$$

262

263 Where σ_{est} corresponds to the mean standard error for the estimated parameter ($\delta^{18}\text{O}_w$). The
264 phosphate-water fractionation equation of extant crocodilians has been applied to crocodylomorphs
265 (Amiot et al., 2007):

266

$$267 \quad \delta^{18}\text{O}_w = 0.823 \pm 0.062 \delta^{18}\text{O}_p - 19.129 \pm 1.076, (\sigma_{\text{est}} = 1.13) \quad (2),$$

268

269 to turtles the phosphate-water fractionation equation of their extant living (Barrick et al. (1999),
270 updated in Pouech et al. (2014)):

271

$$272 \quad \delta^{18}\text{O}_w = 0.994 \pm 0.046 \delta^{18}\text{O}_p - 21.197 \pm 0.755, (\sigma_{\text{est}} = 0.89) \quad (3),$$

273

274 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):

276

$$277 \quad \delta^{18}\text{O}_w = 1.113 \pm 0.003 \delta^{18}\text{O}_p - 26.441 \pm 0.051, (\sigma_{\text{est}} = 0.28) \quad (4).$$

278

279 Calculated local water $\delta^{18}\text{O}_w$ value and associated uncertainties (2σ) range from $-13.3 \pm 1\%$
280 to $-11.1 \pm 1.8\%$ V-SMOW for the Shokawa locality, from $-12.8 \pm 0.6\%$ to $-8.2 \pm 1.8\%$ for the
281 Kuwajima Kaseki-kabe locality, from $-11.3 \pm 1.0\%$ to $-7.8 \pm 2.2\%$ for the Kitadani Dinosaur Quarry,
282 from $-12.3 \pm 1.0\%$ to $-8.4 \pm 1.0\%$ for the Kamitaki locality, and from $-7.6 \pm 1.8\%$ to $-6.4 \pm 1.8\%$ for the
283 Early Late Cretaceous locality of Kumamoto (**Table 2, Fig. 4**). Using the global MAT- $\delta^{18}\text{O}_w$
284 relationship proposed by Lécuyer (2014):

285

$$286 \quad \delta^{18}\text{O}_w = 0.481 \pm 0.02 T(^{\circ}\text{C}) - 14.254 \pm 0.261 \quad (5),$$

287

288 Mean Air Temperatures (MAT) and associated uncertainties (2σ) derived from these $\delta^{18}\text{O}_w$ values
289 respectively range from $2\pm 2^\circ\text{C}$ to $7\pm 4^\circ\text{C}$, from $3\pm 2^\circ\text{C}$ to $13\pm 4^\circ\text{C}$, from $6\pm 2^\circ\text{C}$ to $13\pm 4^\circ\text{C}$ and from
290 $4\pm 2^\circ\text{C}$ to $12\pm 2^\circ\text{C}$, and from $14\pm 4^\circ\text{C}$ to $16\pm 4^\circ\text{C}$ (**Fig. 5; Table 2**). For the three localities of
291 Shokawa, Kuwajima Kaseki-Kabe and Kitadani Dinosaur Quarry (**Fig. 5; Table 2**), surface water
292 temperatures derived from fish $\delta^{18}\text{O}_p$ values have been calculated using local water $\delta^{18}\text{O}_w$ values
293 estimated from dinosaurs, crocodylomorphs and turtles $\delta^{18}\text{O}_p$ values and the phosphate-water
294 temperature scale established for extant fish (Lécuyer et al., 2013):

$$295$$
$$296 \quad T(^{\circ}\text{C}) = 117.4\pm 9.5 - 4.50\pm 0.43 (\delta^{18}\text{O}_p - \delta^{18}\text{O}_w) \quad (6).$$
$$297$$

298 Calculated water temperatures are globally higher than mean air temperatures, ranging from
299 $17\pm 8^\circ\text{C}$ to $27\pm 8^\circ\text{C}$ for the Shokawa locality, from $3\pm 5^\circ\text{C}$ to $27\pm 8^\circ\text{C}$ for the Kuwajima Kaseki-Kabe
300 locality, and from $11\pm 8^\circ\text{C}$ to $36\pm 10^\circ\text{C}$ for the Kitadani Dinosaur Quarry (**Table 2; Fig. 5**). It must
301 be noted that the large ranges of calculated temperatures using fish $\delta^{18}\text{O}_p$ values do not reflect real
302 temperature variability, as fish $\delta^{18}\text{O}_p$ variability is quite low, but variability in calculated water $\delta^{18}\text{O}_w$
303 values from other vertebrates.

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

$$309$$
$$310 \quad \text{Log (MAP)} = 0.0802\pm 0.0102 * \Delta^{13}\text{C}_{\text{C3 plant}} + 1.3726\pm 0.1875 \quad (7),$$
$$311$$

312 with MAP in mm, $\Delta^{13}\text{C}_{\text{C3 plant}} = (\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{plant}}) / (1 + 10^{-3} * \delta^{13}\text{C}_{\text{plant}})$ and atmospheric CO_2 $\delta^{13}\text{C}_{\text{atm}}$
313 values calculated by Barral et al. (2017) for the studied Cretaceous time periods. Estimated MAPs

314 and associated uncertainties (2σ) range from 497 ± 17 mm to 560 ± 50 mm, from 397 ± 12 mm to
315 542 ± 40 mm, from 782 ± 35 mm to 1162 ± 78 mm and from 717 ± 27 mm to 1235 ± 72 mm for the
316 localities of Shokawa, Kuwajima Kaseki-kabe, Kitadani Dinosaur Quarry, Kamitaki and
317 Kumamoto, respectively (**Table 2; Fig. 5**).

318

319 **4 Discussion**

320

321 **4.1 Primary preservation of the stable carbon and oxygen isotope compositions**

322 Biotic and abiotic processes leading to the decomposition, burial and fossilization of living
323 organisms may alter the original isotopic composition of bioapatite through processes of secondary
324 precipitation, ion adsorption or dissolution-recrystallization of bioapatite (Blake et al., 1997;
325 Kolodny et al., 1996; Lécuyer et al., 2003; Trueman et al., 2003; Zazzo et al., 2004b, 2004a).
326 Therefore, pristine preservation of the isotopic records needs to be assessed before discussing the
327 ecological and climatic significance of the oxygen and carbon isotope compositions of fossil
328 vertebrate apatites. Although no method can definitely demonstrate whether the original isotopic
329 compositions have been kept, several ways to assess the preservation state of the isotopic record
330 have been considered (Fricke et al., 1998; Iacumin et al., 1996; Kolodny et al., 1996; Lécuyer et al.,
331 2003; Pucéat et al., 2004; Tütken et al., 2008; Zazzo et al., 2004b). Both phosphate and carbonate in
332 apatite have $\delta^{18}\text{O}$ values reflecting that of the animal's body water, but with a different mineral-
333 water ^{18}O enrichment. Consequently, a positive linear correlation between the $\delta^{18}\text{O}_p$ and the $\delta^{18}\text{O}_c$
334 values with a slope close to unity has been observed on extant vertebrates (Bryant et al., 1996;
335 Chenery et al., 2012; Iacumin et al., 1996; Lécuyer et al., 2010) and used as a test for primary
336 preservation of fossil vertebrate apatites (Amiot et al., 2015; Tütken et al., 2008; Zazzo et al.,
337 2004b). Due to the limited range of apatite $\delta^{18}\text{O}$ values within each Japanese locality, no significant
338 correlation between phosphate and carbonate can be observed. However, a comparison of the
339 distribution of $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ pairs with those of other East Asian Early Cretaceous vertebrates

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

342 A strong case in favor of the preservation of the isotope compositions is the distribution
343 within each locality of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of co-existing vertebrates showing significant
344 differences between taxa (**Fig. 3**). Such a pattern would be a result of differences in ecology,
345 digestive physiology, water strategies and thermophysiology between taxa rather than diagenetic
346 processes that would have more randomly distributed the values. However, the narrow range in $\delta^{13}\text{C}$
347 values observed between taxa of the Kamitaki and Shokawa localities may point to some diagenetic
348 alteration of the carbon isotope composition that would reflect the $\delta^{13}\text{C}$ value of the diagenetic
349 carbon source. Therefore, $\delta^{13}\text{C}$ values from these two localities must be considered with caution.
350 Another clue to primary isotopic preservation is that the carbon isotope compositions of plant diet
351 estimated from plant-eating dinosaurs fall within a range typical of C_3 plants considering the
352 relatively high $\delta^{13}\text{C}_{\text{atm}}$ value of atmospheric CO_2 that was, according to Barral et al. (2017), about
353 3‰ higher than the present-day value of about -8‰ (**Table 2**). It is noteworthy that sample SH20
354 has a $\delta^{13}\text{C}_c$ value anomalously high pointing to a possible diagenetic alteration. This value is treated
355 as an outlier and not considered for subsequent interpretations (**Fig. 3**).

356 Finally, the weight percentage of carbonate in analysed fossil apatites, which ranges from
357 1% to 7%, lies within the expected biological range of modern vertebrate apatites (Brudevold and
358 Soremark, 1967; Rink and Schwarcz, 1995; Tarnowski et al., 2002; Vennemann et al., 2001).

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

362

363 **4.2 Environmental conditions recorded in Cretaceous deposits of Southwest Japan and**
364 **adjacent areas**

365 Fossil plant and vertebrate records within the Tetori Biota hint at a climatic change between
366 the Barremian Kuwajima Formation and the Early Aptian Kitadani Formation. According to
367 differences in floristic composition and physiognomy between the Oguchi flora (found in the
368 Okurodani and Kuwajima formations) and Kitadani flora, a change to warmer and possibly dryer
369 climate has been proposed (Yabe et al., 2003). In contrast with its lower part (Okurodani and
370 Kuwajima formations) which only features the boreal fossil wood genus *Xenoxylon*, the upper part
371 of the Tetori group (Kitadani Formation) yielded beside *Xenoxylon* two more genera, *Brachyoxylon*
372 and *Podocarpoxyton* (Terada and Yabe, 2011; Yamazaki et al., 1990), which thrived under warmer
373 climates (Philippe et al., 2017). A similar switch from *Xenoxylon*-exclusive or dominated fossil
374 wood floras to warmer wood floras with *Agathoxylon* and *Brachyoxylon* is also reported in
375 Southern Korea at the Barremian to Aptian transition (Philippe et al., 2011). Warmer conditions
376 have also been suggested from the occurrence of crocodylomorphs in the Kitadani Formation,
377 whereas they were absent from the underlying Kuwajima and Okurodani formations (Amiot et al.,
378 2011; Matsumoto et al., 2015). Amiot et al. (2011) used a generic phosphate-water oxygen isotope
379 relationship (Amiot et al., 2004) to infer average local meteoric water $\delta^{18}\text{O}$ value from the average
380 $\delta^{18}\text{O}_p$ value of continental vertebrates. Cool temperate climatic conditions with MAT of $10\pm 4^\circ\text{C}$
381 recorded at mid latitudes in East Asia were thus inferred from the oxygen isotope compositions of
382 vertebrates from the Late Barremian Yixian Formation of the Jehol Biota as well as from the
383 Kuwajima Formation. In our study, we have applied available phosphate-water oxygen isotope
384 fractionation equations determined for extant vertebrates (birds, mammals, crocodylians and turtles)
385 to their Cretaceous relatives (dinosaurs, tritylodonts, crocodylomorphs and turtles, **Fig. 4**) and
386 estimated mean air temperature ranges and surface water temperatures using freshwater fish $\delta^{18}\text{O}_p$
387 values (**Table 2, Fig. 6**). Air temperature increase is observed from the Hauterivian to the early Late
388 Cretaceous, however, temperature values comprised between 4°C and 13°C for the Aptian Kitadani
389 Formation and Albian Ohyamashimo Formation seem too low to be considered as realistic
390 estimates. Indeed, the occurrence of crocodylomorphs with a minimum mean living temperature

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

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

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

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

443 both suggest a tropophilous climate with a marked dry season and are only rarely associated to
444 *Xenoxylon* (Oh et al., 2015), possibly only in environments where beside riparian forests existed
445 drier settings. A similar mixture of *Xenoxylon* and more thermophilous element was reported from
446 the coeval Nakdong Formation in South Korea (Jeong et al., 2014). A paleobotanical study of the
447 Sawada Formation of the Sasayama Group documented a flora related to those of the Ryoseki-type
448 usually recorded in the Outer Zone of Japan, with an abundance of xerophytic microphyllous taxa
449 such as *Brachyphyllum* spp. and *Pseudofrenelopsis* sp. (Yamada et al., 2018). These floristic
450 components, together with the overall rarity of fern remains, would indicate the prevalence of a
451 seasonally arid tropophilous climate. The wood genus *Brachyoxylon* was also reported from the
452 Sawada Formation (Terada, 2012), similarly suggesting a subtropical tropophilous climate (Philippe
453 et al., 2017). This interpretation is supported by sedimentary facies observed at the locality of
454 Kamitaki as well as in the Ohyamashimo Formation cropping out at Sasayama city (Hayashi et al.,
455 2017). Mudstone shows features seen in vertisols such as a strong development of slickensides and
456 high smectite content (Saegusa et al., 2010), suggesting that high amount of precipitation occurred
457 during the rainy season, as well as the occurrence of strong shrinkage of clay rich soil indicating a
458 intense dry seasons. The possible intense dry season is also supported by the presence of caliche in
459 other mudstone layers in Kamitaki (Saegusa et al., 2010). Vertebrates from the Ohyamashimo
460 Formation of the Sasayama Group have low apatite carbonate $\delta^{13}\text{C}_c$ values that reflect large
461 amounts of annual precipitation compatible with the existence of a “wet and dry” tropophilous
462 climate.

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

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

472 According to a study based on the reconstruction of spatio-temporal changes in the
473 latitudinal distribution of desert deposits and the prevailing surface-wind patterns recorded in the
474 Asian interior, a humid zone should have existed at mid latitudes during the mid-Cretaceous, as
475 documented by the coal-bearing deposits observed in the Gobi basin of Mongolia (Hasegawa et al.,
476 2012). This would be compatible with the amount of precipitations calculated from the Aptian
477 Kitadani and Albian Sasayama vertebrate $\delta^{13}\text{C}$ values, but not with the drier environments inferred
478 from the Fuxin vertebrates (Amiot et al., 2015). Far-East Asia fossil wood record for the Cretaceous
479 is consistent with the hypothesis that regional paleogeography might explain this peculiar climate
480 pattern (Oh et al., 2011). Indeed, Northeastern China was then bordered on the southeast by the Su-
481 Lu mountain range, locally producing a “rain shadow” that limited air moisture from the Pacific
482 Ocean to enter from the East inlandward. Such topography may have contributed to constitute
483 continental-like climatic conditions with a thermal seasonality enough contrasted to be unsuitable
484 for the presence of crocodylomorphs. Further ecological and environmental studies might elucidate
485 the apparent contradiction between isotopic and paleobotanical data from the Aptian Kitadani and
486 Albian Sasayama fossil assemblages, and help to better understand the mosaic environments that
487 seem to have characterized East Asia during the Cretaceous.

488

489 **5 Conclusion**

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

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

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

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

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

506

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512

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515 **Figure captions**

516 **Figure 1:** Geographic location of the studied localities. 1: Shokawa; 2: Kuwajima Kaseki-Kabe; 3:
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 ($\delta^{18}\text{O}_p$) reported against the
523 carbon isotope compositions of structural carbonate ($\delta^{13}\text{C}_c$) for the five studied Cretaceous
524 localities. Numbers in brackets refer to the locality described in Figure 1. Sample SH20 having an
525 anomalously high $\delta^{13}\text{C}_c$ value is treated as an outlier and not used for subsequent MAP calculations.

526

527 **Figure 4:** Taxon-averaged drinking water $\delta^{18}\text{O}_w$ value and associated standard deviation (horizontal
528 bars) estimated for each studied locality.

529

530 **Figure 5:** Temporal variations of surface temperature and amount of precipitation ranges estimated
531 from vertebrate apatite $\delta^{18}\text{O}_p$ and $\delta^{13}\text{C}_c$ values. Numbers refer to the localities described in Figure 1.
532 Published indicators of qualitative environmental conditions described in the text are figured as
533 symbols.

534

535 **Figure 6:** Oxygen isotope compositions of carbonate ($\delta^{18}\text{O}_c$) of all analyzed vertebrates plotted
536 against their corresponding oxygen isotope compositions of phosphate ($\delta^{18}\text{O}_p$), and compared to the
537 published $\delta^{18}\text{O}_p$ - $\delta^{18}\text{O}_c$ pairs for Early Cretaceous East Asian localities (Amiot et al., 2015). Dashed
538 line with a slope of unity is drawn for reference.

539

540

541 **Table captions**

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

545

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

553