Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climates

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Early Cretaceous vertebrate assemblages from East Asia and particularly the Jehol Biota of northeastern China flourished during a period of highly debated climatic history. While the unique characters of these continental faunas have been the subject of various speculations about their biogeographic history, little attention has been paid to their possible climatic causes. Here we address this question using the oxygen isotope composition of apatite phosphate ($\delta^{18}O_p$) from various reptile remains recovered from China, Thailand, and Japan. $\delta^{18}O_p$ values indicate that cold terrestrial climates prevailed at least in this part of Asia during the Barremian—early Albian interval. Estimated mean air temperatures of about 10 ± 4 °C at midlatitudes (~42 °N) correspond to present day cool temperate climatic conditions. Such low temperatures are in agreement with previous reports of cold marine temperatures during this part of the Early Cretaceous, as well as with the widespread occurrence of the temperate fossil wood genus *Xenoxylon* and the absence of thermophilic reptiles such as crocodilians in northeastern China. The unique character of the Jehol Biota is thus not only the result of its evolutionary and biogeographical history but is also due to rather cold local climatic conditions linked to the paleolatitudinal position of northeastern China and global icehouse climates that prevailed during this part of the Early Cretaceous.

vertebrate phosphate | oxygen isotopes | paleoclimate

Since the last decade, continuous discoveries of Early Cretaceous invertebrates, plants and vertebrates in East Asia, and more particularly exceptionally preserved specimens in northeastern China belonging to the Jehol Biota, have fed numerous current evolutionary debates (1, 2). This latter assemblage is preserved in the lacustrine and volcanic sediments that mainly constitute the Yixian and Jiufotang formations of Liaoning Province. The peculiar character of the Jehol Biota, with "unusual" forms such as feathered dinosaurs, is clearly in part a result of the exceptional preservation of many fossils which show well preserved integumentary structures seldom preserved in other localities. However, it has been suggested that the Jehol Biota show peculiar floral and faunal compositions, which may, for instance, be indicative of a "relict" character (3) although this interpretation has been disputed (1). To date, possible relations between global climatic conditions and the taxonomic composition of the Jehol Biota have not been investigated, and no quantitative local climate reconstruction has been proposed so far. In the marine record, cold climatic intervals have been recognized during the Early Cretaceous period, with two major events occurring (*i*) during the early Valanginian, and (*ii*) from the late Barremian to the early Albian (4, 5). The most recent $^{40}Ar/^{39}Ar$ dating of sanidine crystals from tuff beds within the Yixian Formation and the base of the overlying Jiufotang Formation gave an age bracket of 129.7 ± 0.5 Ma to 122.1 ± 0.3 Ma for the deposition of the Yixian Formation (6). These ages correspond to a Barremian to early Aptian age interval which is encompassed by the second cold interval. We have estimated water $\delta^{18}O$ values and related mean air paleotemperatures at eight contemporaneous localities covering a large range of paleolatitudes in order to define a latitudinal climatic gradient and its influence upon the geographic distribution of East Asian fauna and flora.

Results and Discussion

We have used 99 new and 17 published [(7–9); Table S1] oxygen isotope compositions of apatite phosphate ($\delta^{18}O_p$) measured on dinosaurs, tritylodont synapsids, and freshwater crocodilian teeth, as well as turtles shell bones. These apatitic remains were recovered from deposits of the Yixian Formation and seven other Early Cretaceous formations in China, Japan, and Thailand. All these deposits are dated from the Barremian to the Aptian-Albian intervals and cover palaeolatitudes ranging from 21.0± 7.2 °N to 43.2 ± 8.0 °N (Table 1 and Fig. 1). Oxygen isotope compositions of apatite phosphates were measured using the procedure described in the *Analytical method* section, and are reported on in Table S1.

Preservation of the Original Oxygen Isotope Compositions. Secondary precipitation of apatite and isotopic exchange during microbially mediated reactions may alter the primary isotopic signal (10, 11). However, apatite crystals that make up tooth enamel are large and densely packed, and in the absence of high temperature conditions which Kolodny and others argue that they enable microbial mediated reactions to reset the bone phosphate oxygen isotopic signal, isotopic exchange might not affect the oxygen isotope composition of phosphates even at geological time scales (12, 13). Turtle shell and dinosaur bones should be more susceptible to diagenetic alteration because hydroxylapatite crystals

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Table 1. Formation, age, sample number (N), and computed palaeolatitudes are given along with mean vertebrate $\delta^{18}O_p$ values, environmental water $\delta^{18}O_w$ values obtained by subtracting 21.9 to mean $\delta^{18}O_p$ values (15) and estimated mean air temperatures using the following equation: $\delta^{18}O_w = 0.49(\pm 0.03)T\,°C - 14.18(\pm 0.52)$ (15)

Formation	Age	N	Paleolatitude (°)	$\delta^{18}O_p$ (‰ V-SMOW) Mean	Std. Dev.	$\delta^{18}O_w$ (‰ V-SMOW)	M.A.T. (°C) mean	Std. Dev.
Kuwajima (1)	Barremian-Early Aptian	16	43.2(+8.2/ − 7.8)	12.7	1.8	−9.2	10	4
Fuxin (2)	Aptian-Albian	10	42.1(+6.6/ − 6.5)	11.7	1.6	−10.3	8	3
Shahai (3)	Aptian-Albian	9	42.1(+6.6/ − 6.5)	11.9	0.7	−10.0	9	1
Yixian (4)	Barremian-Early Aptian	16	41.9(+6.6/ − 6.6)	12.7	1.8	−9.2	10	4
Xinminbao (5)	Aptian-Albian	29	35.2(+6.4/ − 6.6)	14.9	2.9	−7.0	15	6
Khok Kruat (6)	Aptian	18	24.3(+1.9/ − 1.8)	15.2	2.8	−6.7	15	6
Sao Khua (7)	Barremian?	11	24.3(+1.9/ − 1.8)	17.0	0.5	−4.9	19	1
Napai (8)	Aptian?	9	21.0(+7.2/ − 7.2)	17.1	2.5	−4.9	19	5

Numbers in brackets associated with Formation names are the same as those displayed in Fig. 1.

of bones are smaller and less densely intergrown than those of enamel (14), even though several case studies have shown that the original oxygen isotope composition can be preserved in Mesozoic reptile remains (7–9, 15–17). Although no method is available to demonstrate definitely whether or not the oxygen isotope composition of fossil vertebrate phosphate was modified by diagenetic processes, several ways to assess the preservation state of the primary isotopic record have been proposed [e.g., (14, 18–21)]. Here the main argument supporting the preservation of the original oxygen isotope composition is the latitudinal variation of the offset observed between the $\delta^{18}O_p$ values of probable endotherms (dinosaurs and trytilodont synapsids) and ectotherms (turtles and crocodilians) that mimics present day variations of the offset observed between the $\delta^{18}O_p$ values of endotherms and ectotherms (Fig. 2). If early diagenetic processes had occurred, they would have erased the expected offsets in $\delta^{18}O_p$ values of vertebrate remains having different ecologies or physiologies (20).

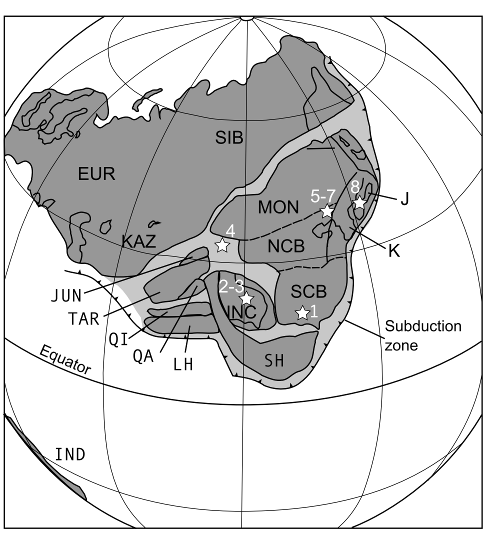

Fig. 1. Palaeogeographic map of eastern Asia in the Early Cretaceous modified from ref. 42. Number refers to the following horizons and localities: 1: Napai Fm., Guangxi, China, Aptian?; 2: Sao Khua Fm., Thailand, Barremian? (43); 3: Khok Kruat Fm., Thailand, Aptian (43); 4: Xinmingbao Fm., Gansu, China, Aptian-Albian (44); 5: Yixian Fm., Liaoning, China, Barremian-early Aptian (6); 6: Shahai and 7:Fuxin formations, Liaoning, China, Aptian-Albian (45); and 8: Kuwajima Fm., Japan, Barremian-early Aptian (46). Palaeolatitude of each locality was calculated using the Apparent Polar Wander Path (APWP) of refs. 47, 48. Abbreviations refer to major tectonic divisions: EUR, Europe; INC, Indo-China; IND, India; J, Japan; JUN, Junggar; K, Korea; KAZ, Kazakhstan; LH, Lhassa; MON, Mongolian; NCB, north China; QI, Qiangtang; SCB, south China; SH, Shan Thai; SIB, Siberian; and TAR, Tarim.

Climatic and Ecologic Implications. Considering at least partial preservation of the primary isotopic compositions of analyzed apatites, mean $\delta^{18}O_{mw}$ values of meteoric waters can be estimated at each site using present day relationships established between vertebrate phosphate and water ($\delta^{18}O_p - \delta^{18}O_w$). Due to ecological differences between herbivorous (sauropods, ornithopods, ceratopsians, and ankylosaurs) and carnivorous (theropods) dinosaurs, systematic offsets in $\delta^{18}O_p$ values between these dinosaur groups that would reflect differences in diet, water strategies, and foraging micro habitats were expected (7, 22, 23). However, the $\delta^{18}O_p$ value differences observed between coexisting theropods, sauropods, ornithopods, ceratopsians, and ankylosaurs appear to be randomly distributed from one site to another (Fig. 2) instead of being ordered the same way at all sites. This observation suggests that these differences are more related to spatial or seasonal variability in ingested water $\delta^{18}O$ values than to taxon-specific ecological differences. Moreover, as dinosaur teeth took from a few months up to more than a year to grow depending on their size (24), significant differences in $\delta^{18}O_p$ values between teeth coming from the same deposit are expected. The same pattern can be observed on crocodilian and turtles $\delta^{18}O_p$ values but with less scattering due to their semiaquatic lifestyle and their living environment consisting of large water bodies (rivers, lakes) that buffer seasonal variations in local meteoric water $\delta^{18}O_{mw}$ values (Fig. 2). From present day data, it has

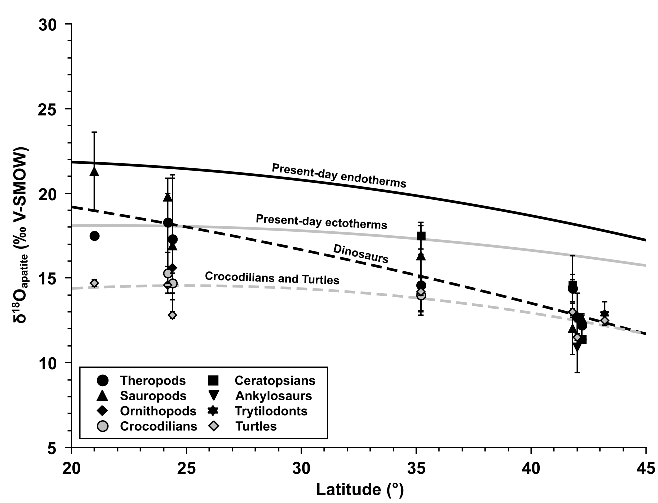

Fig. 2. Latitudinal variations in $\delta^{18}O_p$ values of dinosaurs, crocodilians, and turtles compared to expected latitudinal variations in $\delta^{18}O_p$ values of present day endotherms and ectotherms drawn using $\delta^{18}O_{mw}$ and mean air temperature values of IAEA (International Atomic Energy Agency)/WMO (World Meteorological Organization) (27), and the following equations : $\delta^{18}O_{mw} = 1.11 * \delta^{18}O_p - 26.44$ [endotherms; (15)] and $T = 113.3 - 4.38 * (\delta^{18}O_p - \delta^{18}O_{mw})$ [ectotherms; (12)].

been shown that a first order estimation of $\delta^{18}O_{mw}$ value can be calculated by substracting 21.9‰ to the average $\delta^{18}O_p$ value of both endotherms and ectotherms (15). Based on these considerations, $\delta^{18}O_{mw}$ values were estimated for the eight Early Cretaceous sites (Table 1 and Fig. 3). At the global scale, these values are slightly lower than those found today at similar latitudes, suggesting lower Mean Annual Air Temperatures (MAAT) than present day ones.

Despite the possibility that, at the global scale, Mesozoic hygrometry differed from present day condition, thus affecting the latitudinal distribution of $\delta^{18}O_{mw}$ values, there is no compelling evidence to indicate that the systematics of ancient meteoric waters were radically different from today (25). On the contrary, it was argued that the "$\delta^{18}O_{mw}$-MAAT" relationship may be conservative through time, at least throughout the Quaternary (26). Mean air palaeotemperatures were thus proposed (Table 1 and Fig. 4) using the same present day relationship established between meteoric water and MAAT ($\delta^{18}O_{mw}$—MAAT) that was previously used to establish a terrestrial temperature gradient for the terminal Cretaceous (15; Fig. 4).

The fitted temperature gradient has a curvature similar to that of the present day gradient but shifted towards lower mean temperatures (Fig. 4). For consistency, the same ($\delta^{18}O_{mw}$—MAAT) relationship was used for all sites (Table 1), but this leads to underestimation of mean air temperatures in tropical sites of the Khok Kruat and Sao Khua formations of Thailand, as well as the Napai Formation of Guangxi (China), which were closer to a typical 20–25 °C range because of the possible occurrence in these areas of monsoon-like precipitations having ^{18}O-depleted meteoric waters (7). Calculated mean air palaeotemperatures for the Liaoning region range from 8 ± 3 °C (Fuxin Formation) to 10 ± 4 °C (Yixian Formation), matching modern cool temperate midlatitude climatic conditions (27). These temperature estimates are supported by previous studies (4, 5, 28) that have documented global cold intervals during the Early Cretaceous with subfreezing to freezing conditions in polar regions. Throughout the early Aptian, low latitude surface seawaters of the western Tethys were about 20 °C with high seasonality (4, 28) while polar ice was present at high latitudes (5). The fossil wood genus *Xenoxylon*, recognized as an indicator of temperate to cool temperate climates (29), was widely distributed in northeastern Asia during the Early Cretaceous, where it reached a level of anatomical diversity unmatched elsewhere in the world (30). Most strikingly, no crocodilian remains have been found so far either in northeastern China or Japan in deposits corresponding to the Jehol Biota, whereas they were abundant at lower latitudes, the northernmost occurrence being in the Dongmyeong Formation (Barremian) in the southern part of South Korea (31). During the late Early Cretaceous, crocodilians occurred again in Japan in the Albian Kitadani Formation (32) and colonized higher latitudes during the Late Cretaceous, as shown by their occurrence in the Late Turonian to Early Santonian Nenjiang Formation of Jilin Province (latitude about 44 °N). It is noteworthy that during the Late Campanian-Middle Maastrichtians interval, for which a terrestrial temperature gradient with higher mid- to high-latitudes temperatures was previously established [(Fig. 4; 15)], crocodilians occurred at latitudes up to 60 °N. Because of modern crocodilians restricted temperature requirements, they can live only under climates where mean air temperatures exceed 13–14 °C (33). According to the calculated Early Cretaceous gradient, these minimum mean temperatures tolerated by crocodilians occurred at latitudes of 35 °N, as illustrated by their presence in the Xinminbao Formation of Gansu Province (Fig. 1, Locality 4) and in the Dongmyeong Formation of the southern part of South Korea. Under the cool climatic conditions of the Jehol Biota, ectothermic vertebrates such as turtles, lizards, or amphibians may have hibernated, whereas endothermic animals such as mammals, non avian dinosaurs, birds, and possibly pterosaurs may have benefited from their integumentary structures (hair, feathers, or feather-like structures) as insulation devices, allowing them to keep sustained activity all year round. The occurrence of choristoderes (crocodile–like archosauromorph reptiles) in the Jehol Biota raises the question of whether they can be used as an ecological analogue to crocodilians in terms of temperature tolerance, as has been proposed (34). Choristoderes were semiaquatic active predators and some of them, such as *Ikechosaurus* from the Jehol Biota, resembled modern gharials. Although choristoderes commonly occur along with crocodilians, their presence in assemblages from which crocodilians are absent has led to the hypothesis that they were ecological competitors of crocodilians (35, 36) and had similar environmental temperature requirements (34). On the basis of present data, we argue that choristoderes could tolerate low temperatures, and thus probably occupied the ecological niches of crocodilians in colder environments where the latter could not live, although they definitely occurred together in warmer environments. This interpre-

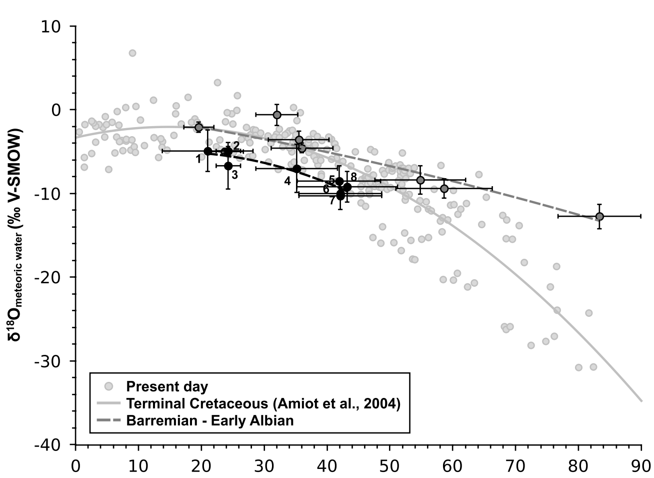

Fig. 3. Calculated mean meteoric water $\delta^{18}O_{mw}$ gradient during the Early Cretaceous of eastern Asia vs. absolute latitudes. The Early Cretaceous thermal gradient was calculated using fossil vertebrate $\delta^{18}O_p$ values and published equations (15). The present day continental temperature gradient for low altitude localities and the calculated Late Campanian—Middle Maastrichtian gradient are given for comparison.

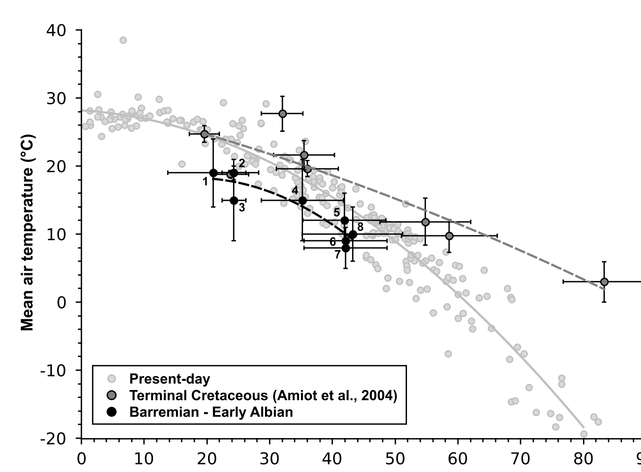

Fig. 4. Estimated mean annual temperatures during the Early Cretaceous of eastern Asia vs. absolute latitudes. The Early Cretaceous thermal gradient was calculated using fossil vertebrate $\delta^{18}O_p$ values and published equations (15). The present day continental temperature gradient for low altitude localities and the calculated Late Campanian—Middle Maastrichtian gradient (15) are given for comparison.

tation suggests that the distribution of choristoderes cannot be used as an indicator of warm climates simply on the basis of a supposed ecological analogy with crocodilians.

The relatively cold climatic conditions under which the formations containing the Jehol Biota were deposited may partly explain their singularity, notably by comparison with assemblages from other parts of Asia, which during the Early Cretaceous were located farther South. Such comparison applies, in particular, to the Barremian (?) Sao Khua and Aptian Khok Kruat formations of northeastern Thailand, which have yielded abundant vertebrate remains, and for which isotopic data are available (7). Although there are a few faunal elements shared by the Jehol Biota and the Khok Kruat Formation, such as the ceratopsian dinosaur *Psittacosaurus* (37), faunal similarities between the two formations seem to be very limited. Such differences may partly be owing to different depositional environments between the fluvial Thai formations and the largely lacustrine formations of northeastern China, with consequences in both composition and preservation. However, the different climatic conditions, themselves linked to geography, may have played a major role by preventing forms restricted to warm environments from entering northeastern Asia during part of the Early Cretaceous. More globally, the palaeotemperatures estimated from the oxygen isotope compositions of Jehol Biota fossils support previous claims that "icehouse" events took place during the Early Cretaceous, resulting in climatic conditions that might have been close to present day global climate but with a lesser extent of polar ice caps (5). The peculiar composition of the Jehol Biota may therefore largely reflect relatively cold climatic conditions in northeastern Asia during part of the Early Cretaceous, which contrasts with the usual "greenhouse" conditions under which many Mesozoic ecosystems flourished. A climatic gradient similar in some respects to the present one may at least partly explain the differences between the Jehol Biota and floral and faunal assemblages from regions located farther South.

Analytical method. Measurements of oxygen isotope compositions of apatite phosphate consist in isolating phosphate ions using acid dissolution and anion-exchange resin, according to a protocol derived from the original method published by Crowson et al. (38) and slightly modified by Lécuyer et al. (39). Silver phosphate was quantitatively precipitated in a thermostatic bath set at a temperature of 70 °C. After filtration, washing with double deionised water, and drying at 50 °C, 15 mg of Ag_3PO_4 were mixed with 0.8 mg of pure powder graphite. Oxygen isotope ratios were measured by reducing silver phosphate to CO_2 using graphite reagent (40, 41). Samples were weighed into tin reaction capsules and loaded into quartz tubes and degassed for 30 min at 80 °C under vacuum. Each sample was heated at 1,100 °C for 1 min to promote the redox reaction. The CO_2 produced was directly trapped in liquid nitrogen to avoid any kind of isotopic reaction with quartz at high temperature. CO_2 was then analyzed with a Thermo-Finnigan MAT253 mass spectrometer at the Institute of Geology and Geophysics, Chinese Academy of Sciences. Isotopic compositions are quoted in the standard δ notation relative to V-SMOW (Vienna Standard Mean Ocean Water). Silver phosphate precipitated from standard NBS120c (natural Miocene phosphorite from Florida) was repeatedly analyzed ($\delta^{18}O = 21.7 \pm 0.2‰$; $n = 37$) along with the silver phosphate samples derived from the fossil vertebrate remains.

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