Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles, and crocodilians

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Abstract

Oxygen isotopes can be used to reconstruct the palaeoenvironmental conditions in which vertebrates lived, and thereby give an indication of their ecology. This has been done for faunas from the famous Late Jurassic lithographic limestones of Western Europe. Oxygen isotope compositions of phosphate from apatite were measured in aquatic or semiaquatic vertebrate remains (fish, turtles, and crocodilians) deposited in these protected coastal marine environments. The unknown water composition in the oxygen isotope fractionation equations between phosphate and water was solved for turtles by assuming that modern relationship between environmental water and turtle bone isotope compositions applies to the past. The results show that: (1) coastal marine waters were thermally homogenous at the regional scale of Western Europe; (2) oxygen isotope data discriminate between coastal marine and freshwater to brackish water inhabitants; (3) the plesiochelyid turtles were coastal marine inhabitants—their $\delta^{18}O$ values allow the calculation of the oxygen isotope compositions of marine waters, thus refining the estimate of water temperatures by combining $\delta^{18}O$ values from fish; and (4) the marine isotopic signature and the cranial anatomy of plesiochelyid turtles lead us to propose that they had a salt-excreting system (i.e., the fundamental physiological feature that controls osmoregulation in the marine environment). These Late Jurassic turtles are proposed to be the first known marine turtles, several tens of million years before the chelonioids or 'sea turtles.'
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1. Introduction

In western Europe, at the end of Jurassic (~144 million years ago; Gradstein et al., 1994), lithographic limestones were deposited in protected coastal marine environments. They contain exceptionally preserved vertebrates, such as the famous bird *Archaeopteryx* in Bavaria, as well as an aquatic or semiaquatic (amphibious) fauna including fish, turtles, and crocodilians (e.g., Barthel et al., 1990). Four well-dated sites have been documented: Cerin, Crayssac, Canjuers (France), and Solnhofen (Germany), all of similar age (Upper Kimmeridgian–Lower Tithonian). They provide an opportunity to characterize the aquatic environments of these vertebrates (Fig. 1). For comparison with a more open coastal marine system (North Atlantic side), vertebrate remains were sampled from a fifth locality, Chassiron, from the Lower Tithonian of France (Fig. 1).

Oxygen isotope compositions of phosphate from marine biogenic apatites have been recognized as proxies of past seawater oxygen isotope compositions and temperatures (Longinelli and Nuti, 1968; Kolodny et al., 1983; Kolodny and Raab, 1988; Kolodny and Luz, 1991; Lécuyer et al., 1993; Picard et al., 1998; Vennemann and Hegner, 1998). Diagenetic alteration may affect isotope compositions (e.g., Longinelli, 1966, 1996; Kolodny et al., 1996; Sharp et al., 2000; Lécuyer et al., 2003a), but the apatite crystals that make up the studied material are large and densely packed, thus minimizing the possibility of oxygen isotope exchange with sediment pore aqueous fluids. The analyzed biogenic apatite remains are tooth enamel (fish, crocodilians), scale ganoine (fish), and dermal bony plates (turtles, crocodilians).

Similar oxygen isotope fractionation equations between phosphate and water have been determined for various invertebrate and vertebrate ectotherms
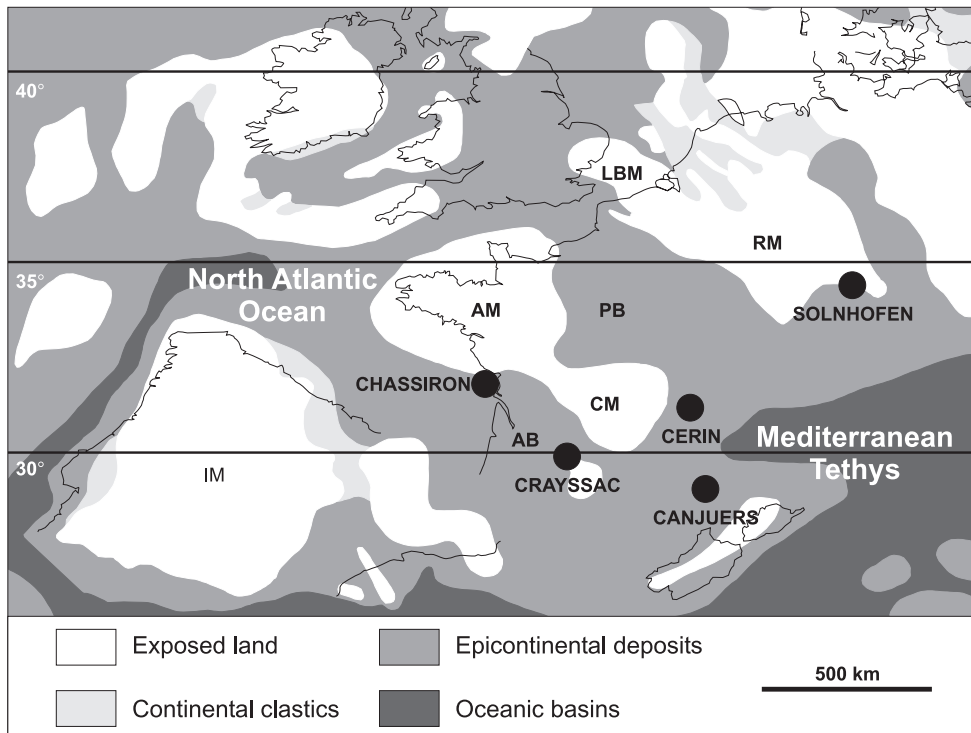

Fig. 1. Locations of studied fossiliferous sites on the Early Tithonian (Late Jurassic) palaeoenvironmental map of western Europe. Map modified from Thierry et al. (2000). Abbreviations: AB, Aquitaine Basin; AM, Armorican Massif; CM, Central Massif; IM, Iberian Massif; PB, Paris Basin; LBM, London Brabant Massif; RM, Rhenish Massif.

(Longinelli and Nuti, 1973; Kolodny et al., 1983; Lécuyer et al., 1996, 2003b). One property of the phosphate–water system is that a single equation describes oxygen isotope fractionations for most ectotherms; the oxygen isotope composition of phosphate from extant fish apatite depends only on the temperature and isotopic composition of drinking water (Longinelli and Nuti, 1973; Kolodny et al., 1983). For example, extant fish and crocodilians living in the same ambient water (Oubangui river, Central Africa) have similar oxygen isotope compositions of phosphate (Lécuyer et al., 2003a). The oxygen isotope composition of crocodilian phosphate also strongly depends on ambient water composition, as shown by Lécuyer et al. (1999) and Stoskopf et al. (2000). More generally, some large fish or reptiles are characterized by a mass homeothermy where the skeleton grows at a rather constant temperature, as in the case of turtles (Hutchison, 1977). Consequently, as shown by Barrick et al. (1999), the $\delta^{18}O$ value of turtle apatite is a simple function of the $\delta^{18}O$ of ambient water, hence constituting a potential powerful proxy for identifying fresh and marine waters (assuming that extinct turtles were basking as modern ones). Knowing the composition of water, the fractionation equation determined for ectotherms (poikilotherms) can be solved for the temperature at which the fauna lived in the same environment.

The oxygen isotope measurements performed on the phosphate of both fish and reptiles allowed us to investigate environmental, ecological, and taphonomical aspects of the Late Jurassic coastal deposits of western Europe: (1) The thermal homogeneity of coastal marine waters at the regional scale of western Europe will be tested because these environments were more or less influenced by the North Atlantic and Tethyan oceanic domains, and more or less protected. (2) The autochthony of fish and reptiles will be tested to sort out this concentration of coastal marine vertebrates. (3) The modern relationship between environmental water and turtle bone isotope compositions will be applied to solve the unknown water composition in the oxygen isotope fractionation equations, to improve the estimate of past water temperatures. (4) The marine status of some Late Jurassic turtles will be tested both from their isotopic signature and their anatomy, several tens of million years before the first known marine turtles.

2. Palaeogeography and depositional environments

During the Late Jurassic, western Europe was an archipelago located on the northern margin of the Tethys (Fig. 1), between the opening North Atlantic ocean (western Tethys) and the Mediterranean Tethys (central Tethys). It consisted of islands and shallow carbonate platforms (Fourcade et al., 1993a; Thierry, 2000); the studied sites were lying between palaeolatitudes ~29°N and 35°N (Fourcade et al., 1993b; Thierry et al., 2000), a latitudinal belt that corresponds to the modern subtropical semiarid zone. Consequently, it was supposed that the climate was relatively warm and dry, as supported by the presence of xerophytic plants at several sites (e.g., Solnhofen) (Barthel et al., 1990).

Reconstructions of ocean circulations based on Nd isotope ratios of biogenic apatites and results obtained from global circulation models (GCMs) support the presence of a permanent westward-flowing Tethys Circumglobal Current (TCC) during the Late Jurassic and Early Cretaceous (Barron et al., 1981; Barron and Peterson, 1989; Stille et al., 1996). This surface current would have allowed large masses of Pacific waters to flow into the Tethys and the young North Atlantic Ocean, which was still quite narrow in the earliest Cretaceous. The reported depositional environments can be divided into two types according to their palaeogeographic location and marine connections: those from southeastern France and Bavaria (Cerin, Canjuers, and Solnhofen), which are essentially sourced by the Mediterranean Tethys; and those from the Aquitaine Basin (Crayssac, Chassiron), which are influenced both by waters from the opening North Atlantic ocean and the Mediterranean Tethys (Fig. 1). The Aquitaine basin was likely occupied by a gulf (SE–NW orientation) during the Tithonian, the 'Charentais Gulf' (Delfaud and Gottis, 1966; Hantzpergue and Lafaurie, 1994), fed mainly by waters from the opening North Atlantic Ocean. However, this hypothesis is not supported by a recent palaeogeographic reconstruction (Thierry, 2000; Thierry et al., 2000; Fig. 1), which shows the possibility of a connection southward and eastward between the Aquitaine Basin and the Mediterranean Tethys. According to their respective geographical positions, Chassiron was probably principally connected to the

Table 1

Systematics, material, location, age, and oxygen isotope compositions of phosphate from Late Jurassic vertebrate remains of western Europe

Sample	Taxon	Taxon abbreviation	Family	Group	Material	Locality	Stage	Ammonite zone	Ammonite subzone	$\delta^{18}O_p$ (‰ SMOW)	T (°C) using $\delta^{18}O_w$=−1 ‰[a]	$\delta^{18}O_w$ (‰ SMOW) from turtles[b]	T (°C) using $\delta^{18}O_w$ from plesiochelyid turtles[c]
BG32	*Proscinetes* sp.	Pro.	Pycnodontidae	Osteichthyes	Tooth	Canjuers	Lower Tithonian	Mucronatum	Indet.	19.9	21.8		
BG38	*Proscinetes* sp.	Pro.	Pycnodontidae	Osteichthyes	Tooth	Canjuers	Lower Tithonian	Mucronatum	Indet.	19.8	22.2		
BG36	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scales	Canjuers	Lower Tithonian	Mucronatum	Indet.	20.1	20.9		
BG37	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scales	Canjuers	Lower Tithonian	Mucronatum	Indet.	20.4	19.6		
BG39	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scales	Canjuers	Lower Tithonian	Mucronatum	Indet.	20.6	18.7		
BG33[d]	*Steneosaurus priscus*	Ste.	Teleosauridae	Crocodylia	Osteoderm	Canjuers	Lower Tithonian	Mucronatum	Indet.	19.9			
BG50[d]	*Steneosaurus priscus*	Ste.	Teleosauridae	Crocodylia	Tooth	Canjuers	Lower Tithonian	Mucronatum	Indet.	20.3			
BG35	*Eurysternum* sp.	Eur.	'Thalassemydidae'	Chelonia	Osteoscute	Canjuers	Lower Tithonian	Mucronatum	Indet.	18.9		−3.2	
BG41	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Tooth	Chassiron	Lower Tithonian	Gigas	Gravesiana	22.8	9.0		11.3 (a)/12.6 (b)
BG42	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.7	13.9		16.1 (a)/17.5 (b)
BG43	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.5	14.8		17.0 (a)/18.3 (b)
BG11	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Chassiron	Lower Tithonian	Gigas	Gravesiana	22.0	12.6		14.8 (a)/16.1 (b)
BG14	Semionotidae	Sem.	Semionotidae	Osteichthyes	Tooth	Chassiron	Lower Tithonian	Gigas	Gravesiana	22.1	12.1		14.4 (a)/15.7 (b)
BG17	Semionotidae	Sem.	Semionotidae	Osteichthyes	Tooth	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.3	15.6		17.9 (a)/19.2 (b)
BG29	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Tooth	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.1			
BG12	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Osteoderm	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.9			
BG16	'Thalassemys' moseri	Ple.	Plesiochelyidae	Chelonia	Osteoscute	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.6		−0.2	
BG10	'Thalassemys' moseri	Ple.	Plesiochelyidae	Chelonia	Osteoscute	Chassiron	Lower Tithonian	Gigas	Gravesiana	21.9		−0.5	
BG25	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.3	20.0		
BG20	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.7	18.3		
BG28	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.2	20.4		
BG44	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Crayssac	Lower Tithonian	Gigas	Gravesiana	22.8	9.1		
BG05	Semionotidae	Sem.	Semionotidae	Osteichthyes	Tooth	Crayssac	Lower Tithonian	Gigas	Gravesiana	22.6	9.9		
BG23	Semionotidae	Sem.	Semionotidae	Osteichthyes	Tooth	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.3	20.0		

BG24	Osteichthyes	Ost.	Osteichthyes indet.	Osteichthyes	Scale	Crayssac	Lower Tithonian	Gigas	Gravesiana	19.7	22.6		
BG21	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Osteoderm	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.2			
BG22	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Tooth	Crayssac	Lower Tithonian	Gigas	Gravesiana	21.7			
BG31	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Osteoderm	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.5			
BG34	Chelonia	Che.	Chelonia indet.	Chelonia	Osteoscute	Crayssac	Lower Tithonian	Gigas	Gravesiana	20.3		−1.8	
BG67	*Gyrodus circularis*	Gyr.	Gyrodontidae	Osteichthyes	Scale	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	19.9	21.8		22.9
BG72	*Lepidotes maximus*	Lep.	Semionotidae	Osteichthyes	Tooth	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	21.0	16.9		18.2
BG68	*Lepidotes maximus*	Lep.	Semionotidae	Osteichthyes	Scale	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	20.8	17.8		19.0
BG62	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Osteoderm	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	21.3			
BG63	*Steneosaurus* sp.	Ste.	Teleosauridae	Crocodylia	Tooth	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	21.0			
BG65	Plesiochelyidae	Ple.	Plesiochelyidae	Chelonia	Osteoscute	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	21.4		−0.7	
BG64	'Thalassamydidae'	'Tha.'	'Thalassamydidae'	Chelonia	Osteoscute	Solnhofen	Lower Tithonian	Hybonotum	Gravesiana	19.2		−2.9	
BG48	Pycnodontiformes	Pyc.	Pycnodontiformes indet.	Osteichthyes	Tooth	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	20.8	17.8		
BG49	Pycnodontiformes	Pyc.	Pycnodontiformes indet.	Osteichthyes	Tooth	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	20.2	20.4		
BG45	Pycnodontiformes	Pyc.	Pycnodontiformes indet.	Osteichthyes	Teeth	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	20.2	20.4		
BG70	*Lepidotes* sp.	Lep.	Semionotidae	Osteichthyes	Scale	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	20.3	20.0		
BG47	Osteichthyes	Ost.	Osteichthyes indet.	Osteichthyes	Tooth	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	19.7	22.6		
BG46	Osteichthyes	Ost.	Osteichthyes indet.	Osteichthyes	Scales	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	22.3	11.2		
BG71	*Idiochelys fitzingeri*	Idi.	'Thalassemydidae'	Chelonia	Osteoscute	Cerin	Upper Kimmeridgian–Lower Tithonian	Beckeri–Hybonotum	Irius–Gigas	19.5		−2.6	

[a] Water temperatures calculated using Kolodny et al.'s (1983) equation: T (°C)$=113.4−4.38(\delta^{18}O_p−\delta^{18}O_w)$ with a $\delta^{18}O_w$ of −1‰.

[b] $\delta^{18}O_w$ calculated with the $\delta^{18}O_p$ of turtles by using Barrick et al.'s (1999) equation: $\delta^{18}O_w$ (‰ SMOW)$=1.01\delta^{18}O_p−22.3$.

[c] Water temperatures calculated using Kolodny et al.'s (1983) equation and with $\delta^{18}O_w$ derived from the $\delta^{18}O_p$ of plesiochelyid turtles. (a) and (b): temperatures calculated using the $\delta^{18}O_w$ inferred from turtle samples BG16 and BG10, respectively.

[d] BG33 and BG50 were sampled from the same *Steneosaurus* specimen (collection no. CNJ78).

North Atlantic, whereas Crayssac was possibly linked to the Mediterranean Tethys.

Cerin (Upper Kimmeridgian–Lower Tithonian, Ain, France) corresponds to a back-insular complex lagoon (Bernier et al., 1982). Canjuers (Lower Tithonian, Var, France) corresponds to a back-coral reef lagoon (Atrops, 1994; Roman et al., 1994). Solnhofen (Lower Tithonian, Solnhofen sensu lato, i.e., sites from the Solnhofen area, Bavaria, Germany) corresponds to back-coral reef lagoons, with higher marine influences than in Canjuers (Barthel et al., 1990). Crayssac (Lower Tithonian, Lot, France) was a coastal mudflat (Mazin et al., 1995). Chassiron (Lower Tithonian, Oléron island, Charente–Maritime, France) was a relatively open shallow marine environment (Hantzpergue et al., 2004).

3. Taxa and purported ecology

The analyzed taxa are exclusively aquatic or semiaquatic (amphibious) vertebrates: fish, turtles, and crocodilians from genera or families that were reported at most studied sites (Table 1).

The fish remains (Osteichthyes, Actinopterygii) belong to the Pycnodontiformes (Gyrodontidae, Pycnodontidae, and Pycnodontiformes indet.) and Semionotidae. These are durophagous forms (hard-prey feeders), considered to have lived in reef environments and shallow marine bottoms rich in shells (Wenz et al., 1994), although the semionotid *Lepidotes* is known to be highly euryhaline (Kriwet, 2000).

The marine crocodilian *Steneosaurus* (Thalattosuchia, Teleosauridae) is a piscivorous crocodilian, supposed to be an inhabitant of the shelf sea but probably capable of incursions into the open sea (Buffetaut, 1982; Hua, 1997). At Solnhofen and Canjuers, the occurrence of *Steneosaurus* is interpreted as that of a crocodilian living around the coral reefs before being carried away into the lagoon through passes during storms (Barthel et al., 1990; Roman et al., 1994).

Two families of turtles are documented: the Plesiochelyidae and the 'Thalassemydidae.' The systematic validity of the latter is dubious; it could be a junior synonym of Plesiochelyidae (Gaffney and Meylan, 1988; de Broin, 1994; Lapparent de Broin et al., 1996). These turtles are considered amphibious based on their skull and carapace (de Broin, 1994; Buffetaut, 1994). Their depositional environment is commonly shallow marine waters, but they were not anatomically adapted to a pelagic lifestyle: they had limbs with enlarged autopods but that were not modified into paddles, as encountered later in the chelonioid sea turtles (de Broin, 1994; Buffetaut, 1994). Only the 'Thalassemydidae' occur generally in the protected environments where lithographic limestones were deposited, whereas the Plesiochelyidae are usually found in more open marine environments (de Broin, 1994). An exception is Solnhofen, where the plesiochelyid *Plesiochelys* has been reported (Barthel et al., 1990), as well as some indeterminate plesiochelyid remains, including a specimen analyzed in this study (BG65). Although the supposed aquatic environment of these turtles is still questioned, from fresh continental to coastal marine waters (de Broin, 1994; Buffetaut, 1994), they are commonly regarded as coastal marine inhabitants (Bardet, 1995).

4. Sample collection, analytical techniques, and diagenetic alterations

The studied vertebrate fossil samples come from five well-dated localities based on ammonite zones from the Upper Kimmeridgian to the Lower Tithonian (Table 1). Specimens were collected from private collections (Crayssac, Chassiron), institutional collections (Cerin, Canjuers, Solnhofen), and excavations (Crayssac, Chassiron). Forty-three samples were analyzed: they include twenty-seven fish, seven turtles, and nine crocodilians (Table 1). The phosphatic biogenic remains include fish teeth and ganoid scales, turtle osteoscutes, and crocodilian teeth and osteoderms (osteoscutes and osteoderms are mineralized dermal bony plates). Highly mineralized tissues such as tooth enamel and ganoine layers of scales (=stratified enamel) were preferentially analyzed to avoid diagenetic alteration. In the same way, only the cortical zones of turtle and crocodilian dermal bony plates were selected for oxygen isotope analysis.

Measurements of oxygen isotope ratios in apatite start with isolating PO_4^{3-} using acid dissolution and anion exchange resin, according to a protocol derived from the original method published by Crowson et al.

(1991) and slightly modified by Lécuyer et al. (1993). Silver phosphate is quantitatively precipitated in a thermostatic bath set at a temperature of 70 °C. After filtration, washing with double deionized water, and drying at 50 °C, 15 mg of Ag_3PO_4 is mixed with 0.8 mg of pure powder graphite. $^{18}O/^{16}O$ ratios are basically measured by reducing silver phosphates to CO_2 using graphite reagent (O'Neil et al., 1994; Lécuyer et al., 1998). Samples are weighed into tin reaction capsules and loaded into quartz tubes and degassed for 30 min at 80 °C in vacuum. Each sample was heated at 1100 °C for 1 min to promote the redox reaction. The CO_2 produced during this reaction 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 Finnigan DeltaE™ mass spectrometer at the Laboratory UMR CNRS 5125 'PEPS' at the University of Claude Bernard Lyon 1. Isotopic compositions are quoted in the standard δ

notation relative to V-SMOW. Silver phosphate precipitated from standard NBS120c (natural Miocene phosphorite from Florida) was repeatedly analyzed ($\delta^{18}O=21.72\pm0.14$; $n=20$) along with the silver phosphate samples derived from the Late Jurassic vertebrates from western Europe.

We cannot exclude the possibility that some processes of diagenetic alteration could have disturbed the pristine oxygen isotope compositions of studied phosphatic vertebrate remains. Well-preserved and unbroken teeth were systematically selected for the isotopic measurements of enamel. Osteoscutes and osteoderms from turtles and crocodilians constitute highly mineralized apatites that are less sensitive to postdepositional isotopic exchange than other porous bones. Based on the phosphate chemical yields measured during the wet chemistry procedure, clustered P_2O_5 contents from 35% to 40% indicate that the original stoichiometry of studied Late Jurassic bio-
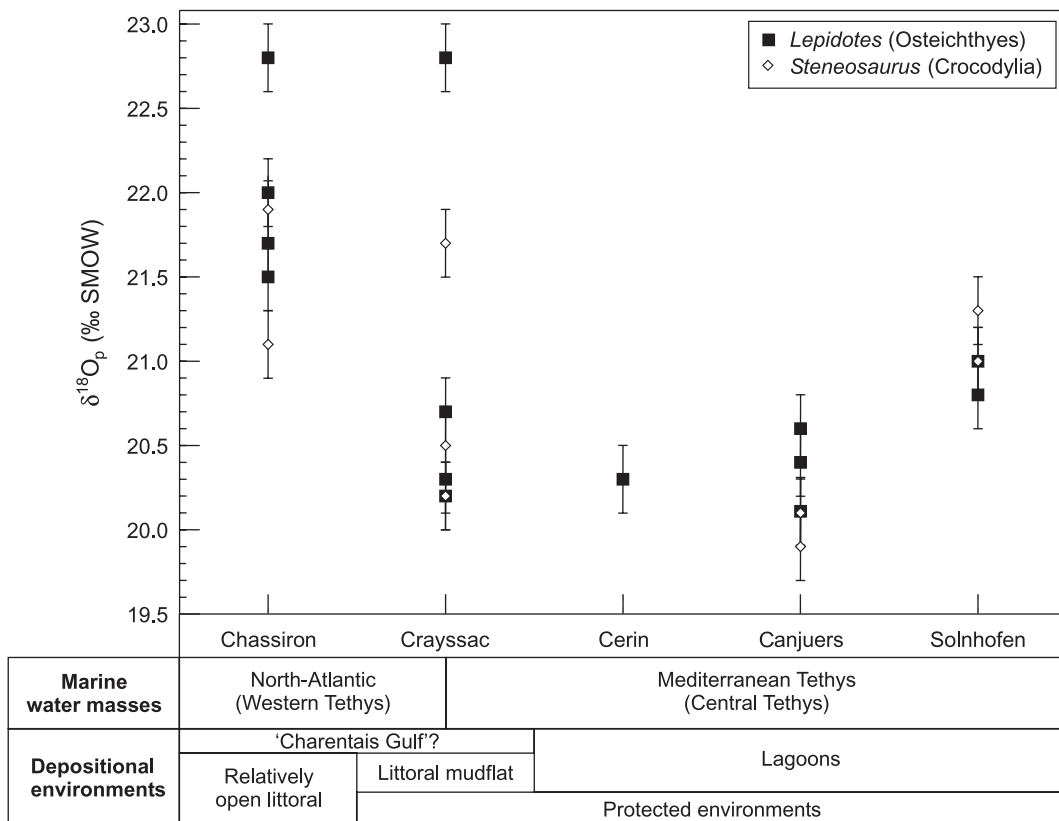

Fig. 2. Comparison of $\delta^{18}O_p$ values of Late Jurassic vertebrate genera sampled from the different localities. Water masses and depositional environments are also indicated for each studied site from western Europe.

genic apatites was preserved in the limestone deposits. Only sample BG05 was excluded from the dataset because its low silver phosphate chemical recovery of

60% can be related to a replacement of apatite by calcium carbonate and metaloxides. Moreover, the oxygen isotope compositions of fish teeth from the
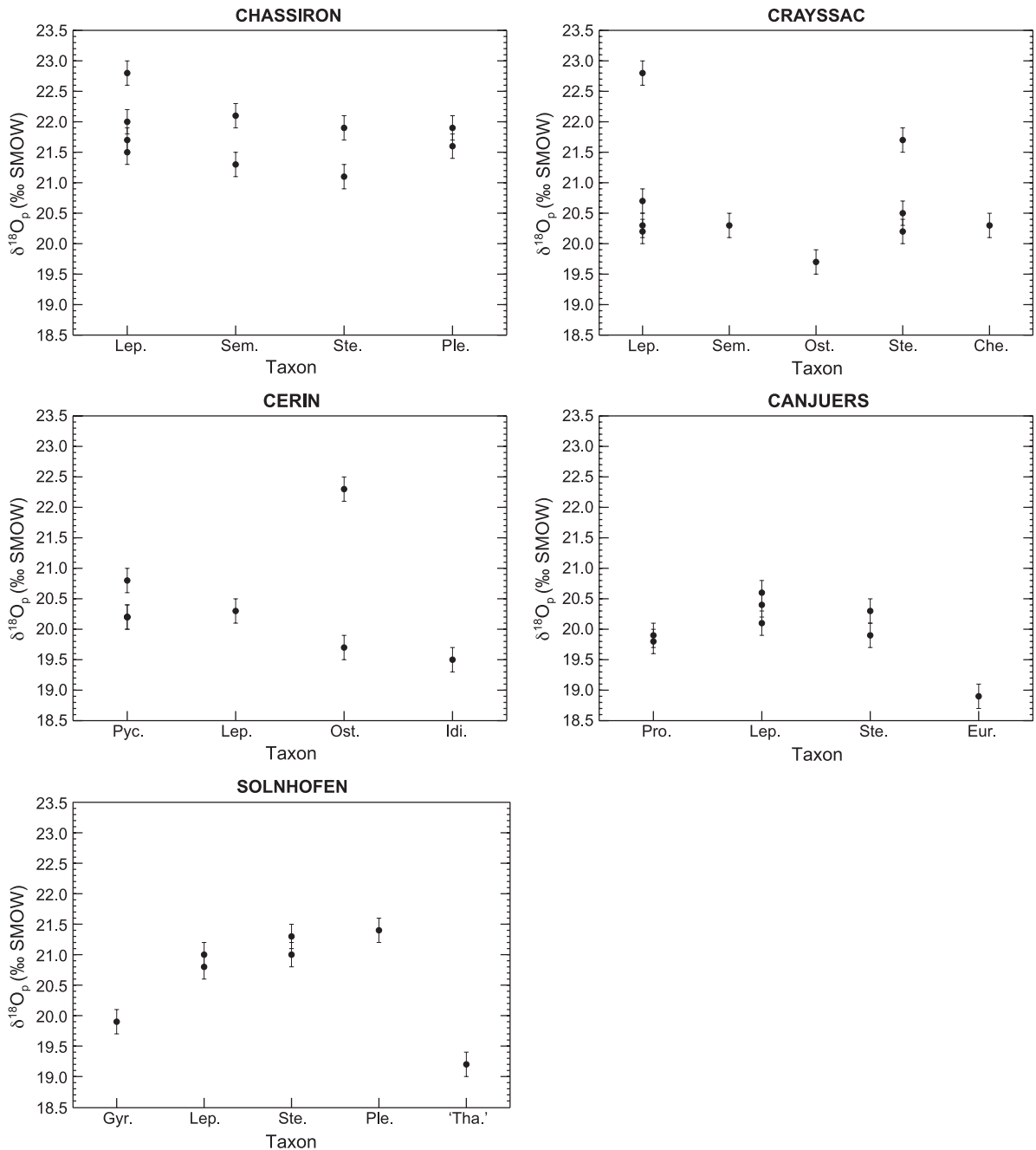

Fig. 3. $\delta^{18}O_p$ values of various Late Jurassic vertebrate taxa of western Europe from the site of Chassiron and from the four lithographic limestone sites of Crayssac, Cerin, Canjuers, and Solnhofen (see Table 1 for abbreviations of taxa).

relatively open coastal environment of Chassiron match well the oxygen isotope compositions of fish teeth from the Late Jurassic (Lécuyer et al., 2003b) or Early Cretaceous (Pucéat et al., 2003) of France, for which REE contents or $\delta^{18}O$ values of apatite carbonate suggest that most samples escaped diagenetic alteration processes.

5. Results

The $\delta^{18}O$ values (‰ SMOW) measured in phosphates from Late Jurassic biogenic apatites (fish, turtles, and crocodilians) of west European coastal marine environments are reported in Table 1. Sample BG05 was excluded from the dataset because of evidence of diagenetic alteration (see Sample Collection, Analytical Techniques, and Diagenetic Alterations). These Late Jurassic vertebrates have a wide range (4‰) of $\delta^{18}O$ values, from 18.9‰ to 22.8‰. To compare the five sampling sites, the $\delta^{18}O$ values of ubiquitous genera, such as *Lepidotes* and *Steneosaurus*, are illustrated in Fig. 2 according to marine water masses, palaeogeographic connections, and depositional environments. Samples from the four lithographic

limestone sites, which correspond to protected environments (Cerin, Solnhofen, Crayssac, and Canjuers), have a mean $\delta^{18}O$ value of 20.4±0.8‰, significantly lower than that of Chassiron (relatively open littoral), which has a mean $\delta^{18}O$ value of 21.8±0.5‰. This difference is well supported in comparing the $\delta^{18}O$ values from similar genera, reaching about 1‰. In the two lagoonal environments of the Mediterranean Tethys domain, Solnhofen samples have $\delta^{18}O$ values about 0.5–1‰ higher than those from Canjuers.

The $\delta^{18}O$ values of various taxa from the five studied sites are illustrated in Fig. 3. The $\delta^{18}O$ values of fish from the lithographic limestone sites include the highest values of analyzed vertebrates and are highly variable (especially in Cerin and Crayssac), ranging from 19.7‰ to 22.8‰, with a mean value of 20.8±0.9‰. This large variability is also observed at the genus level for *Lepidotes* (20.7±0.8‰), especially at Crayssac (20.2–22.8‰). In Chassiron, the $\delta^{18}O$ values of *Lepidotes* are also highly variable (21.5–22.8‰). The Pycnodontiformes from the lithographic limestones have rather constant $\delta^{18}O$ values (20.1±0.4‰), slightly lower in Solnhofen and Canjuers, or equivalent in Cerin to *Lepidotes*. The marine crocodilian *Steneosaurus* has $\delta^{18}O$ values close to the

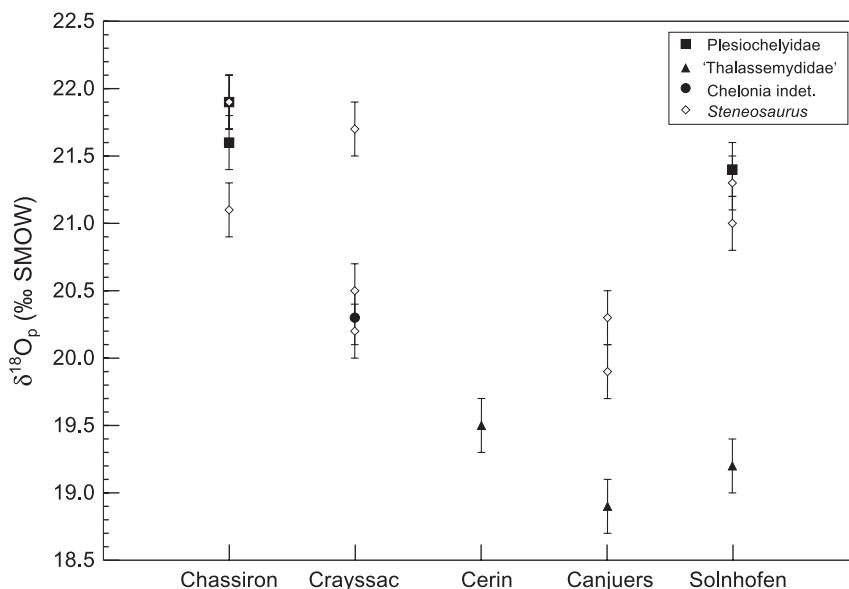
Fig. 4. Comparison of the $\delta^{18}O_p$ values between the crocodilian *Steneosaurus* and the turtle families for all the reported localities (from Late Jurassic remains of western Europe).

fish *Lepidotes*, ranging from 19.9‰ to 21.9‰ (see also Fig. 2), with a mean $\delta^{18}O$ value of 20.7±0.7‰ for the lithographic limestone sites. At Canjuers, osteoderm and tooth samples from the same specimen of *Steneosaurus* (BG33, BG50) have comparable $\delta^{18}O$ values of 19.9‰ and 20.3‰, respectively. At Crayssac, the tooth sample from *Steneosaurus* has a $\delta^{18}O$ value 1.2–1.5‰ higher than the two associated osteoderms, a feature already recognized in a living crocodilian from the Oubangui river (Central Africa) (Lécuyer et al., 2003a). The turtles of the Plesiochelyidae family have $\delta^{18}O$ values (21.4–21.9‰) close to *Lepidotes* and to *Steneosaurus*, as shown for Solnhofen and Chassiron (Figs. 3 and 4). Conversely, the sample of 'Thalassemydidae' from Solnhofen obviously differs from the 'isotopic faunal group' of '*Lepidotes*, *Steneosaurus*, and Plesiochelyidae,' with a $\delta^{18}O$ value of at least 1.5‰ lower, and a difference of 2.2‰ from the plesiochelyid specimen. The 'Thalassemydidae' have low and constant $\delta^{18}O$ phosphate values (18.9–19.5‰), and represent the lowest vertebrate $\delta^{18}O$ values among the related sites (Cerin, Solnhofen, and Canjuers) (Figs. 3 and 4). The indeterminate turtle from Crayssac has an intermediate $\delta^{18}O$ value of 20.3‰, close to *Steneosaurus* values (Fig. 4).

6. Discussion

6.1. Coastal water temperatures and vertebrate ecology

Temperatures of Late Jurassic marine waters (Table 1) were calculated by using the oxygen isotope fractionation equation determined by Kolodny et al. (1983), which gives results similar to those obtained with equations determined by Longinelli and Nuti (1973) and Lécuyer et al. (2003b):

$$T(°C) = 113.3 - 4.38(\delta^{18}O_p - \delta^{18}O_w) \qquad (1)$$

where T is the ambient water temperature (more exactly the average temperature of fish apatite deposition), and $\delta^{18}O_p$ and $\delta^{18}O_w$ are the oxygen isotope compositions of phosphate and water, respectively. The composition of water is classically assumed to be equal to $-1‰$ according to the hypothesis of a continental ice-free Earth (e.g., Shackleton and Kennett, 1975), although recently, Lécuyer et al. (2003b) recommended the use of a $\delta^{18}O$ of surface seawater equal to 0‰ because evaporation dominates precipitation at low latitudes. We also emphasize that the hypothesis of a constant seawater isotope composition for the various marine environments throughout the Upper Kimmeridgian–Lower Tithonian interval is an unlikely scenario.

Mean calculated marine temperatures that correspond to the various lithographic limestone deposits (including all fish) remain in a narrow range (~18.5–20.5 °C), consistent with their close latitudinal positions. These protected environments of shallow carbonate platforms are characterized by higher temperatures than those calculated for the relatively open coastal environment of Chassiron (~13 °C). The low mean temperature of seawater at Chassiron could be interpreted as an influence of cooler waters from the opening North Atlantic. The close $\delta^{18}O$ values between Crayssac and the other lithographic limestone sites (Fig. 2) are consistent with the recent Early Tithonian palaeogeographical map (Thierry, 2000; Thierry et al., 2000) (Fig. 1). It shows that Crayssac was probably fed both by the North Atlantic Ocean and the Mediterranean Tethys waters, a scenario at variance with the hypothesis of the 'Charentais Gulf' (Delfaud and Gottis, 1966; Hantzpergue and Lafaurie, 1994). In the Mediterranean Tethys domain, although Canjuers and Solnhofen are relatively similar back-coral reef lagoons, they present a slight difference in marine temperatures. The mean marine temperatures derived from Pycnodontiformes and *Lepidotes* $\delta^{18}O$ values at Canjuers (20.6±1.5 °C) are higher than in Solnhofen (18.8±2.6 °C). Nevertheless, the $\delta^{18}O$ values of Pycnodontiformes from these two sites resemble each other, highlighting that the difference is due to *Lepidotes* from Solnhofen, which lived either in cooler waters or in more marine waters than in Canjuers. This behaviour was likely governed by its relative tolerance to water temperature and salinity.

The protected environments that deposited the lithographic limestones are characterized by an important range of apparent marine temperatures (9.1–22.6 °C), but the mean temperatures are quite uniform and high (~18.5–20.5 °C). The explanation of this variability lies in fish samples that record the

lowest isotopic marine temperatures. The relatively homogeneous temperatures documented at Canjuers (18.7–22.2 °C; 20.6±1.5 °C) and at Solnhofen (16.9–21.8 °C; 18.8±2.6 °C) are consistent with the studied fish (Pycnodontiformes and *Lepidotes*), whose living environment is supposed to be restricted to the coral reef system. Conversely, large temperature ranges are observed at Cerin (11.2–22.6 °C, 18.7±4 °C) and at Crayssac (9.1–22.6 °C; 18.4±4.8 °C), only because of one analyzed fish sample in each site (BG46 and BG44, respectively). These observations suggest the presence of beached fish that originated from offshore deeper and cooler waters. The Pycnodontiformes from the lithographic limestones have comparable $\delta^{18}O$ values (20.1±0.4‰), constituting a reliable proxy of the temperature range of shallow coastal marine waters (18–22 °C). This palaeotemperature range of sea surface is consistent with those derived from belemnites for the Late Jurassic of western Europe (Gröcke et al., 2003). However, on the basis of a $\delta^{18}O$ of seawater set at −1‰, the calculated isotopic temperatures inferred from fish are rather low, considering the tropical palaeolatitudes of studied sites. They are barely compatible with the presence of corals (in Solnhofen and Canjuers), which are interpreted as indicators of relatively warm waters (~20–30 °C; e.g., Barthel et al., 1990). On the other hand, they may be considered high enough to accommodate the occurrence of crocodilians if we agreed on extant forms that require a minimum mean air temperature of ~5.5 °C for the coldest month, corresponding to an annual mean air temperature of at least ~14 °C (Markwick, 1998).

According to their quite similar oxygen isotope compositions, fish (except beached fish), the crocodilian *Steneosaurus*, and the plesiochelyid turtles were inhabitants of these coastal marine environments.

6.2. The dichotomy of turtle aquatic environments and the improvement of seawater palaeotemperature estimates

Oxygen isotope compositions of modern aquatic turtles are directly related to ambient water compositions (Barrick et al., 1999) according to the following equation:

$$\delta^{18}O_w = 1.01\delta^{18}O_p - 22.3 \qquad (2)$$

where $\delta^{18}O_w$ and $\delta^{18}O_p$ are the oxygen isotope compositions of water and phosphate, respectively. The use of Eq. (2) suggests that Plesiochelyidae and 'Thalassemydidae' lived in aquatic environments of contrasting oxygen isotope compositions, a discrimination clearly illustrated at Solnhofen where the two turtle families coexisted (Fig. 5). The $\delta^{18}O$ values of water calculated from Plesiochelyidae range from −0.7‰ to −0.2‰ (Table 1; Fig. 5), indicating a marine environment. This was already suggested from their usual coastal marine depositional environments (de Broin, 1994), but it could have been due to a taphonomical bias. The $\delta^{18}O$ values of ambient waters derived from 'Thalassemydidae' are between −3.2‰ and −2.6‰ (Table 1; Fig. 5). These oxygen isotope compositions are compatible with the compositions of freshwaters or brackish waters at low latitude and altitude (see e.g., Bowen and Wilkinson, 2002). The 'oxygen isotopic geological noise' has been quantified for recent fish teeth in the range 0.6–1.1‰ according to Venneman et al. (2001), and Pucéat et al. (2003) observed an envelope of ±0.8‰ around the $\delta^{18}O$ tendency Cretaceous curve. This natural 'noise' is significantly lower than the average isotopic difference documented for the studied samples of Plesiochelyidae and 'Thalassemydidae.' Therefore, we consider that the isotopic signal is contrasted enough to propose two different environmental waters: a marine water for Plesiochelyidae and a freshwater or brackish water for 'Thalassemydidae'. This ecological difference was not deciphered from the quite similar anatomy of these two turtle families (Gaffney and Meylan, 1988; de Broin, 1994; Lapparent de Broin et al., 1996). The recovered 'Thalassemydidae' from the lithographic limestones are well-preserved, subcomplete, articulated, and not water-worn specimens (de Broin, 1994; Buffetaut, 1994), suggesting a restricted transport before deposition.

Furthermore, the $\delta^{18}O$ values of ambient waters derived from 'Thalassemydidae' indicate that the coastal environments of Solnhofen, Cerin, and Canjuers were somewhat supplied by freshwater, whereas terrigenous sediments are scarce in Solnhofen (Barthel et al., 1990) and not mentioned at Cerin and Canjuers. A freshwater supply matches well with the presence of common terrestrial vertebrates such as the Sphenodontidae (Lepidosauria) in these three sites, the
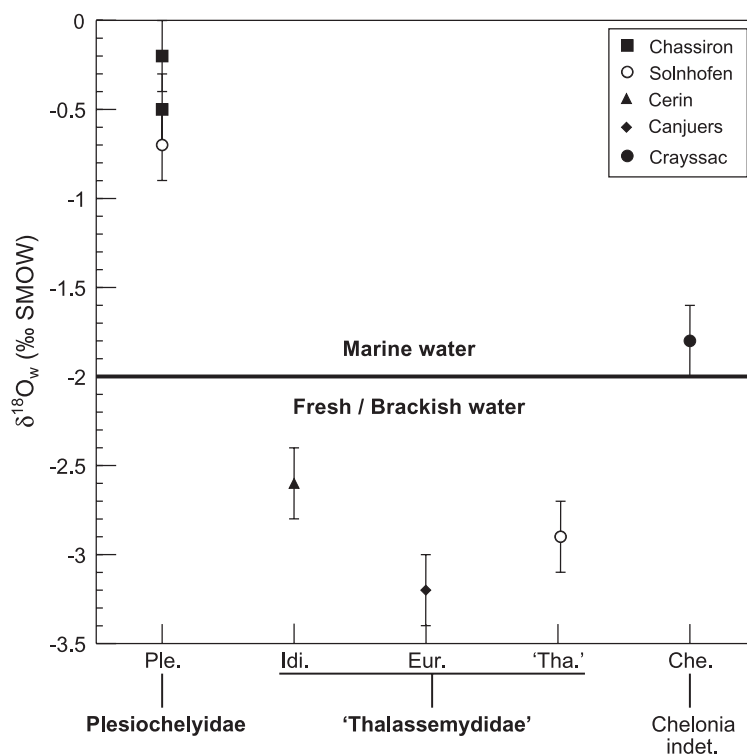
Fig. 5. Determination of the aquatic environment of turtles from the Late Jurassic of western Europe. The δ^{18}O values of ambient waters were calculated from the $\delta^{18}O_p$ of turtles using Barrick et al.'s (1999) equation: $\delta^{18}O_w$ (‰ SMOW)=$1.01\delta^{18}O_p-22.3$ (see Table 1 for abbreviations of taxa).

Atoposauridae (Crocodylia) in Cerin and Solnhofen, or the theropod dinosaur *Compsognathus* in Canjuers and Solnhofen (Buffetaut, 1994; Billon-Bruyat, 2003). It is also consistent with the presence of insects in Solnhofen, which are most dependent on a freshwater habitat for the larval stages of their life cycle (Barthel et al., 1990).

Seawater palaeotemperature estimates may be refined by using the calculated δ^{18}O values of seawater from the plesiochelyids to solve Kolodny et al.'s (1983) equation. Combining fish and turtle δ^{18}O values provides an improved picture of temperatures and isotopic compositions (and indirectly salinity) of water masses. Compared to the classical hypothesis of a δ^{18}O seawater=-1‰ assumed for Mesozoic times (ice-free Earth), computed temperatures in this study are found from 1 to 3.5 °C higher (1 °C at Solnhofen and 2–3.5 °C at Chassiron; Table 1), and are more compatible with the low palaeolatitudes of western Europe at the Jurassic/Cretaceous boundary.

6.3. Marine turtles as early as the Late Jurassic?

A surprising result obtained in this study is the marine 'isotopic signature' of plesiochelyid turtles. The oxygen isotope composition of phosphate of ectotherms mainly depends on temperature and isotopic composition of drinking water (see Introduction). Plesiochelyids certainly did not drunk marine water except during feeding, the aim of turtles in the marine environment being to excrete marine salts to maintain their osmoregulation. According to their clearly marine 'isotopic signature,' we propose that plesiochelyids mainly or exclusively depended on marine resources for feeding; hence, they represented an important member of coastal marine trophic webs, an ecological condition defining them as marine organisms (see e.g., Hémery, 2001 for the concept of marine birds).

Like several groups of tetrapods (e.g., crocodilians, cetaceans), turtles were secondarily adapted to
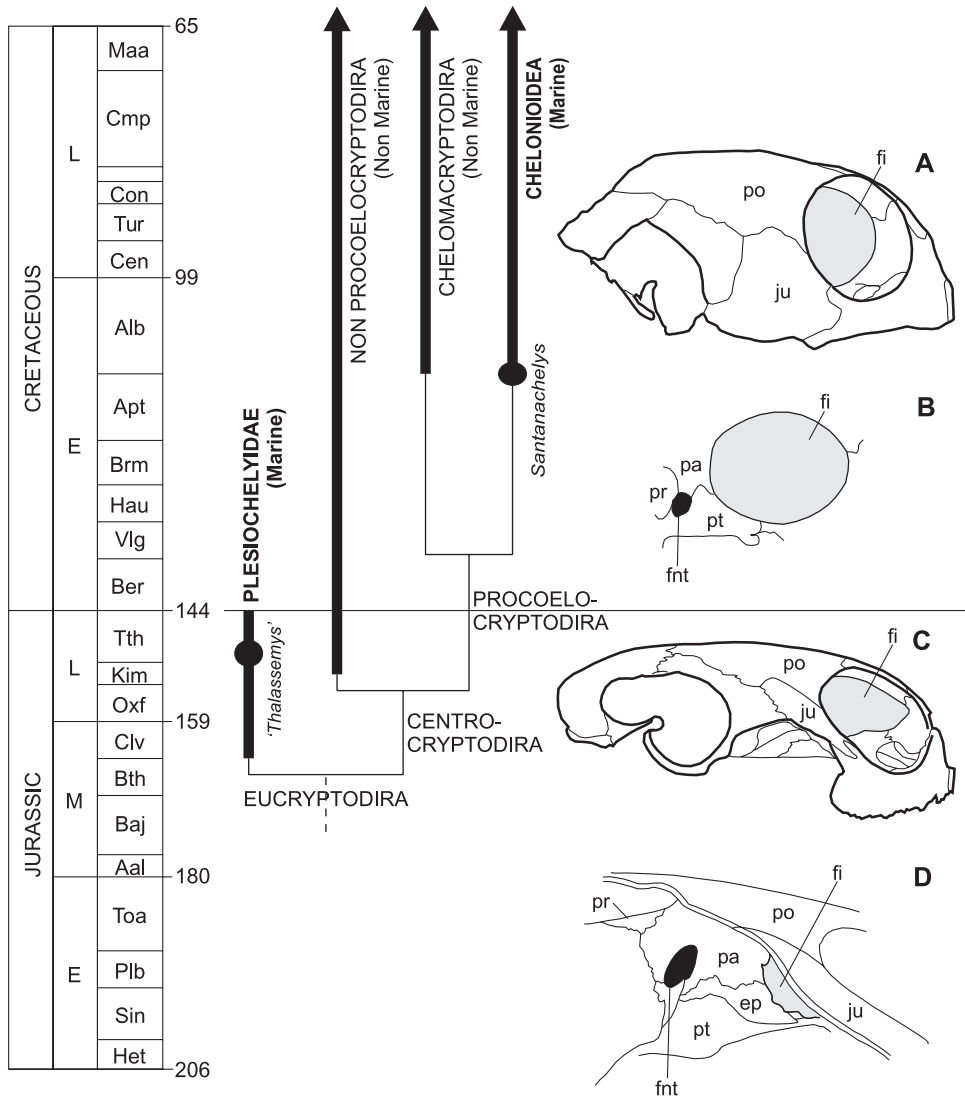
Fig. 6. Simplified calibrated phylogeny of the higher categories of eucryptodiran turtles and illustration of the foramen interorbitale in chelonioid and plesiochelyid turtles. Black bars indicate stratigraphic ranges of turtle groups; arrows indicate that the groups have extant relatives; nodes indicate the occurrence of reported genera. (A) Skull of *Santanachelys* (Chelonioidea) in right lateral view and (B) the right ethmoid region of this skull; (C) skull of '*Thalassemys*' (Plesiochelyidae, from the site of Chassiron) in right lateral view and (D) the 'right' (reversed from the left) ethmoid region of this skull, with a part of the braincase wall. Abbreviations: ep, epipterygoid; fi, foramen interorbitale; fnt, foramen nervi trigemini; ju, jugal; pa, parietal; po, postorbital; pr, pro-otic; pt, pterygoid. Only the ventral vertical plate of the parietal (dermal roofing bone principally formed by a dorsal plate) or processus inferior parietalis is represented in (B) and (D). The posterior margin of the foramen interobitale is formed by the anterior margins of the processus inferior parietalis dorsally and of the epipterygoid (in '*Thalassemys*') or pterygoid (in *Santanachelys*) ventrally. (A) and (B) are adapted from Hirayama (1998); (C) and (D) adapted from Rieppel (1980). Phylogeny was modified from Gaffney and Meylan (1988) and Hirayama (1998). Stratigraphic ranges were from Benton (1993), Bardet (1995) and Hirayama (1998). Time scale was based on Gradstein et al. (1994). Numbers indicate geological age in millions of years.

life in the marine environment. Although these Late Jurassic turtles (Callovian–Tithonian) have been considered coastal marine inhabitants based on their usual depositional environments (de Broin, 1994; Bardet, 1995), they have never been recognized with certainty as marine turtles. The marine turtles sensu stricto are defined as a monophyletic group, the Chelonioidea (including fossil and extant sea turtles). They appeared after the plesiochelyids in the fossil record; their first occurrence is *Santanachelys*, a primitive chelonioid recently reported from the Late Aptian or Early Albian (Hirayama, 1998; Fig. 6).

Plesiochelyids and *Santanachelys* still have limbs with movable digits as in freshwater turtles (i.e., they were not totally modified into paddles as in later chelonioids). *Santanachelys* has large interorbital foramina, indicative of huge lachrymal glands surrounding the eyes (Fig. 6), which function as salt glands in chelonioids for excreting marine salts, a key adaptation to marine life (Hirayama, 1998). One of the diagnostic features of chelonioids is that the large foramen interorbitale is formed by a relatively narrow processus inferior parietalis, as narrow as the foramen nervi trigemini or absent (Gaffney, 1976, 1979; Hirayama, 1998; Fig. 6). Surprisingly, this processus inferior parietalis has been recognized in plesiochelyids as intermediate in size between those of chelonioids and those of other turtles (Gaffney, 1976; Fig. 6). Because plesiochelyids have quite large interorbital foramina, the presence of relatively important lachrymal salt glands can be inferred. This physiological adaptation to the marine environment deduced from the anatomy fits the marine oxygen isotope 'signature' of the osteoscutes. Hirayama (1998) concluded from the study of *Santanachelys* that the salt-excreting system and the occupation of the marine environment preceded the evolution of paddles in chelonioids. In the same way, the plesiochelyids lived in a marine environment without evolving paddles. According to the phylogeny of eucryptodiran turtles (Gaffney and Meylan, 1988; Hirayama, 1998), the plesiochelyids are considered the sister group of all other eucryptodires (i.e., a basal group compared to chelonioids) (Fig. 6). This phylogenetic dichotomy, combined with the marine character of plesiochelyids, supports a scenario in which eucryptodiran turtles were adapted twice independently to marine life. Although turtles have adapted several times to life in the marine domain (Bardet, 1995), the most ancient marine turtles known so far are the Late Jurassic plesiochelyids.

7. Conclusions

Following the objectives presented in the Introduction, we can conclude that:

(1) The oxygen isotope analysis of fish showed that coastal marine waters were thermally homogenous at the regional scale of western Europe during the Late Jurassic. The protected coastal marine environments are characterized by higher mean marine temperatures (~18.5–20.5 °C) than that calculated for Chassiron (~13 °C), more open and likely influenced by cooler waters from the opening North Atlantic.

(2) In the protected deposits, some fish samples record the lowest isotopic marine temperatures, suggesting the presence of beached fish that originated from offshore deeper and cooler waters. On the basis of their distribution of $\delta^{18}O$ values, fish (except beached fish), the crocodilian *Steneosaurus*, and plesiochelyid turtles are considered autochthonous fauna of the reported coastal marine environments. The 'thalassemyid' turtles have $\delta^{18}O$ values between −3.2‰ and −2.6‰, suggesting that they lived in fresh or at least in brackish waters that were likely present in the coastal environments of Cerin, Canjuers, and Solnhofen.

(3) Considering the marine $\delta^{18}O$ values of plesiochelyid turtles (−0.7‰ to −0.2‰), the combined oxygen isotope analysis of turtle and fish phosphate allowed us to refine estimates of isotopic compositions of water masses and temperatures in coastal marine environments. Estimates of isotopic temperatures increased by about 1 and 2–3.5 °C in Solnhofen and Chassiron, respectively.

(4) The Late Jurassic plesiochelyids can be considered both from oxygen isotope (marine 'isotopic signature') and cranial anatomy (presence of a salt-excreting system) data as the first turtles to

be secondarily adapted to the marine environment, several tens of million years before the chelonioids or 'sea turtles.'

Acknowledgments

References

Atrops, F., 1994. Présence d'ammonites du Tithonien inférieur dans les calcaires lithographiques de Canjuers (Var, France): conséquences stratigraphiques et paléogéographiques. Géobios, Mém. Spéc. 16, 137–146.

Bardet, N., 1995. Évolution et extinction des reptiles marins au cours du Mésozoïque. Palaeovertebrata 24, 177–283.

Barrick, R.E., Fischer, A.G., Showers, W.J., 1999. Oxygen isotopes from turtle bone: applications for terrestrial paleoclimates? Palaios 14, 186–191.

Barron, E.J., Peterson, W.H., 1989. Model simulation of the Cretaceous ocean circulation. Science 244, 684–686.

Barron, E.J., Harrison, C.G.A., Sloan, J.L., Hay, W.W., 1981. Paleogeography, 180 million years ago to the present. Eclogae Geol. Helv. 74, 443–470.

Barthel, K.W., Swinburne, N.H.M., Conway Morris, S., 1990. Solnhofen: a study in mesozoic palaeontology. Cambridge Univ. Press, Cambridge.

Benton, M.J., 1993. Reptilia. In: Benton, M.J. (Ed.), The Fossil Record, vol. 2. Chapman & Hall, London, pp. 681–715.

Bernier, P., Barale, G., Bourseau, J.-P., Buffetaut, E., Demathieu, G., Gaillard, C., Gall, J.-C., 1982. Trace nouvelle de locomotion de Chélonien et figures d'émersion associées dans les calcaires lithographiques de Cerin (Kimméridgien supérieur, Ain, France). Geobios 15, 447–467.

Billon-Bruyat, J.-P., 2003. Les écosystèmes margino-littoraux du Jurassique terminal et du Crétacé basal d'Europe occidentale: biodiversité, biogéochimie et l'événement biotique de la limite Jurassique/Crétacé. PhD thesis, Univ. Poitiers, France.

Bowen, G.J., Wilkinson, B., 2002. Spatial distribution of $\delta^{18}O$ in meteoric precipitation. Geology 30, 315–318.

Buffetaut, E., 1982. Radiation évolutive, paléoécologie et biogéographie des crocodiliens mésosuchiens. Mém. Soc. Géol. Fr. 142 (88 pp.).

Buffetaut, E., 1994. Tetrapods from the Late Jurassic and Early Cretaceous lithographic limestones of Europe: a comparative review. Géobios, Mém. Spéc. 16, 259–265.

Crowson, R.A., Showers, W.J., Wright, E.K., Hoering, T.C., 1991. A method for preparation of phosphate samples for oxygen isotope analysis. Anal. Chem. 63, 2397–2400.

de Broin, F., 1994. Données préliminaires sur les chéloniens du Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France). Géobios, Mém. Spéc. 16, 167–175.

Delfaud, J., Gottis, M., 1966. Sur quelques figures de sédimentation dans le Portlandien du Lot et sur leur cadre paléogéographique en Aquitaine septentrionale. Acta Soc. Linn. Bordeaux B7 103, 3–9.

Fourcade, E., Azema, J., Cecca, F., Dercourt, J., Guiraud, R., Sandulescu, M., Ricou, L.-E., Vrielynck, B., Cottereau, N., Petzold, M., 1993a. Late Tithonian (138 to 135 Ma). In: Dercourt, J., Ricou, L.-E., Vrielynck, B. (Eds.), Atlas tethys palaeoenvironmental maps, Explanatory Notes. Gauthier-Villars, Paris, pp. 113–134.

Fourcade, E., Azema, J., Cecca, F., Dercourt, J., Vrielynck, B., Bellion, Y., Sandulescu, M., Ricou, L.-E., 1993b. In: Dercourt, J., Ricou, L.-E., Vrielynck, B. (Eds.), Atlas Tethys Palaeoenvironmental Maps, BEICIP-FRANLAB, Rueil-Malmaison, Map Late Tithonian Palaeoenvironments (138 to 135 Ma).

Gaffney, E.S., 1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys*. Bull. Am. Mus. Nat. Hist. 157, 489–543.

Gaffney, E.S., 1979. Comparative cranial morphology of recent and fossil turtles. Bull. Am. Mus. Nat. Hist. 164, 65–375.

Gaffney, E.S., Meylan, P.A., 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.), The Phylogeny and Classification of the Tetrapods: Vol. 1. Amphibians, Reptiles, Birds, Systematics Association Special Volume, vol. 35A, pp. 157–219.

Gradstein, F.M., Agterberg, F.P., Ogg, J.G., Hardenbol, J., Veen van, P., Thierry, J., Huang, Z., 1994. A Mesozoic time scale. J. Geophys. Res. 99, 24051–24074.

Gröcke, D.R., Price, G.D., Ruffell, A.H., Mutterlose, J., Baraboshkin, E., 2003. Isotopic evidence for Late Jurassic–Early Cretaceous climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 202, 97–118.

Hantzpergue, P., Lafaurie, G., 1994. Les calcaires lithographiques du Tithonien quercynois: stratigraphie, paléogéographie et contexte biosédimentaire. Géobios, Mém. Spéc. 16, 237–243.

Hantzpergue, P., Boullier, A., Colin, J.-P., Abit, D., 2004. Nouveaux repères biostratigraphiques à Terebratulidés (Brachiopodes) dans le Tithonien inférieur ouest-européen. Geobios 37, 361–375.

Hémery, G., 2001. Biodiversity and adaptation of extant marine birds: an overview. In: Mazin, J.-M., Buffrénil, V. de (Eds.),

Secondary Adaptation of Tetrapods to Life in Water. Pfeil, München, pp. 119–139.

Hirayama, R., 1998. Oldest known sea turtle. Nature 392, 705–708.

Hua, S. 1997. Adaptation des crocodiliens mésosuchiens au milieu marin. PhD thesis, Pierre et Marie Curie Univ. Paris, France.

Hutchison, V.H., 1977. Thermoregulation. In: Harless, M., Morlock, H. (Eds.), Turtles, Perspectives and Research. John Wiley & Sons, New York, pp. 207–228.

Kolodny, Y., Luz, B., 1991. Oxygen isotopes in phosphates of fossil fish—Devonian to Recent. In: Taylor, H.P., O'Neil, J.R., Kaplan, I.R. (Eds.), Stable Isotope Geochemistry: A Tribute to Samuel Epstein, Geochem. Soc. Spec. Publ. 3, 105–119.

Kolodny, Y., Raab, M., 1988. Oxygen isotopes in phosphatic fish remains from Israel: paleothermometry of tropical Cretaceous and Tertiary shelf waters. Palaeogeogr. Palaeoclimatol. Palaeoecol. 64, 59–67.

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

Kolodny, Y., Luz, B., Sander, M., Clemens, W.A., 1996. Dinosaur bones: fossils or pseudomorphs? The pitfalls of physiology reconstruction from apatitic fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126, 161–171.

Kriwet, J., 2000. The fish fauna from the Guimarota mine. In: Martin, T., Krebs, B. (Eds.), Guimarota—A Jurassic Ecosystem. Pfeil, München, pp. 41–50.

Lapparent de Broin, F. de, Lange-Badré, B., Dutrieux, M., 1996. Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. Rev. Paléobiol. 15, 533–570.

Lécuyer, C., Grandjean, P., O'Neil, J.R., Capetta, H., Martineau, F., 1993. Thermal excursions in the ocean at the Cretaceous–Tertiary boundary (northern Morocco): the δ^{18}O record of phosphatic fish debris. Palaeogeogr. Palaeoclimatol. Palaeoecol. 105, 235–243.

Lécuyer, C., Grandjean, P., Emig, C.C., 1996. Determination of oxygen isotope fractionation between water and phosphate from living lingulids: potential application to palaeoenvironmental studies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126, 101–108.

Lécuyer, C., Grandjean, P., Barrat, J.-A., Emig, C.C., Nolvak, J., Paris, F., Robardet, M., 1998. δ^{18}O and REE contents of phosphatic brachiopods: a comparison between modern and Lower Paleozoic populations. Geochim. Cosmochim. Acta 62, 2429–2436.

Lécuyer, C., Grandjean, P., Mazin, J.-M., Buffrénil, V. de, 1999. Oxygen isotope compositions of reptile bones and teeth: a potential record of terrestrial and marine paleo-environments. In: Hoch, E., Brantsen, A.K. (Eds.), Secondary Adaptation to Life in Water. Copenhagen Univ., Geologisk Museum, Denmark, p. 33.

Lécuyer, C., Bogey, C., Garcia, J.-P., Grandjean, P., Barrat, J.-A., Floquet, M., Bardet, N., Pereda-Superbiola, X., 2003a. Stable isotope composition and rare earth element content of vertebrate remains from the Late Cretaceous of northern Spain (Laño): did the environmental record survive? Palaeogeogr. Palaeoclimatol. Palaeoecol. 193, 457–471.

Lécuyer, C., Picard, S., Garcia, J.-P., Sheppard, S.M.F., Grand-jean, P., Dromart, G., 2003b. Thermal evolution of Tethyan surface waters during the Middle–Late Jurassic: evidence from δ^{18}O values of marine fish teeth. Paleoceanography 18, 1076.

Longinelli, A., 1966. Ratios of oxygen-18: oxygen-16 in phosphate and carbonate from living and fossil marine organisms. Nature 211, 923–927.

Longinelli, A., 1996. Pre-Quaternary isotope palaeoclimatological and palaeoenvironmental studies: science or artifact? Chem. Geol. 129, 163–166.

Longinelli, A., Nuti, S., 1968. Oxygen isotope composition of phosphates from marine formations. Earth Planet. Sci. Lett. 5, 13–17.

Longinelli, A., Nuti, S., 1973. Revised phosphate–water isotopic temperature scale. Earth Planet. Sci. Lett. 19, 373–376.

Markwick, P.J., 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 137, 205–271.

Mazin, J.-M., Hantzpergue, P., Lafaurie, G., Vignaud, P., 1995. Des pistes de ptérosaures dans le Tithonien de Crayssac (Querçy, France). C. R. Acad. Sci., Paris IIa 321, 417–424.

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

Picard, S., Garcia, J.-P., Lécuyer, C., Sheppard, S.M.F., Cappetta, H., Emig, C.C., 1998. δ^{18}O values of coexisting brachiopods and fish: temperature differences and estimates of paleo-water depths. Geology 26, 975–978.

Pucéat, E., Lécuyer, C., Sheppard, S.M.F., Dromart, G., Reboulet, S., Grandjean, P., 2003. Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels. Paleoceanography 18, 1029–1040.

Rieppel, O., 1980. The skull of the Upper Jurassic cryptodire turtle Thalassemys, with a reconsideration of the chelonian braincase. Palaeontogr. Abt. A 171, 105–140.

Roman, J., Atrops, F., Arnaud, M., Barale, G., Barrat, J.-M., Boullier, A., de Broin, F., Gill, G.A., Michard, J.-G., Taquet, P., Wenz, S., 1994. Le gisement Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France): état actuel des connaissances. Géobios, Mém. Spéc. 16, 126–135.

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

Sharp, Z.D., Aturodel, V., Furrer, H., 2000. The effect of diagenesis on oxygen isotope ratios of biogenic phosphates. Am. J. Sci. 300, 222–237.

Stille, P., Steinmann, M., Riggs, S.R., 1996. Nd isotope evidence for the evolution of the paleocurrents in the Atlantic and Tethys Oceans during the past 180 Ma. Earth Planet. Sci. Lett. 144, 9–19.

Stoskopf, M.K., Barrick, R.E., Showers, W.J., 2000. Oxygen isotope variability in bones of wild caught and constant temperature reared sub-adult American alligators. J. Therm. Biol. 26, 183–191.

Thierry, J., 2000. Early Tithonian (141–139 Ma). In: Crasquin, S. (Ed.), Atlas péri-téthys, palaeogeographical maps—explanatory notes. CCGM/CGMW, Paris, pp. 99–110.

Thierry, J., et al., 2000. Early Tithonian (141–139 Ma). In: Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.-P., Crasquin, S., Sandulescu, M. (Eds.), Atlas Péri-Téthys, Palaeogeographical Maps, Map, vol. 11. CCGM/CGMW, Paris.

Vennemann, T.W., Hegner, E., 1998. Oxygen, strontium, and neodymium isotope composition of fossil shark teeth as a proxy for the palaeoceanography and palaeoclimatology of the Miocene northern Alpine Paratethys. Palaeogeogr. Palaeoclimatol. Palaeoecol. 142, 107–121.

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

Wenz, S., Bernier, P., Barale, G., Bourseau, J.-P., Buffetaut, E., Gaillard, C., Gall, J.-C., 1994. L'ichthyofaune des calcaires lithographiques du Kimméridgien supérieur de Cerin (Ain, France). Géobios, Mém. Spéc. 16, 61–70.