



Strontium isotopes and the long-term residency of thalattosuchians in the freshwater environment

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Abstract.—Thalattosuchians are crocodylomorphs mainly known from marine strata of Early Jurassic to Early Cretaceous age. They represent the earliest crocodylomorph radiation to an aquatic habitat and their evolutionary history offers very few records from freshwater settings. Here, we report several exquisitely preserved thalattosuchian skulls attributed to a derived teleosaurid from a pedogenic horizon located at the base of a fluvial series of alternating silts and sandstones of the Phu Kradung Formation (Upper Jurassic) of northeastern Thailand. Using laser ablation multicollector inductively coupled mass spectrometry (MC-ICP-MS) on tooth enamel and dentine, we measured isotopic ratios of strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) to test the habitat of these teleosaurids. In addition, Sr concentrations of the dental tissues were estimated from the calibrated signal intensities of the Sr isotope measurements. The dataset includes bioapatite (teeth or scales) of eight terrestrial and five aquatic vertebrates. Theropods exhibit lower Sr concentrations both in enamel and dentine compared to others groups, a pattern in accordance with the calcium biopurification process, which predicts that Sr concentrations in the body of vertebrates decrease up the trophic chain. It also excludes the possibility that diagenesis has completely overprinted the Sr isotope compositions of the fossil assemblage, which exhibits a homogeneous $^{87}\text{Sr}/^{86}\text{Sr}$ signature above the Late Jurassic seawater value. Values for teleosaurid teeth are in the range of other values for vertebrates in the continental assemblage and imply that these crocodylomorphs did not migrate between freshwater and marine habitats at least in the time constraint of the mineralizing tooth. This result represents the first demonstration that a population of teleosaurids was established for a prolonged time in a freshwater environment. Whether the ability of teleosaurids to inhabit freshwater habitats is a secondary adaptation or whether it is plesiomorphic and inherited from freshwater ancestors is discussed.

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Introduction

The name *Thalattosuchia* translates as 'marine crocodiles' and refers to their frequent occurrence in near-shore and pelagic deposits of Early Jurassic to Early Cretaceous age (e.g., Martin et al. 2014). *Thalattosuchia* comprise *Pelagosaurus typus* representing a monospecific group (Pierce and Benton 2006), the monophyletic *Metriorhynchoidea* (Young and Andrade 2009) and *Teleosauridae*, a clade of uncertain monophyletic content according to recent hypotheses (Mueller-Töwe 2005;

Jouve 2009; Young and Andrade 2009). The *Metriorhynchoidea* exhibit a number of morphological and physiological specializations (paddle-like limbs, salt-excreting gland, a fluked tail) that are assumed to have been associated with a pelagic lifestyle (e.g., Hua and de Buffrénil 1996; Fernández and Gasparini 2008). On the other hand, *Pelagosaurus* and the *Teleosauridae*, although not exhibiting such derived features are nonetheless adapted to a highly specialized aquatic lifestyle as exhibited by the size contrast between forelimbs and hind limbs. Their general appearance is reminiscent

of that of modern gharials, their terrestrial locomotion was most probably restricted to crawling on sandy banks (Westphal 1962a). Teleosaurids occur in a variety of proximal deposits such as coastal or lagoonal sediments, therefore presumably in close proximity to emerged lands for laying eggs or basking. In addition, the teleosaurid *Machimosaurus hugii* has been reported from a brackish deposit in the lignite seam of Guimarota, Portugal (Krebs 1967, 1968) and this is probably also the case for some fragmentary remains of indeterminate teleosaurids from the Jurassic Khlong Min Formation of Peninsular Thailand (Buffetaut et al. 1994). More exceptional are the occurrences of teleosaurids in fully continental formations. This is the case for the Jurassic *Peipehsuchus teleorhinus* from the Ziliujing Formation of China (Young 1948).

Here, we document the unambiguous occurrence of a teleosaurid taxon in Late Jurassic freshwater deposits of northeastern Thailand (Fig. 1) providing a brief description and discussing its affinities. Then, we explore habitat preferences of these animals using strontium isotopes (Schmitz et al. 1997; Balter et al. 2008, 2012; Tütken et al. 2011) and discuss the adaptation of thalattosuchians to the freshwater environment.

Institutional abbreviations.—KS, collection numbers for fossils from Kalasin Province at Sirindhorn Museum, Sahatsakhan, Thailand; PRC, Palaeontological Research and Education Centre, Maha Sarakham University, Thailand

Methods

Geological setting.—The age of the Phu Kradung Formation is not precisely defined and has either been considered as Late Jurassic on the basis of vertebrate assemblages (Buffetaut et al. 2001; Buffetaut and Suteethorn 2007; Tong et al. 2009) or Early Cretaceous on the basis of detrital mineralogy and palynomorphs (Carter and Bristow 2003; Racey and Goodall 2009). Teleosaurids are unknown in Cretaceous deposits and if the presently described specimens are not an exception, their presence at Phu Noi may reject a Cretaceous age for this

locality. On the basis of freshwater sharks, a Late Jurassic age has been suggested for most of the Phu Kradung Formation (Cuny et al. 2014). The Phu Noi fossil site is located in the upper part of the Phu Kradung Formation but lies stratigraphically below most of the early Cretaceous fossiliferous localities of the Phu Phan Range (Liard and Martin 2011), therefore a Late Jurassic age for the Phu Noi locality is likely.

Two skulls (KS33-209 and PRC-8) were surface collected during prospecting work on the Phu Noi hill. Subsequently, excavation of a single silty pedogenic horizon (surface area approximately 20 m × 15 m) led to the discovery of several teleosaurid specimens (see description below). In this horizon, some dinosaur bones, ribs, and limbs bear on their external surface peculiar marks (Fig. 1) comparable in morphology to the rosettes described on sauropod bones from the Jurassic of Wyoming (Bader et al. 2009). Accordingly, the most likely trace makers are dermestid larvae in pupation chambers developing on decaying carcasses. This indicates that the fossiliferous horizon at Phu Noi was exposed under aerial conditions for extended periods of at least a few weeks, as implied by the development of necrophagous arthropods on the dinosaur carcasses. Gleyey structures (Fig. 1) indicative of temporarily waterlogged conditions are found at several horizons below and above the vertebrate-bearing horizon. This fossiliferous horizon is part of a thick sequence of alternating sandstone bars and silts, typical of floodplain deposits, which is thought to be indicative of a lake-dominated floodplain (Racey and Goodall 2009). Estimating a rough distance to the nearest coast is difficult, but according to paleogeographic reconstructions for the Late Jurassic, the Phu Noi locality was located far from the coast (>100 km?) when the Indochinese block was already connected to the South China block (Metcalf 2009).

Laser ablation.—All fossil teeth analyzed in this study originate from a single horizon of the Phu Noi excavation site (Fig. 1), part of the Phu Kradung Formation of northeastern Thailand. Fossil specimens include three teleosaurid teeth; four sauropod teeth; four theropod teeth; two *Lepisosteiformes* scales;

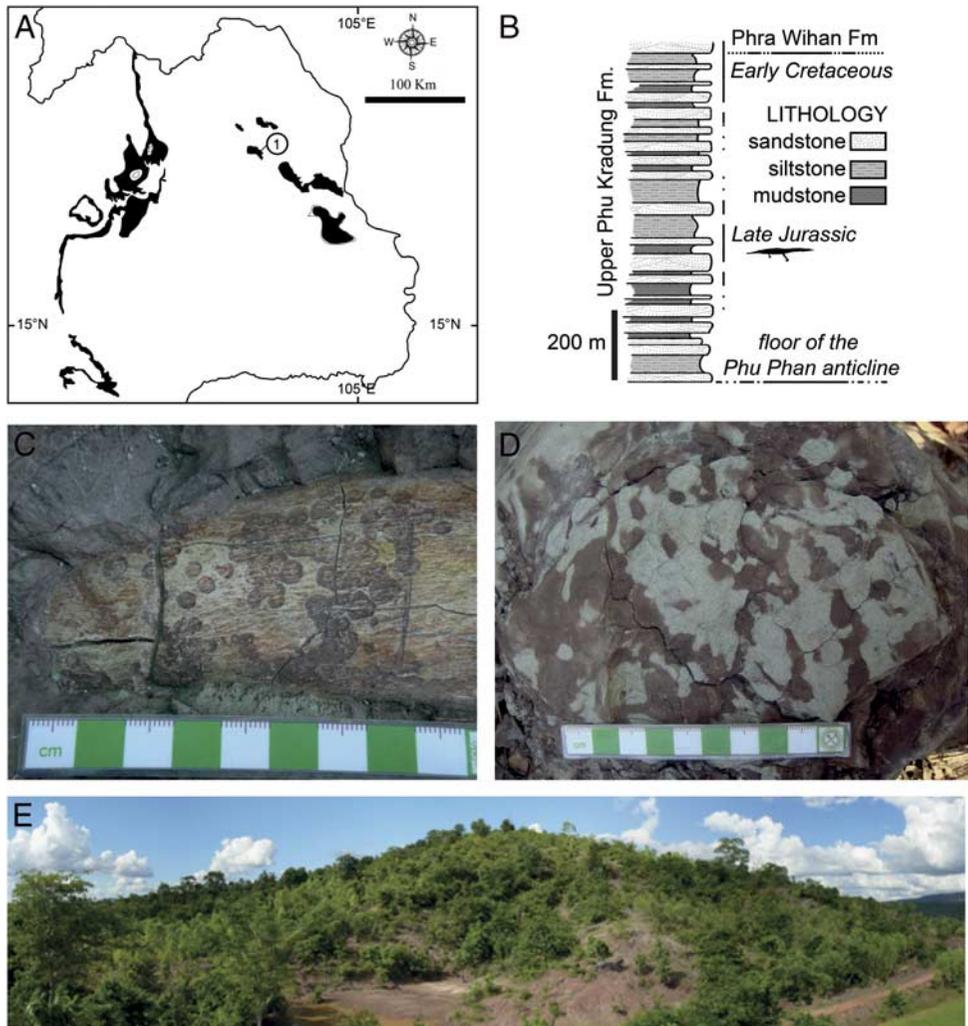


FIGURE 1. The geographic and geological context of the locality of Phu Noi. A, Geographic situation in northeastern Thailand with outcrops of the Phu Kradung Formation indicated in black. Number 1 refers to Phu Noi; B, Simplified stratigraphic framework; C, Traces fossils (rosettes) on the surface of a sauropod rib, indicating developmental activity of dermestid beetles; D, Gleyey structures part of a paleosol horizon; E, General view of the locality of Phu Noi, Thailand.

two *Hybodus* teeth and one turtle bone. Teeth were broken and fixed in epoxy resin before polishing so as to obtain a flat surface of the sectioned enamel-dentine junction. Sintered SRM-1400 (Bone Ash) served as a bracketing reference, correcting instrumental biases during isotopic measurements (Balter et al. 2008). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio was measured at the LGLTPE, ENS Lyon on a Nu instrument-500 HR multicollector-ICP-MS (Inductively Coupled Plasma – Mass Spectrometer) with an Excite laser ablation system (193 nm excimer, Photon

Machines/Cetac Analyte Teledyne). The standard SRM-1400 contains 249 $\mu\text{g}/\text{g}$ of strontium, which yields about 3 volts on mass ^{88}Sr for a laser power of 9 mJ with a spot diameter of 40 to 65 μm , a fluence of 15 J/cm^2 and a repetition rate of 30 Hz. The strontium concentration was evaluated using the total strontium voltage, which was set at the certified value of 249 $\mu\text{g}/\text{g}$ for the standard SRM-1400. Each sample was ablated at least three times across the dentine-enamel junction for teeth and across the ganoin-dentine junction

for ganoid scales of lepisosteids (supplementary material). The turtle bone was ablated at eight different locations. In order to test for changes in $^{87}\text{Sr}/^{86}\text{Sr}$ during the mineralization of the teleosaurid teeth, two teeth were sectioned along a base-apex axis and were ablated across the dentine-enamel junction at eight different locations (Supplementary Appendix). The crown height of each tooth is about 20 mm and teeth were selected from specimen PRC-239. Finally, a polished section of a belemnite from the Lower Jurassic strata of Beaujolais, France (Toarcian, Suan et al. 2013) was ablated in order to have a marine reference in the sample list. An aliquot of this belemnite sample was dissolved in concentrated nitric acid, purified through a strontium-specific resin (Sr-Spec Eichrom[®]) and analyzed for $^{87}\text{Sr}/^{86}\text{Sr}$ ratios at the LGLTPE, ENS Lyon on a Neptune Plus multicollector-ICP-MS (Thermo Scientific).

Sediments were not rich enough to yield sufficient Sr voltage using laser ablation. Therefore, about 400 mg of sediment was leached over three days in 1M HCl. The leachate was centrifuged and purified through a strontium-specific resin (Sr-Spec Eichrom[®]). The purified sample was then analyzed for $^{87}\text{Sr}/^{86}\text{Sr}$ ratios at the LGLTPE, ENS Lyon on a Neptune Plus multicollector-ICP-MS (Thermo Scientific).

Results

Systematic paleontology.—Superorder Crocodylomorpha Hay, 1930; Suborder Thalattosuchia Fraas, 1901; Family Teleosauridae Geoffroy Saint-Hilaire, 1825

(Fig. 2)

Referred material.—KS33-209, a skull with part of the mandible in occlusion lacking the rostrum (maxillary and mandibular), PRC-238, PRC-239, PRC-240, three complete skulls with mandibles in occlusion; PRC-8, right skull table and basicranium and associated osteoderms; PRC-9, a fragmented skull table.

Geographic occurrence.—Phu Noi, Phu Phan Range, Kham Muang district, Kalasin province, Thailand.

Geological provenance.—Upper part of the Phu Kradung Formation, Upper Jurassic (?Tithonian).

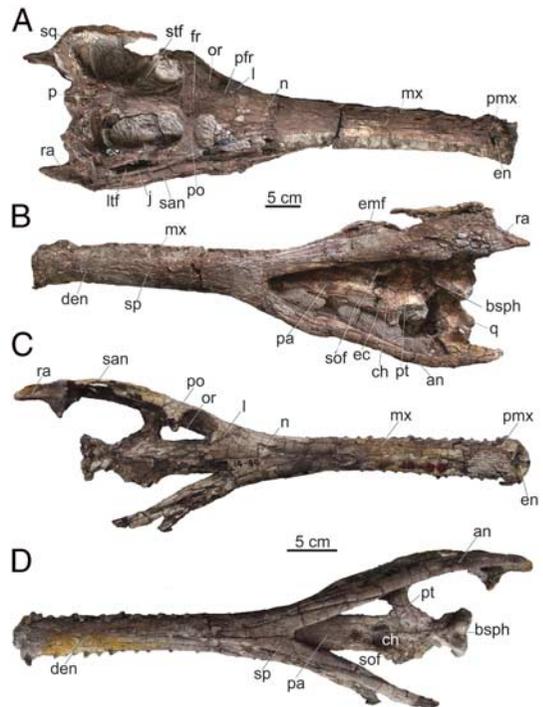


FIGURE 2. Two examples of teleosaurid skulls from Phu Noi. Dorsal (A) and ventral (B) views of PRC-239; dorsal (C) and ventral (D) views of PRC-238. Abbreviations: an, angular; bsph, basisphenoid; ch, choana; den, dentary; emf, external mandibular fenestra; ec, ectopterygoid; en, external nares; fr, frontal; j, jugal; l, lacrimal; ltf, lower temporal fenestra; mx, maxilla; n, nasal; or, orbit; p, parietal; pa, palatine; pfr, prefrontal; pmx, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; ra, retroarticular process; san, surangular; sp, splenial; sof, suborbital fenestra; stf, supratemporal fenestra; sq, squamosal.

Comparative description and affinities.—The best preserved and most complete skulls including mandibles are PRC-238 and PRC-239 (Fig. 2) and four other skulls are currently under technical preparation and study. An in-depth description will be presented elsewhere.

The taxon from Phu Noi displays a combination of apomorphies for Thalattosuchia (Young and Andrade 2009) such as the absence of contact between nasal and premaxilla, a nearly tubular rostrum, a complex dorsal surface of the supratemporal roof, the post-orbital located laterally to the jugal, a post-orbital longer than the squamosal, a long mandibular symphysis about half of the skull

length, a non-planar posterior margin of the skull table, the dorsal primary head of the quadrate contacting only the squamosal and not the laterosphenoid, the absence of a squamosal groove for the external earflap musculature and large pendulous basioccipital tubera. Furthermore, the taxon from Phu Noi is referred to Teleosauridae on the basis of the following apomorphies: the basisphenoid is long and projects further anteriorly than the quadrates and the cranial nerve XII opens in line with the foramen magnum.

The taxon from Phu Noi is longirostrine with a tubular rostrum that is ovoid in cross section. Its supratemporal fenestrae are longer than wide in dorsal view as in most teleosaurids except *Teleosaurus cadomensis*, which possesses large and as long as wide supratemporal fenestrae (Eudes-Deslongchamps 1870). Within members of the genus *Steneosaurus*, the supratemporal fenestrae are indeed longer than wide but appear also longer than in the taxon from Phu Noi. One exception concerns *Steneosaurus bollensis*, presenting supratemporal fenestrae of similar proportions to those of *Peipehsuchus teleorhinus* and the taxon from Phu Noi (Westphal 1962b: Figs. 1–2). *Machimosaurus hugii* also possesses longer supratemporal fenestrae than those of the taxon from Phu Noi. Also, the posterior margin of the fenestrae of *Machimosaurus hugii* are convex in dorsal view whereas in the taxon from Phu Noi and *Peipehsuchus teleorhinus* they widely expose the squamosal in this area, thus giving to the posterior margin of the fenestrae a concave outline in dorsal view, a condition moderately expressed among species of the genus *Steneosaurus*.

The orbits of the taxon from Phu Noi are circular as in all other teleosaurids. Their ventral margin is slightly protruding, a condition difficult to assess in other teleosaurids due to the dorsoventral compression of most specimens. However, a similar condition was reported for a nicely preserved skull of *Machimosaurus hugii* (Buffetaut 1982). The orbits of the Phu Noi teleosaurid are relatively large but their size does not depart much from the condition in *Steneosaurus* or *Teleosaurus cadomensis*. On the other hand, the orbits of *Machimosaurus hugii* are smaller relative to the total skull length.

The palate of the Phu Noi taxon is reminiscent of other teleosaurids in presenting choanae that are wide and opening both on the pterygoids and palatines. Among teleosaurids, the only exception is *Teleosaurus cadomensis*, which possesses choanae wider than the palatines (Jouve 2009). Another similarity of the Phu Noi taxon with teleosaurids concerns the presence of a relatively large external mandibular fenestra.

In teleosaurids, the antorbital fenestra is present but can easily be overlooked due to its small size. On the other hand, the antorbital fenestra consists of a large slit-like opening and is bordered dorsally by the lacrimal in the taxon from Phu Noi. This is also the case in *Peipehsuchus teleorhinus* from China. Further similarities between the two taxa are listed as follows: the nasal contributes to most of the rostrum length but is excluded from the narial border by a posteriorly V-shaped premaxilla; wide and dorsally facing posterolateral wall of the supratemporal fenestra, mostly built by the squamosal. The maxillary alveolar count in *Peipehsuchus teleorhinus* is 27 and the maxillary count in the taxon from Phu Noi is at least 25. As a comparison, this count can be approaching or surpassing 30 alveoli in *Steneosaurus* (Andrews 1913). Therefore, the taxon from Phu Noi exhibits characters reminiscent of the genus *Peipehsuchus* Young (Young 1948). As a side note, *Peipehsuchus teleorhinus* is possibly as old as Toarcian (Wang et al. 2008). An in-depth description and phylogenetic analysis of the younger (?Tithonian) Phu Noi taxon is pending and for the moment, it is provisionally referred to Teleosauridae indet.

Phylogenetic analysis.—The Phu Noi teleosaurid was coded and included in a matrix for a total of 73 taxa and 240 characters (Young et al. 2012) using the software TNT (Goloboff et al. 2003). The analysis resulted in a strict consensus of 10 trees with a best tree length of 663 steps. Bremer decay indices were computed and are superimposed on Figure 3. The recovered topology follows what has been reported previously (Young et al. 2012; Martin and Vincent 2013); only the Thalattosuchia are represented in figure 3 because this work focuses on the intrarelations of teleosaurids, not on the interrelationships of Thalattosuchia with

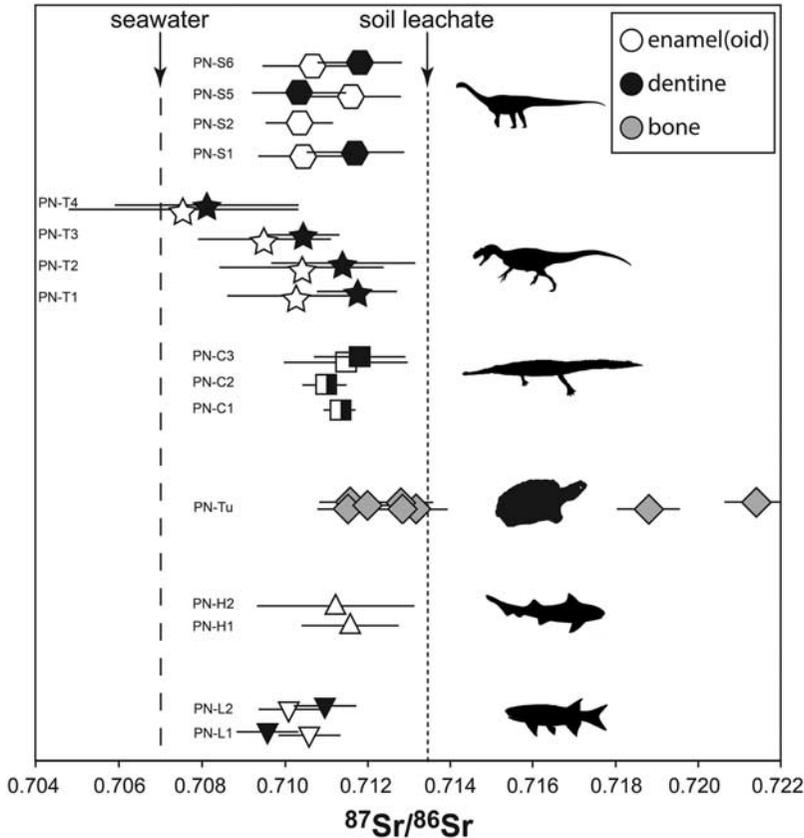


FIGURE 5. Strontium isotopic variability ($^{87}\text{Sr}/^{86}\text{Sr}$) in the Upper Jurassic vertebrate continental assemblage of the locality of Phu Noi. Sample names of individual taxa are indicated on the left hand side. The vertical stipple line on the left is the approximate $^{87}\text{Sr}/^{86}\text{Sr}$ value for the marine environment during the Late Jurassic (after Prokoph et al. 2008). Error bars represent 2SD.

the crystal lattice of bioapatite during mineralization of teeth and bones (Reynard and Balter 2014) and therefore its isotopic composition reflects that of the environment in which the animal lived, as derived from food and drinking water (e.g., Graustein 1989; Blum et al. 2000; Maurer et al. 2012). That fossil teeth do not retain an *in vivo* strontium signal is always an issue because biogenic strontium may be rapidly replaced after burial by diagenetic strontium (e.g., Nelson et al. 1986; Sillen 1986; Hoppe et al. 2003). Diagenesis can be detected by several means, but here we take advantage of the lower Sr concentrations in theropod teeth to assume, as a general rule, that the Phu Noi assemblage has not been overprinted significantly by diagenesis. Strontium, and barium concentrations decrease up the trophic

chain because these are two non-essential trace elements that tend to mimic Ca, which is bio-essential (Elias et al. 1982; Burton et al. 1999; Balter 2004). Although interpretations can be complicated by the ingestion of trace elements from dust or soil (Kohn et al. 2013), this process has been widely used as a paleodietary tool, but has been restricted to the reconstruction of the diet of Late Paleolithic Neanderthals (Balter et al. 2001, 2002) and of Early Pleistocene hominins (Sillen 1986; Sponheimer et al. 2005; Balter et al. 2012), i.e., of Quaternary age. Thus, the low Sr concentrations in the teeth of theropods compared to other taxa reflect that the most parsimonious interpretation is that these animals were feeding at a higher trophic level. It is noteworthy that the preservation of a Ca biopurification pattern in the Phu Noi assemblage dated at about 150 Ma is

exceptional and to our knowledge, has never been described before for Mesozoic fossils. Also, the large range of strontium isotope values in the various fossils analyzed here argue that all the samples have not converged on a single diagenetic value. However, possible diagenetic effects have to be scrutinized sample by sample in order to discard samples suspected of diagenetic overprinting. Diagenetic process can be modeled as a conventional mixing balance between biogenic and diagenetic end-members with distinct strontium concentrations [Sr] and isotopic ratios $^{87}\text{Sr}/^{86}\text{Sr}$: samples affected by diagenesis would fall on a mixing hyperbola in a [Sr] vs $^{87}\text{Sr}/^{86}\text{Sr}$ space (Albarède 1995; Balter et al. 2012). Here, no such correlation is observed, except for the two turtle bone outliers PN-TU1-6 and PN-TU1-7 (Fig. 4; Supplementary Appendix, Table S1), for which both the strontium concentration and the isotopic ratio are different from the rest of the samples. Both samples have more radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ values than the soil strontium soluble fraction (Fig. 5). The $^{87}\text{Sr}/^{86}\text{Sr}$ values of the two turtle bone outliers must have been driven by another diagenetic pool with a higher $^{87}\text{Sr}/^{86}\text{Sr}$ value, at least ~ 0.722 , possibly a secondary mineral phase that precipitated in the porous structure of bone (e.g., calcite, gypsum). In this condition, the soil strontium soluble fraction (i.e., “soil water” on Fig. 5) cannot be considered as the prevalent diagenetic end-member for the PN-TU1-6 and PN-TU1-7 samples. However, three other turtle bone samples exhibit suspicious $^{87}\text{Sr}/^{86}\text{Sr}$ value, i.e., higher than ~ 0.711 (which is the average value of the dataset) and lower than the soil soluble fraction value at 0.71334. These samples are PN-TU1-2, PN-TU1-3 and PN-TU1-8 (Supplementary Appendix, Table S1). For these three samples, slight diagenetic strontium overprinting originating from the “soil water” strontium can be suggested, but is not demonstrated, as no increase of strontium concentration is concomitantly observed. In the present study, diagenesis has affected bone samples, leaving dentine and enamel seemingly unaffected by diagenetic overprints. This is in contrast, for instance, with the results obtained at the

Middle Eocene conservation-Lagerstätte Messel site, Germany (Tütken 2014), where dentine samples have systematically lower $^{87}\text{Sr}/^{86}\text{Sr}$ values (~ 0.706) than related enamel (~ 0.711). Dentine are thus lower by ~ 0.06 units of $^{87}\text{Sr}/^{86}\text{Sr}$ as compared with enamel, which is an important offset that is not observed in the present study, indicating very different diagenetic processes observed for the fossils of the Messel deposits and those of the Phu Kradung Formation. Moreover, that enamel and dentine strontium isotope values are not significantly different from each other is in agreement with an in vivo signature, as reported in modern faunas (Budd et al. 2000).

For the reasons presented above, we consider at least our enamel data to be most likely representative of an in-vivo signal. On average, the $^{87}\text{Sr}/^{86}\text{Sr}$ values measured on the vertebrate assemblage (~ 0.711 , Fig. 5, Supplementary Data, tables S1 and S2) reflect a continental environment, with values significantly more radiogenic than the values reported for marine environment of Late Jurassic age (~ 0.707 as compiled in McArthur et al. 2001). This implies that vertebrates recovered from Phu Noi mineralized their teeth locally in a freshwater setting incorporating the isotopic ratio of 0.71334. This is in line with sedimentological and petrographic observations of polycrystalline quartz grains and lithic fragments of quartz-mica schists that indicate a crystalline, metamorphic bedrock substrate as a source area for the clastic sediments of the Phu Kradung Formation (Racey et al. 1996: p. 20).

The outlier theropod with the lowest strontium value (~ 0.708) mineralized its tooth on a different substrate, possibly reflecting migration from another area. From the general distribution of $^{87}\text{Sr}/^{86}\text{Sr}$, there is no indication that the teleosaurid material is allochthonous. A detailed sampling of two teleosaurid teeth belonging to PRC-239 along incremental growth lines allows tracking the evolution of the strontium isotope signal (and therefore of the provenance) during the time necessary for mineralization. Tooth replacement takes about two months to complete as reported from a study on a meter long extant *Alligator mississippiensis* (Erickson 1996). Erickson (1996) also concluded that tooth replacement slows

down during ontogeny. Although not assessed for large animals, it is reasonable to admit that in several meter long specimens, several months are necessary to renew teeth. In the case of PRC-239 representing an adult, it is reasonable to assume that the teeth analyzed here did record more than two months of environmental signal. Electronic supplementary material, table S2 reports strontium isotope values, which are all around 0.711 ($n=48$) for these two teeth with a minimum value of 0.710 and a maximum value of 0.712. These $^{87}\text{Sr}/^{86}\text{Sr}$ values fall in the range of the seasonal variability of the weathering flux of a homogeneous catchment, which is about $2 \cdot 10^{-3}$ in the study of the Xijiang River (Wei et al. 2013). Indeed, the timeline of the mineralizing tooth is perhaps too short to capture significant shifts in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that would provide evidence for migration. Therefore, it cannot be excluded that migration between the freshwater and the marine habitat could take place in the Phu Noi teleosaurid. Nevertheless, it can be said that in the time necessary to mineralize the teeth (over 2 months), there is no evidence of migration of teleosaurids between the freshwater environment of Phu Noi and a marine environment. Thus, the strontium isotopic values of the Phu Noi teleosaurid fall in the range of values retrieved for the other vertebrates from Phu Noi, and the most probable conclusion is that this teleosaurid is a long-term (over 2 months) resident of this continental freshwater paleoenvironment.

Colonization of freshwater drainages.—The earliest known thalattosuchians are Early Jurassic in age (early Toarcian) and are exclusively recorded from marine deposits. Several million years later, the teleosaurid from northeastern Thailand illustrates an unambiguous example of a thalattosuchian recovered from a freshwater setting. From an evolutionary perspective, a reconstruction of the evolution of osmoregulation in thalattosuchians is hampered by the unclear interrelationships of its main lineages (*Pelagosaurus*, Teleosauridae, Metriorhynchoidea). Therefore, osmoregulation within Thalattosuchia and more specifically within Teleosauridae can only be tentatively superimposed on an evolutionary hypothesis,

as has been implied for the capacity of members of this clade to osmoregulate (Fernández and Gasparini 2008). Based on a transitional stage model (Mazzotti and Dunson 1989), Fernández and Gasparini (2008) consider teleosaurids to be estuarine/marine and metriorhynchoids to be pelagic swimmers. The presence of salt-excreting glands in *Geosaurus* and *Metriorhynchus* represents a solid basis for the latter assumption (Fernández and Gasparini 2000, 2008; Gandola et al. 2006; Herrera et al. 2013). However, characterization of a marine versus estuarine lifestyle for teleosaurids and *Pelagosaurus* is impossible based solely on morphology, hence there is a lack of resolution regarding their adaptation to transitional paleoenvironments. As a comparison, salt-excreting glands are active in extant *Crocodylus* (Mazzotti and Dunson 1989), but do not leave any osteological information because they occur on the tongue.

According to our results, three hypotheses could be advanced for the occurrence of some teleosaurids in riverine/lacustrine habitats. First, an adaptation to the freshwater environment could be an autapomorphy of some teleosaurids and evolved once in the derived teleosaurid from Thailand (and possibly also in *Machimosaurus*) (Fig. 3) as a secondary adaptation from a primitively marine teleosaurid ancestor. A second possibility is the retention of an adaptation inherited from a basal member of Thalattosuchia or from the ancestors of Thalattosuchia, if we assume they lived in freshwater environments during the Late Triassic-Early Jurassic time interval. In the latter hypothesis, metriorhynchoids were exclusively living in the marine environment (supported by the presence of salt-excreting glands (Fernández and Gasparini 2008) and we could predict that all other thalattosuchians (*Pelagosaurus* and Teleosauridae) would likely be recovered in riverine environments during the Toarcian-Tithonian interval. The latter two hypotheses seem likely, considering *Peipehsuchus teleorhinus* from the Ziliujing Formation of China as the oldest representative of a freshwater thalattosuchian (Lower Jurassic, Peng et al. 2005). Nevertheless, it should be stressed that the capacity to tolerate salt may not have been lost at all as is seen today with

the following example: the extant species of *Crocodylus* do have a capacity for salt excretion although many of them spend their entire life in freshwater environments. This does not prevent many individuals of *Crocodylus porosus* or *Crocodylus acutus* to spend a considerable amount of time in brackish or marine habitats. Therefore, a third possibility may be that teleosaurids were able to migrate between marine and freshwater habitats without losing the capacity for salt excretion.

Whether those teleosaurids recovered in marine deposits were temporarily visiting freshwater ecosystems, for example to seek food, reproduce or avoid competitive interactions with other marine reptiles is plausible (see below for examples of extant taxa that migrate in freshwater ecosystems). The fact is that two teleosaurid genera have been recorded in non-marine habitats. The oldest record appears to be *Peipehsuchus teleorhinus* from the Lower Jurassic Ziliujing Formation of China, which originates from a lacustrine deposit (Wang et al. 2008) (a freshwater plesiosaur was also reported from this same formation by Sato and Wu (2003)). Secondly, the present study reports a teleosaurid from a freshwater habitat of the Late Jurassic, therefore younger than the Chinese occurrence of *Peipehsuchus*. In addition, fragmentary remains of teleosaurids have been reported from a brackish environment of the Middle to Upper Jurassic Khlong Min Formation in Peninsular Thailand (Buffetaut et al. 1994). These few records indicate a capacity for some teleosaurids to live in non-marine habitats, at least for a few months as highlighted with the present study. Conversely, do the abundant teleosaurids recovered in coastal deposits of Europe preserve a trace of their passage in freshwater habitats? The Kimmeridgian *Machimosaurus hugii* occurs in the lignite deposits of Guimarota, Portugal (Krebs 1967, 1968), which has been interpreted as a brackish environment (Buffetaut 1982). This taxon is often recovered in marine deposits (Martin and Vincent 2013) and the occurrence of the Portuguese specimen in a transitional environment might be viewed as an evidence for migration between marine and brackish habitats and questions its ability to visit freshwater environments.

For historical reasons, more teleosaurids have been discovered in Europe than in other parts of the world. The vast majority of Jurassic and Lower Cretaceous sediments of Europe were deposited in marine environments. Thus, with the exception of terrestrial faunas washed into marine environments (e.g., Buffetaut 1994), fossil vertebrates including teleosaurids found in such deposits most likely have a marine origin. Whether teleosaurids were present in contemporaneous drainage basins has been questioned (Westphal 1962b). That teleosaurids spent some time of their life in the freshwater habitat could be tested by analyzing the strontium isotopic composition of their teeth.

Other predominantly marine predators are also mentioned in freshwater settings of Jurassic and Cretaceous age. Plesiosaurs have been reported from non-marine Lower Cretaceous deposits of Australia (Bartholomai 1966; Kear 2006), Britain (Andrews 1922; Kear and Barrett 2011), Germany (Wegner 1914), Canada (Sato et al. 2005; Vavrek et al. 2014) and China (Sato and Wu 2003). Mosasaurs have also been reported from the Upper Cretaceous (Santonian) freshwater deposits of Hungary (Makádi et al. 2012) and strontium and oxygen isotope studies confirmed they remained in this freshwater setting for some time (Kocsis et al. 2009). There are also undescribed large isolated varanoid vertebrae from Campano-Maastrichtian freshwater deposits of southern France (Buffetaut et al. 1999). Hybodont sharks derive from a marine ancestor (Cuny et al. 2014) and are frequently recovered in Mesozoic brackish and freshwater deposits (Klug et al. 2010; Fischer et al. 2012; 2013; Cuny et al. 2014). Our results, including strontium isotope measurements on two hybodont teeth confirm the long-term occurrence of hybodonts in the freshwater habitats of Phu Noi (Fig. 5).

Colonization of the freshwater environment by marine vertebrates could be tied to a variety of ecological factors including new available niches, lack of competition on newly available resources, or refuges from predators. Beside thalattosuchians, members of another clade of marine crocodylomorphs, Dyrosauridae, have been recorded from transitional environments

(an account is presented elsewhere (Hastings et al. 2011)) and from freshwater deposits in the Maastrichtian of India (Khosla et al. 2009) and in the Eocene of Punjab, Pakistan (Buffetaut 1977, 1978). The rarity of large specimens and the abundance of small ones led Buffetaut (1977) to hypothesize that those freshwater environments were used as refuges for juveniles against large marine predators represented at that time by eusuchians. Sato et al. (2005) observed that freshwater plesiosaurs from the Cretaceous of Canada are of small size, and possibly represent juveniles. More recently Vavrek et al. (2014) interpreted a new freshwater locality from the Canadian High Arctic as a possible plesiosaur nursery. The situation for the Phu Noi teleosaurid is however different with specimens representing different size classes. The abundance of large gynglymodian fish skeletons in this locality (Deesri 2012) hints at the availability of food resources for these teleosaurids.

Modern-day species of *Crocodylus* and cetaceans offer interesting ecological parallels with extinct marine reptiles. Out of the 23 species of living crocodylians, only two species, *C. porosus* and *C. acutus* are frequently found in estuarine or marine habitats and two others, *C. niloticus* and *C. johnstoni* have known estuarine populations (e.g., Mazzotti and Dunson 1989; Wheatley et al. 2012). Occasional accounts also exist for other members of Crocodylinae in brackish environments. There are four extant species of freshwater cetaceans (including the recently extinct Chinese species *Lipotes vexillifer*) living permanently in large fluvial systems of South America and Asia (Cassens et al. 2000; Hamilton et al. 2001). Because it spent a considerable amount of time in freshwater, the Phu Noi teleosaurid could be considered an ecological equivalent of these freshwater dolphins. A closely related species to the freshwater dolphins (see debate about monophyly (Cassens et al. 2000; Hamilton et al. 2001), *Pontoporia blainvillei* inhabits coastal and estuarine habitats of Argentina and Brazil but does not venture far inland. This species represents the marine/estuarine equivalent of teleosaurids following the interpretation of (Fernández and Gasparini (2008). A last case is represented by the delphinid *Orcaella*

brevirostris, which is euryhaline (Baird and Beasley 2005): this species spreads along the shorelines of SE Asia and penetrates deep within the Mahakam, Mekong, and Irrawaddy rivers. The species of cetaceans mentioned above are found in a variety of habitats, some living permanently in freshwater habitats, other migrating back and forth between marine and freshwater habitats and others not venturing inland but having a distribution in estuaries and coastal environments. It is therefore probable that thalattosuchians and particularly teleosaurids were exploiting such a variety of environments too. Further isotopic studies on various fossil assemblages may reveal specific migratory patterns. According to the present study, the Phu Noi teleosaurid could either be viewed as a pioneering taxon into a novel habitat or as an evidence for the widespread behavior of teleosaurids to visit and durably inhabit riverine ecosystems of the Jurassic. Strontium isotope studies provide a means with which to test these hypotheses through the analysis of tooth enamel from the numerous specimens recovered throughout European Jurassic localities.

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