

# Early Cretaceous vertebrates from the Xinlong Formation of Guangxi (southern China): a review

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(Received 26 February 2015; accepted 11 May 2015; first published online 2 July 2015)

**Abstract** – The vertebrate assemblage from the Early Cretaceous non-marine Xinlong Formation of the Napai Basin, in the south-western part of Guangxi Zhuang Autonomous Region (southern China), is reviewed. The assemblage includes chondrichthyans (at least six species of hybodont sharks including *Hybodus*, *Thaiodus*, *Heteroptychodus* and *Acrorhizodus*), actinopterygians (Halecomorphi and Ginglymodi), turtles (the adocid *Shachemys* and the carettochelyid *Kizylkumemys*), crocodylians (cf. *Theriosuchus*) and dinosaurs (the sauropods *Fusuisaurus* and *Liubangosaurus*, carcharodontosaurid and spinosaurid theropods, iguanodontians and a possible psittacosaurid). This assemblage shows many similarities to those from non-marine formations of the Khorat Group of north-eastern Thailand. It seems to be particularly close to that from the Khok Kruat Formation, considered as Aptian in age, as shown especially by sharks and turtles and by the presence of iguanodontians. An Aptian age is therefore proposed for the Xinlong Formation. A study of the stable oxygen and carbon isotope compositions of reptile apatite suggests that this part of South China experienced subtropical arid conditions during the deposition of the Xinlong Formation. In its composition, the vertebrate fauna from the Xinlong Formation seems to be more similar to coeval faunas from SE Asia than to assemblages from northern China (including the Jehol Biota). Although this may partly reflect different depositional and taphonomic environments (fluvial for the Xinlong Formation versus lacustrine for the Jehol Biota) it seems likely that, during Early Cretaceous time, southern China and SE Asia were part of a distinct zoogeographical province, different from that corresponding to northern China. This may be the result of both climatic differences (with relatively cool climates in northern China versus a subtropical climate in the south) and geographical barriers such as mountain chains.

Keywords: Xinlong Formation, Early Cretaceous, Vertebrata, Guangxi, China.

## 1. Introduction

Whereas many recent and detailed studies on the so-called 'Jehol Biota' have enormously increased our knowledge of the Early Cretaceous vertebrates of north-eastern China, the vertebrate assemblages of similar age from southern China have remained comparatively poorly known, despite recent descriptions of various faunal elements. One of the most significant sources of Early Cretaceous fossil vertebrates in southern China is the Xinlong Formation of Guangxi Zhuang Autonomous Region.

Fossil vertebrate remains were first described from the Xinlong Formation (then known as the Napai Formation) of south-western Guangxi by Hou, Yeh & Zhao

(1975), who briefly mentioned the occurrence of shark teeth and turtle remains and gave more detailed descriptions of several reptilian teeth. For more than a decade, research conducted by the Natural History Museum of Guangxi from the early 2000s has resulted in a considerable increase in our knowledge of the fossil vertebrates from the Xinlong Formation. In recent years, French and Thai palaeontologists have collaborated with their Chinese colleagues in order to assess the similarities between the faunal assemblage from the Xinlong Formation and the Early Cretaceous vertebrate faunas of SE Asia. The present paper reviews the fossil vertebrates from the Xinlong Formation and discusses their stratigraphical and biogeographical implications.

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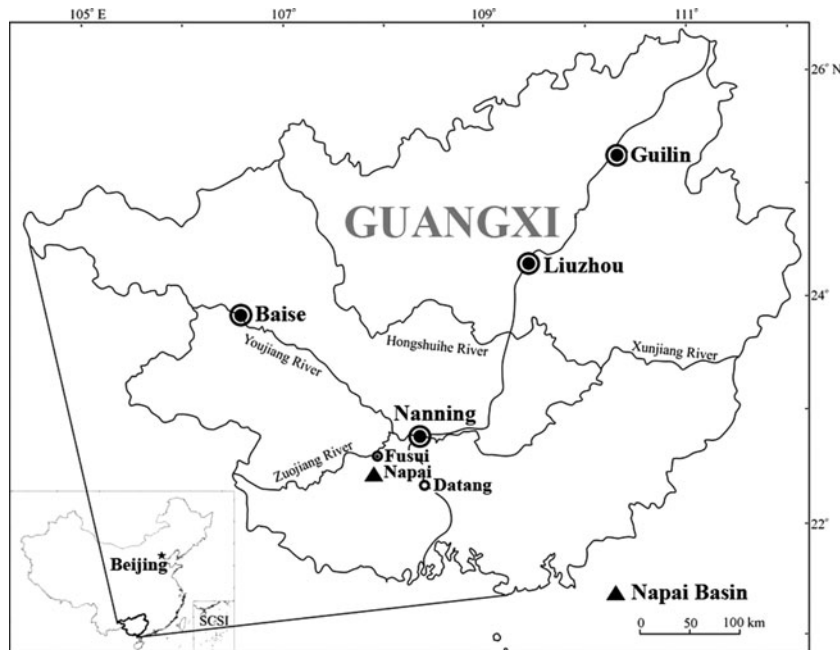


Figure 1. Map showing the location of the Napai Basin in Guangxi Zhuang Autonomous Region, China.

## 2. Geographical and geological setting

The fossils discussed in the present paper were collected from exposures of the Xinlong Formation in the Napai Basin in the south-western part of Guangxi Zhuang Autonomous Region, about 60 km SW of the city of Nanning (Fig. 1). The red beds of the Xinlong Formation can be seen at several localities in the basin. However, the whole area is intensively cultivated and the outcrops tend to be small patches among the sugar-cane fields.

The name ‘Napai Formation’ (misspelled ‘Napan’ by Dong, 1992, 1993 and Weishampel *et al.* 2004) has often been used to designate the Early Cretaceous vertebrate-bearing red beds of the Napai Basin (e.g. Mo *et al.* 2006; Buffetaut *et al.* 2008). However, the name ‘Xinlong Formation’ is more precise and has precedence over ‘Napai Formation’ (Guangxi Bureau of Geology and Mineral Resources, 1985); we therefore follow Mo, Xu & Buffetaut (2010) and Mo *et al.* (2014a) in using it here.

According to the Guangxi Bureau of Geology and Mineral Resources (1985) the Xinlong Formation, which varies in thickness from 80 to 2445 m, consists of purple-red, yellow-grey siltstones, fine sandstones, some mudstones and sandy conglomerates, the latter being found in the lower part of the formation (Fig. 2c). As well as vertebrates, the Xinlong Formation has yielded plants (including charophytes), estheriids, ostracodes, gastropods and bivalves. In some conglomeratic levels, thick-shelled bivalves form lumachelles (Fig. 2c). Vertebrate remains occur in various types of sediments, including conglomerates as well as siltstones. Vertebrate fossils found in conglomerates are mostly isolated teeth (shark teeth being especially abundant), fish scales and bone fragments. In-

complete dinosaur skeletons have been found in finer-grained sediments.

Hou, Yeh & Zhao (1975) considered the Xinlong Formation as Early Cretaceous in age on the basis of the bivalves (*Trigonioides*, *Plicatounio*, etc.) and the reptile remains. As discussed in Section 5, this age assignment is certainly correct. Moreover, newly discovered vertebrate fossils provide additional evidence and allow a more accurate dating, namely Aptian (see discussion in Section 5).

## 3. Review of vertebrate groups from the Xinlong Formation

The groups of vertebrates discovered in the Xinlong Formation are reviewed below. Groups that have so far received little attention, notably fishes and turtles, are discussed at greater length than those that have already been described in some detail (dinosaurs). Where comparisons with fossils from other areas have led to biostratigraphic conclusions concerning the age of the Xinlong Formation, this has been discussed at some length to avoid lengthy discussions in Section 5 (on the age and biogeographical relationships of the Xinlong assemblage).

### 3.a. Chondrichthyes

Hybodont sharks are represented at Tan Gao by at least six species (Fig. 3), one of which is new and will be described in detail in a forthcoming article. The five others are: *Hybodus aequitridentatus*, *Heteroptychodus steinmanni*, *Acrorhizodus khoratensis*, *Thaiodus ruchae* and *Khoratodus foreyi*. *Hybodus aequitridentatus* is represented only by isolated cusps showing a dense pattern

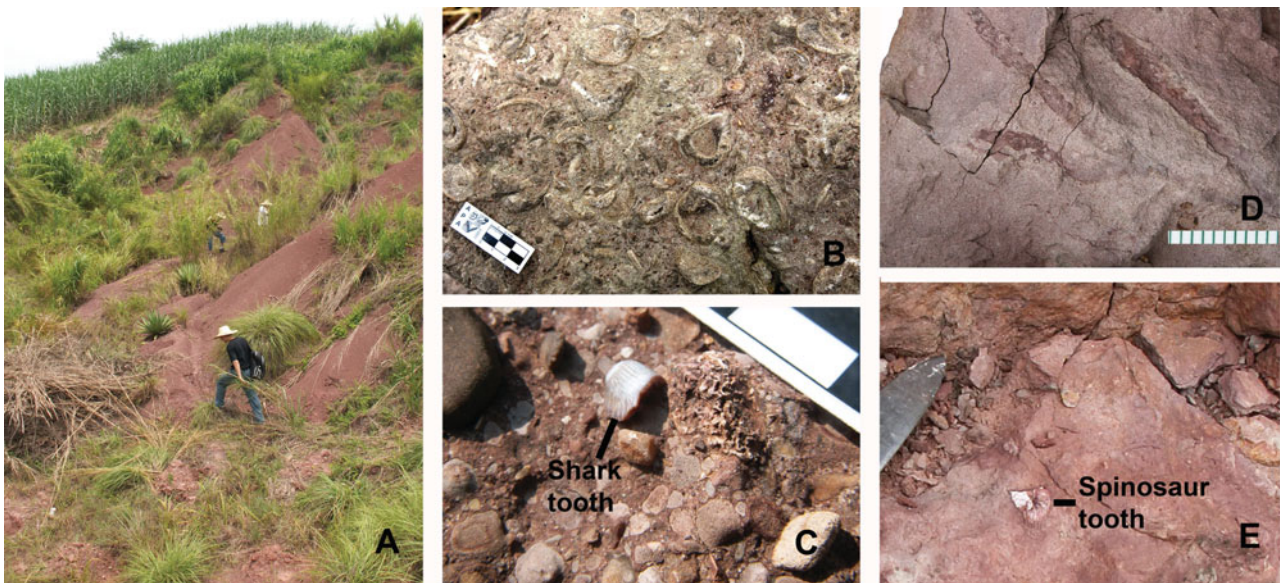


Figure 2. (Colour online) Facies of the Xinlong Formation: (a) red clays; (b) lumachelle with thick-shelled freshwater bivalves; (c) conglomerate with hybodont shark tooth; (d) siltstone with plant impression; and (e) sandstone with spinosaur tooth in cross-section.

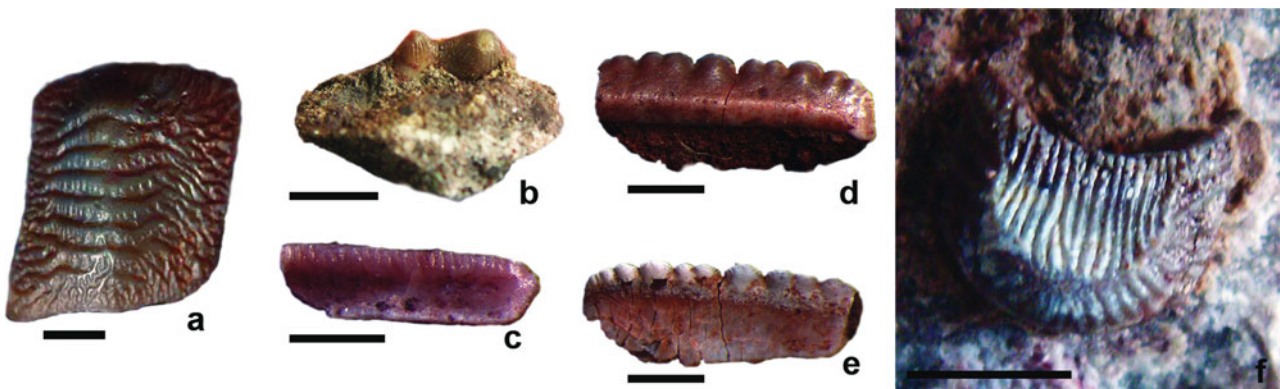


Figure 3. (Colour online) Hybodont shark teeth from the Xinlong Formation of the Napai Basin. (a) Anterior tooth of *Heteroptychodus steinmanni* in apical view. (b) Incomplete tooth of *Hybodus aequitridentatus* still embedded in matrix in apical view. (c) Incomplete tooth of *Khoratodus foreyi* in labial view. (d, e) Incomplete tooth of *Thaiodus ruchae* in (d) lingual and (e) labial views. (f) Tooth of *Acrorhizodus khoratensis* still embedded in matrix in apical view. Scale bars: 1 mm for (a, c–e) and 5 mm for (b, f).

of fine anastomosed ridges similar to that observed in the teeth of the same species from the Khok Kruat Formation in Thailand (Cuny *et al.* 2008).

*Heteroptychodus steinmanni* is represented by teeth with a characteristic, dense ornamentation: several parallel longitudinal ridges, each bearing short perpendicular ridges on their lingual side, together with a marginal area, ornamented by radiating, anastomosed ridges. The anterior teeth are less flat and less expanded mesio-distally than the lateral and posterior teeth.

Teeth of *Acrorhizodus khoratensis* show a convex labial outline and a concave lingual outline with a U-shaped longitudinal crest. The crown is ornamented with a dense pattern of primary anastomosed ridges originating from the longitudinal crest (Cappetta *et al.* 2006).

*Thaiodus ruchae* is represented by asymmetric teeth possessing a well-developed labial flange and up to 12 coarsely serrated cusps. Another member

of the family Thaiodontidae in Tan Gao is *Khoratodus*, represented by a broken, mesio-distally elongated and labio-lingually asymmetric tooth, very similar to those of *Khoratodus foreyi* (Cuny *et al.* 2008).

*Hybodus aequitridentatus*, *Acrorhizodus khoratensis* and *Khoratodus foreyi* were previously restricted to the Khok Kruat Formation (Aptian–?Albian) of Thailand, whereas *Thaiodus ruchae* was known in the Khok Kruat Formation and the Aptian deposits of Tibet (Cappetta, Buffetaut & Suteethorn, 1990) and *Heteroptychodus steinmanni* has been recorded in Lower Cretaceous deposits of Thailand and Japan (Cuny *et al.* 2008). The record of these five taxa of predominantly freshwater hybodont sharks in southern China significantly expands their palaeogeographic distribution. The shark assemblage from Tan Gao, except for the new taxon, is exactly the same as that recovered from the Khok Kruat Formation in Thailand.



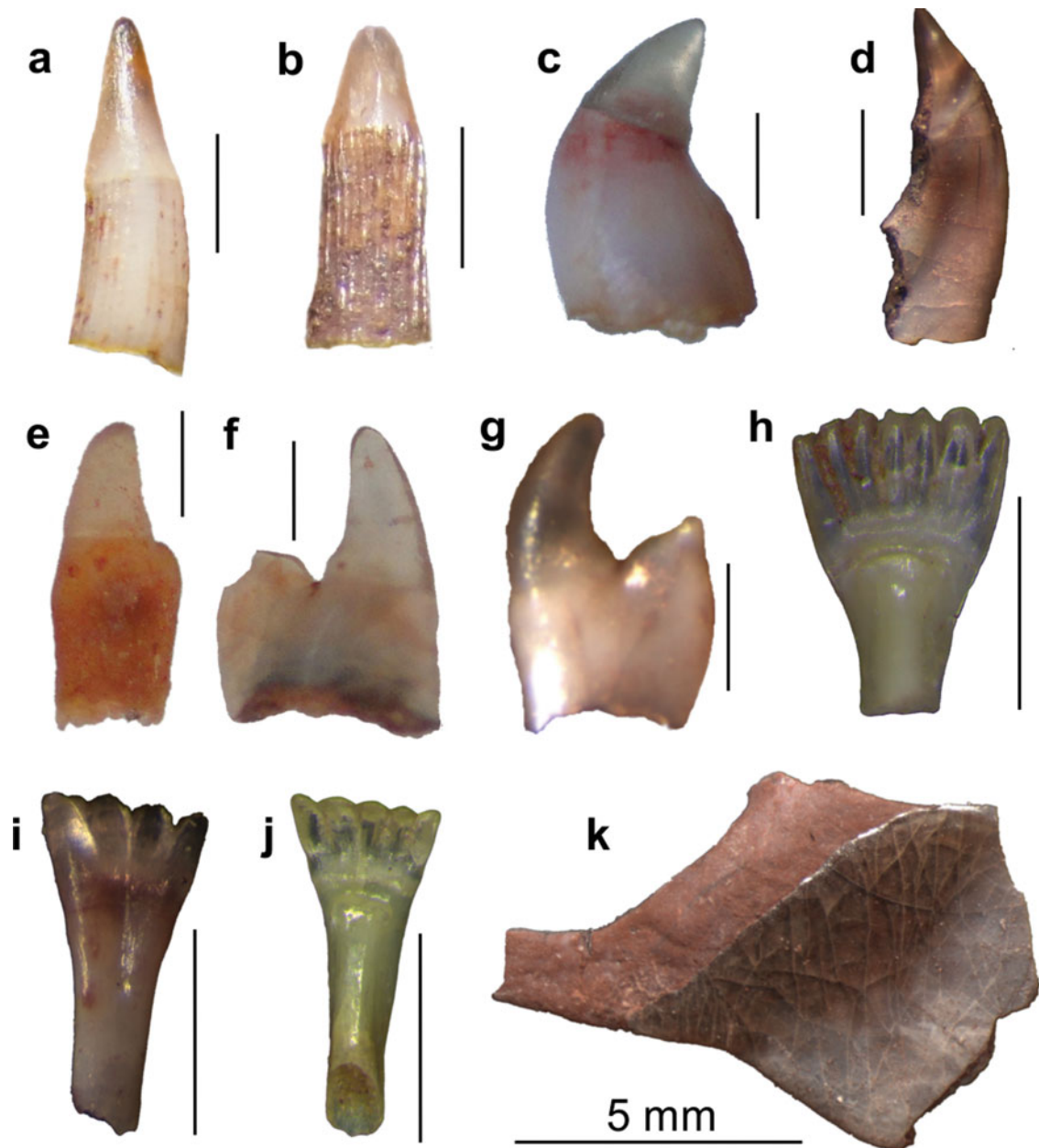


Figure 4. (Colour online) Actinopterygian remains from the Xinlong Formation of the Napai Basin: (a, b) Halecomorphi indet., oral teeth; (c–k) Ginglymodi indet.; (c–g) pharyngeal teeth; (h–j) oral teeth; and (k) scale fragment.

### 3.b. Actinopterygii

The most abundant ray-finned fish (Actinopterygii) remains from the Xinlong Formation are isolated teeth and fragmentary scales (Fig. 4). Except for some exceptional cases, these elements are not diagnosable and identification, if possible, remains vague.

#### 3.b.1. Halecomorphi indet.

Fragments of slightly curved teeth, with a pointed acrodine tip and a shaft circular in cross-section ornamented with elongated grooves are present (Fig. 4a, b). The acrodine cap is either conical or lanceolate.

Lanceolate teeth from Late Jurassic – Early Cretaceous times are generally referred to the genus *Caturus*, but in this genus the shaft is smooth (Thies & Mudroch,

1996) and there is a constriction between the cap and the shaft (Klug & Kriwet, 2013). In *Ionoscopus*, from Upper Jurassic deposits of Europe, the cap is also lanceolate but the cutting edges are fainter than in *Caturus* and there is no constriction between the cap and the shaft (Thies & Mudroch, 1996). The shaft may bear an ornamentation of grooves, but they are less marked than in the specimens described here. These teeth are referred to indeterminate halecomorphs.

#### 3.b.2. Ginglymodi indet.

Several teeth are characterized by a curved apex of acrodine supported by a bulbous shaft, which might be circular in cross-section (Fig. 4c) or flattened (Fig. 4d–g). The bulge of the shaft varies from a faint convexity

(Fig. 4d, e) to a well-developed hooked process that may form a second cusp on the tooth (Fig. 4f, g). The bulging teeth with a flattened shaft and a hooked apex are pharyngeal teeth. Those with a circular section shaft and curved apex might possibly be oral teeth by comparison with oral teeth of the ginglymodian *Thaichthys buddhabutrensis* from basal Cretaceous deposits of Thailand (Cavin, Deesri & Suteethorn, 2013).

A few teeth from the Xinlong Formation show a very peculiar morphology (Fig. 4h, i), with the basal half forming a slightly compressed cylindrical shaft and an apical part being spatulated. The apical margin forms a curved cutting edge with blunt denticles as grooves extending along the lingual face. The number of the denticles varies from 4 to 7.

Ganoid scales, with a flat and shiny surface and some of them with the typical double anterior processes (Fig. 4k), are assigned to a ginglymodian fish.

The association of both dental morphologies, that is, flat and bulging pharyngeal teeth and crenulated oral teeth, is found in several Upper Cretaceous localities of Africa such as in Nigeria (White, 1934), Egypt (Stromer & Weiler, 1930; Weiler, 1935), Tunisia and Morocco (Arambourg, 1952) and Niger (Tabaste, 1963; Cappetta, 1972) as well as in the terminal Cretaceous deposits of India (Prasad & Sahni, 1987). These teeth are usually referred to the genus *Stephanodus*, family Eotrigonodontidae. The taxonomic status of eotrigonodontid genera and the phylogenetic relationships of this extinct family have been much debated for more than a century (Murray & Thewissen, 2008 for a review). It is likely that the family artificially gathers pharyngeal dentitions from different groups with similar gross morphology. While the Cenozoic eotrigonodontids are probable tetraodontiformes (Monsch, 1998), Mesozoic forms are likely non-teleostean fishes, and might be referred to pycnodonts and/or to ginglymodians. Because ganoid scales are found in association with the teeth, and because no typical pycnodont teeth have been found so far in the Xinlong Formation, it is more parsimonious to refer this material to *Stephanodus*, regarded here as an indeterminate ginglymodian. The stratigraphical implication of this taxon is weak because this association of morphology is found in a wide range of Upper Cretaceous localities. The Aptian age of the Xinlong Formation indicated by other elements of the assemblage would make this typical morphology among the oldest known worldwide. This dental morphology has never been found in Lower Cretaceous localities of Thailand.

It is worth noting that multidenticate teeth have recently been described on articulated specimens of *Hemicalypterus weiri* from the Upper Triassic continental Chinle Formation in the United States, a species with ganoid scales of uncertain affinities possibly related to the holosteans (Gibson, 2015). Gibson suggests that this dental morphology, which occurs in several extant teleostean lineages, is associated with a kind of herbivory performed by scraping algae on the substrate. The occurrence of *Stephanodus*-like teeth in several Creta-

ceous localities, including that described here, indicates the persistence of this mode of feeding from Triassic time to the present, although the involved taxa do not belong to a single lineage. Contrary to a statement made by Gibson (2015), her description of multidenticate teeth in the Triassic *Hemicalypterus* was not the first observation of such a kind of teeth in Mesozoic deposits; the first teeth with comparable morphology were recorded more than 80 years ago from Cretaceous rocks of North Africa (Stromer & Weiler, 1930).

### 3.c. Testudines

Turtle remains from the Xinlong Formation in the Napai Basin are fragmentary, consisting of less than a dozen isolated shell plates and fragments of shell plates (Fig. 5). They belong to two families of Trionychoidea: Adocidae and Carettochelyidae.

#### 3.c.1. Adocidae Cope, 1870

*Shachemys* sp.: The material includes an almost complete bridge peripheral from Paimang locality; a complete left peripheral 1, a complete left costal 8 and an incomplete bridge peripheral from Xiamiao locality. The outer surface of these plates is smooth with numerous tiny pores, typical of the adocid *Shachemys*.

The costal 8 has double rib heads on the anteromedial part of the inner surface. On the dorsal surface, the fourth vertebral scute covers the anteromedial corner of the plate. The interpleural sulcus between the third and fourth pleurals runs from the fourth vertebral posterolaterally to the lateral end of the plate. The eleventh marginal extends onto the posterolateral corner of the plate as in *Shachemys baibolatica* Kuznetsov, 1976 and *S. ancestralis* Nessov & Krasovskaya, 1984 from Upper Cretaceous deposits of central Asia. In *Shachemys laosiana* from the middle Cretaceous deposits of Laos, the extension of the 11th marginal onto costal 8 seems to be less important (Lapparent de Broin de, 2004; Danilov, Syromyatnikova & Sukhanov, 2007).

The peripheral 1 is roughly triangular and longer than wide, with an oblique suture with the nuchal and a short suture with the costal 1 as in other *Shachemys* species.

The bridge peripheral is located on the middle part of the bridge, with open anterior and posterior ends. The width of the dorsal portion is more than twice that of the ventral portion. The angle between the dorsal and ventral sheets is 90 degrees. The medial edge of the ventral sheet shows the ligamentous attachment to the plastron as in other *Shachemys* spp. On the inner surface of the dorsal sheet at about the mid-length of the plate, there is a mediolaterally directed elongate scar for the insertion of a long free rib end from the costal plate.

The marginals are included in the peripheral. The pleuromarginal sulcus is angled with the tip extending to more than one-third of the width of the peripheral. In comparison, both *Shachemys baibolatica* and *S.*



Figure 5. (Colour online) Turtle remains from the Xinlong Formation of Napai Basin: (a) *Shachemys* sp., right peripheral 1; and (b) *Kizylkumemys* sp. left hypoplastron. Scale bar: 20 mm.

*ancestralis* have narrower marginals with straight lateral sulci, while in *S. laosiana* the marginals are wider with the pleuromarginal sulci almost lining up the costoperipheral sutures. The condition in the Xinlong *Shachemys* therefore seems to be intermediate.

### 3.c.2. *Carettochelyidae* Boulenger, 1887

*Kizylkumemys* sp.: The material includes a complete right hypoplastron, an almost complete peripheral and an incomplete costal from Xiamiao locality; an incomplete peripheral is partly preserved as an imprint from Liubangcunxi locality.

The outer surface of the costal plate is covered with anteroposteriorly directed vermiculated ridges, typical of *Kizylkumemys* (Tong *et al.* 2005).

The dorsal surface of a small bridge peripheral is covered with anteroposteriorly directed vermiculated parallel ridges, while irregular tubercles cover the ventral surface. The dorsal and ventral sheets form an angle of 45 degrees. A pocket is visible on the border for reception of the free rib end of the costal. A clear sulcus runs transversally through the dorsal surface of the plate.

The hypoplastron is 28 mm wide, 14 mm long at midline and 11 mm long on the lateral border. The outer surface is covered with a pitted ornamentation as in *Kizylkumemys*. There are no sulci, which indicates that scutes were absent from the plastron. The plate is thick, with the thickest point (6 mm) at the middle of the medial border. The plate becomes thinner laterally. The bridge is wide and short. The posterior lobe is very narrow at the base. The lateral margin of the plate bears a series of pegs; the most posterior peg is the largest. On the inner surface, there is a groove located on the posterior part close to the lateral border for the insertion of a peg from the xiphiplastron.

Although turtle remains from the Xinlong Formation of the Napai Basin are fragmentary, which prevents a more precise assignment, this turtle assemblage is interesting in several respects. From a stratigraphical point

of view, the composition of the turtle assemblage from the Xinlong Formation closely resembles that from the mid-Cretaceous Khok Kruat Formation, NE Thailand, in the presence of the adocid *Shachemys* and the carettochelyid *Kizylkumemys* (Tong *et al.* 2005, 2009). A close resemblance is also noticed between the Xinlong turtle fauna and that of the Grès supérieurs Formation in Savannakhet Province, Laos, a lateral equivalent of the Khok Kruat Formation of Thailand (Bufetaut, 1991), where both *Shachemys* and small carettochelyid turtles are present (Lapparent de Broin *de*, 2004). In the underlying Sao Khua Formation in Thailand, the presence of *Kizylkumemys* is attested but no *Shachemys* is reported; instead, there is a more primitive adocid, *Isanemys* (Tong *et al.* 2004; Tong, Bufetaut & Suteethorn, 2006). This supports the conclusion that the Xinlong Formation is coeval with the Khok Kruat Formation in Thailand and the 'Grès supérieurs' Formation in Laos, which are Aptian in age.

### 3.d. Crocodylia

Crocodylian remains are not abundant in the Xinlong Formation. Only a few small isolated teeth have been discovered. Some are conical and pointed and show few distinguishing features; others have a low rounded, laterally compressed crown and bear ridges on their lingual and labial faces, as well as coarse serrations along their carinae (Fig. 6d). The proposal that both types of teeth belong to the same taxon cannot be ruled out since such heterodonty is known to occur in various crocodylians, the pointed conical teeth being in a more mesial position than the blunt teeth which are located in the posterior part of the jaws.

The blunt teeth are reminiscent in their shape and ornamentation of the teeth of atoposaurid crocodylians, in particular *Theriosuchus*. The latter genus is known from the Mesozoic succession of Thailand (Lauprasert *et al.* 2011) with the species *Theriosuchus grandinaris*,



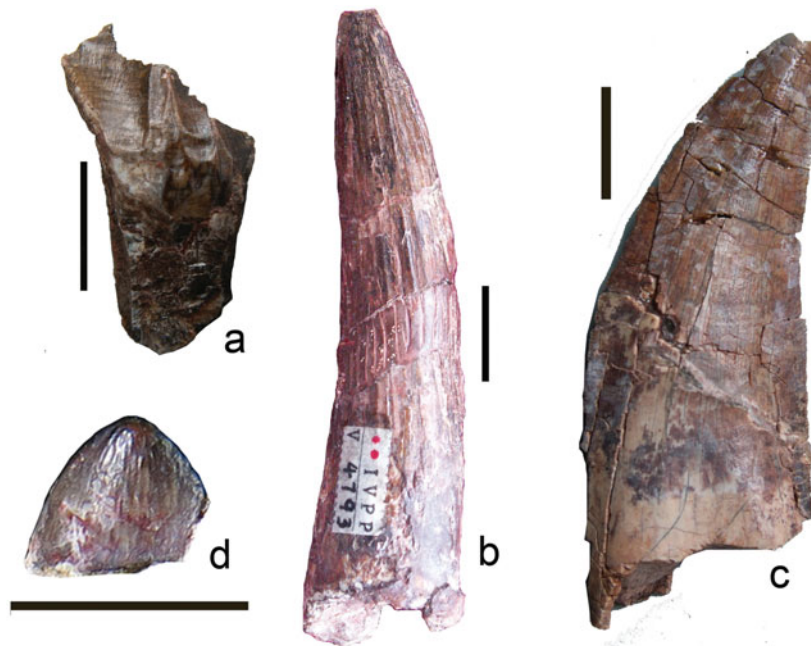


Figure 6. (Colour online) Archosaur teeth from the Xinlong Formation of the Napai Basin: (a) iguanodontian; (b) spinosaurid; (c) carcharodontosaurid; and (d) *Theriosuchus*-like crocodylian. Scale bars: 10 mm.

based on a skull from the Barremian Sao Khua Formation, a dentary from the Phu Kradung Formation (latest Jurassic – basal Cretaceous) and an isolated tooth from the Khok Kruat Formation (Aptian). The latter tooth shows strong similarities with one of the specimens from the Xinlong Formation.

### 3.e. Dinosauria

The dinosaur remains from the Xinlong Formation belong to Theropoda, Sauropoda and Ornithischia. A recent review was published by Mo, Huang & Xie (2013).

#### 3.e.1. Sauropoda

The first sauropod specimens reported from the Xinlong Formation were an isolated spatulate tooth, three broken cervical vertebrae and ribs described by Hou, Yeh & Zhao (1975) as belonging to a new species, *Asiatosaurus kwangshiensis*. *Asiatosaurus* is a sauropod genus originally described by Osborn (1924), with *Asiatosaurus mongoliensis* based on isolated spatulate teeth from the Lower Cretaceous rocks of Mongolia, as type species. Both *Asiatosaurus mongoliensis* and *A. kwangshiensis* are considered as *nomina dubia* by Upchurch, Barrett & Dodson (2004). Some more recently discovered sauropod teeth from the Xinlong Formation are spatulate, such as that described by Hou, Yeh & Zhao (1975). However, peg-shaped teeth also occur, indicating that more than one taxon is present.

More complete sauropod material was discovered in the Xinlong Formation, near the village of Liubang. Remains of three individuals were recovered from the quarry (Mo, Xu & Buffetaut, 2010). A partial skeleton from Liubang consisting of vertebrae, ribs and pelvic

and limb elements was described by Mo *et al.* (2006) as *Fusuisaurus zhaoi*, considered as a basal titanosauriform (Fig. 7). Also from the Liubang quarry, *Liubangosaurus hei* was described by Mo, Xu & Buffetaut (2010) on the basis of five articulated dorsal vertebrae showing distinctive features (Fig. 8). This taxon is considered as a relatively basal eusauropod. Reasons for considering *Fusuisaurus zhaoi* and *Liubangosaurus hei* as two distinct taxa were provided by Mo, Xu & Buffetaut (2010).

The sauropod assemblage from the Xinlong Formation therefore includes at least two distinct taxa as shown by both teeth and skeletal remains, although it is not possible to clearly associate the different types of teeth with the taxa based on skeletal remains. As noted by Mo, Xu & Buffetaut (2010), basal titanosauriforms are common in the Lower Cretaceous deposits of Asia, but they are not the only group of sauropods to have been reported. Both *Fusuisaurus* and *Liubangosaurus* are currently known only from the Xinlong Formation, so that comparisons with sauropods from other regions are difficult. *Phuwiangosaurus sirindhornae*, a basal titanosauriform (Suteethorn *et al.* 2009, 2010) with peg-like teeth, is abundant in the Barremian Sao Khua Formation in SE Asia, but at least one more sauropod is present (Buffetaut *et al.* 2002). The sauropods from the Aptian Khok Kruat Formation of Thailand are still poorly known, although peg-like teeth are relatively common. In Laos, the titanosauriform *Tangvayosaurus hoffeti* (Allain *et al.* 1999) is known from the Grès Supérieurs Formation that should be considered as a lateral equivalent of the Khok Kruat Formation (Buffetaut, 1991). The sauropod assemblage from the Xinlong Formation therefore does not seem unusual for the Lower Cretaceous deposits of Asia in general

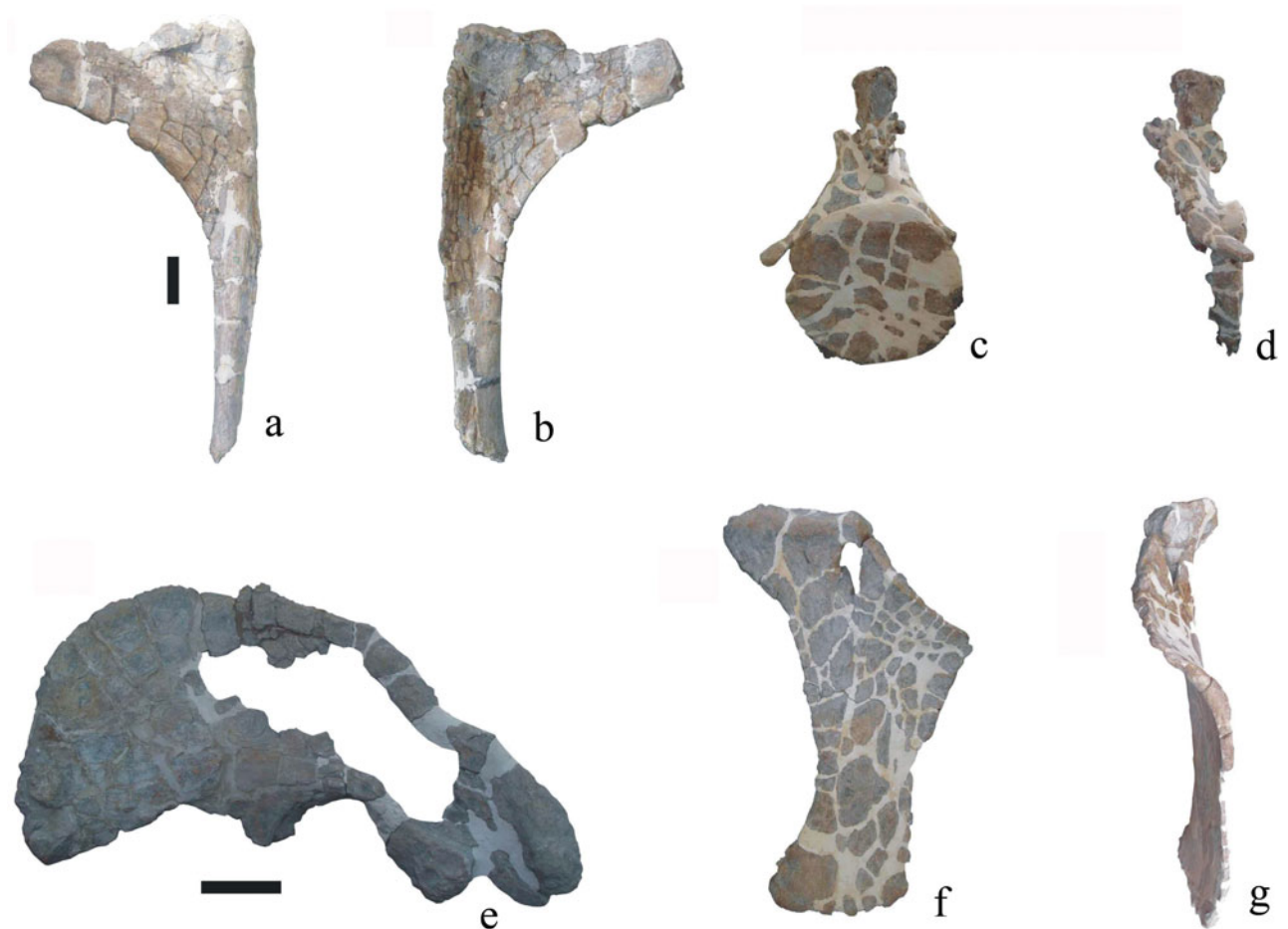


Figure 7. (Colour online) Skeletal elements of the sauropod dinosaur *Fusuisaurus zhaoi*, from the Xinlong Formation of the Napai Basin (after Mo *et al.* 2006): (a, b) left anterior dorsal rib in anterior (a) and posterior (b) views; (c, d) anterior caudal vertebra in posterior (c) and lateral (d) views; (e) left ilium (lateral view); and (f, g) left pubis in lateral (f) and posterior (g) views. Scale bars: 10 cm for (a–d) and 20 cm for (e–g).

and does not seem to indicate special biogeographical affinities.

### 3.e.2. Theropoda

Carcharodontosauridae: Hou, Yeh & Zhao (1975) described four isolated theropod teeth from the Xinlong Formation as a new species of the genus *Prodeinodon*, *P. kwangshiensis*. The genus *Prodeinodon*, with *P. mongoliensis* as type species, was erected by Osborn (1924) on the basis of isolated teeth from Lower Cretaceous deposits of Mongolia. It is considered as a *nomen dubium* by Holtz, Molnar & Currie, 2004. Teeth generally similar to those described by Hou, Yeh & Zhao (1975) are fairly common in the Xinlong Formation (Fig. 6c). They are strongly compressed laterally, with a convex mesial margin and a nearly straight distal margin. The carinae bear well-marked serrations. Mo *et al.* (2014 a) described an especially large tooth of that type as Carcharodontosauridae gen. et sp. indet., noting that it differs in some respects from the teeth described by Hou, Yeh & Zhao (1975). It should be noted that carcharodontosaur postcranial remains from the Xinlong Formation of the Datang Basin of Guangxi, east of the Napai Basin, were described as *Datanglong*

*guangxiensis* by Mo *et al.* (2014 b). The occurrence of carcharodontosaurs in the Xinlong Formation is therefore well established. Carcharodontosaurids are now known from various Cretaceous localities in China, including Inner Mongolia (Upper Cretaceous: Brusatte *et al.* 2009), Henan (Lower Cretaceous: Lü *et al.* 2009) and Xinjiang (Lower Cretaceous: Brusatte, Benson, & Xu, 2012). In SE Asia, carcharodontosaurids have been reported from the Barremian Sao Khua Formation (Buffetaut & Suteethorn, 2012) and the Aptian Khok Kruat Formation (Azuma *et al.* 2011) of Thailand.

Spinosauridae: As shown by Buffetaut *et al.* (2008), the isolated teeth originally described as the putative freshwater pliosaur *Sinopliosaurus fusuiensis* by Hou, Yeh & Zhao (1975) actually belong to spinosaurid theropods. Isolated spinosaurid teeth (Fig. 6b) are relatively common in the Xinlong Formation. The characters of these teeth are similar to those of spinosaurid teeth from Thailand (Buffetaut & Ingavat, 1986) and Japan (Hasegawa *et al.* 2003), with well-developed longitudinal ridges on both faces of the crown and a finely wrinkled enamel (also reported in North African spinosaurids: Hasegawa *et al.* 2010). In Thailand, spinosaurids are known from both the Sao Khua and Khok Kruat formations. As it is currently not possible to



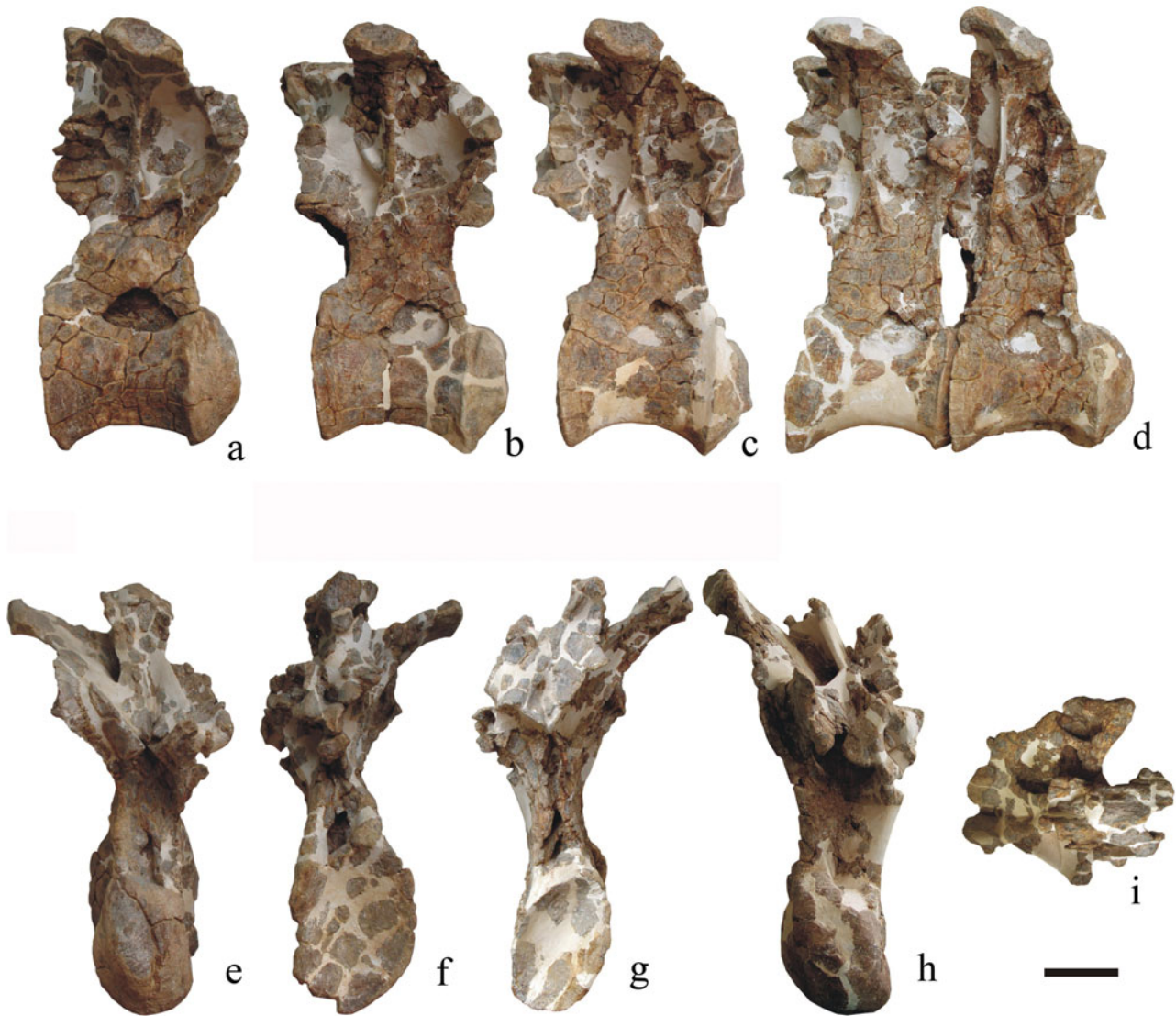


Figure 8. (Colour online) Skeletal elements of the sauropod dinosaur *Liubangosaurus hei*, from the Xinlong Formation of the Napai Basin (after Mo, Xu & Buffetaut, 2010): (a–d) 5th to 9th dorsal vertebrae in right lateral view; (e, f) 9th dorsal in (e) anterior and (f) posterior views; (g) 6th dorsal in posterior view; (h) 5th dorsal in anterior view; and (i) 7th dorsal in dorsal view. Scale bar: 10 cm.

distinguish the spinosaurids from these two formations on the basis of tooth morphology, it cannot be determined whether the form from the Xinlong Formation is more reminiscent of those from one Thai formation or another. Comparisons with the spinosaur *Ichthyovenator* from Laos (Allain *et al.* 2012) are not currently possible because no teeth have yet been described for that taxon.

It may be noted that tooth material from the Xinlong Formation was used for the geochemical study of oxygen isotopes in spinosaurid teeth that led to the demonstration of semi-aquatic habits in these dinosaurs (Amiot *et al.* 2010).

### 3.e.3. *Ornithischia*

Ornithopoda: Dong (1979) was the first to report the occurrence of ornithopod dinosaurs in the Xinlong Formation. However, he provided very little information about the available material. Since then, vari-

ous ornithopod remains have been collected from the Xinlong Formation. Most are isolated postcranial elements, including vertebrae and incomplete limb bones (Fig. 9a–d), which indicate the presence of iguanodontians but cannot be identified more precisely. A few teeth have also been found, but they are not well preserved. The best specimen is a lower tooth showing part of the root and crown (Fig. 6a). The crown seems to have been somewhat fan-shaped and bears a strong median primary ridge and at least one subsidiary ridge (there may have been more, but the apical region of the crown is missing). The morphology of this tooth suggests a relatively advanced iguanodontian, but it is too incomplete to warrant a more precise identification.

Advanced iguanodontians sometimes referred to as ‘basal hadrosauroids’ were widespread in Asia during the later part of Early Cretaceous time (see review in Buffetaut & Suteethorn, 2011) and their presence in the Xinlong Formation is not surprising, especially considering that they are known from SE Asia. In Thailand,

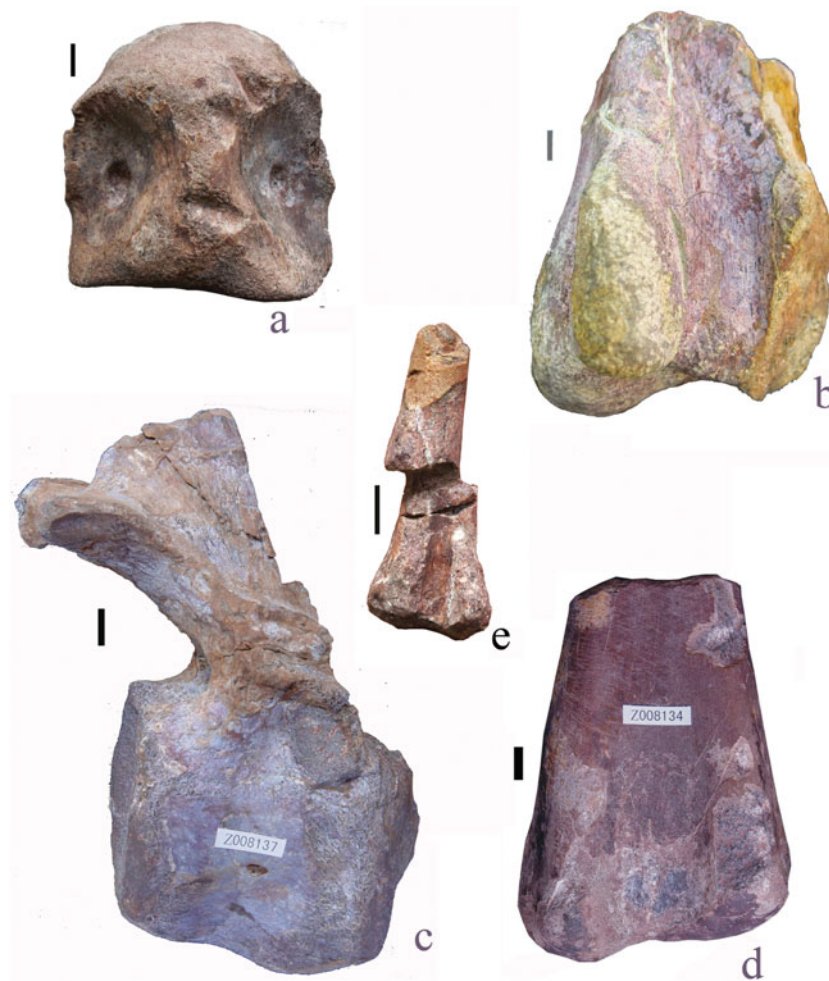


Figure 9. (Colour online) Ornithischian bones from the Xinlong Formation of the Napai Basin: (a) iguanodontian cervical vertebra, ventral view; (b) distal end of iguanodontian left femur, posterior view; (c) iguanodontian dorsal vertebra, right lateral view; (d) distal end of iguanodontian left humerus, anterior view; and (e) distal end of small ornithischian (psittacosaurid?) right femur, posterior view. Scale bars: 10 mm.

they are conspicuously absent from the Barremian Sao Khua Formation but occur in the Aptian Khok Kruat Formation with at least two taxa: *Siamodon nimngami* Buffetaut & Suteethorn, 2011 and *Ratchasimasaurus suranareae* Shibata, Jintasakul & Azuma, 2011. Advanced iguanodontians are also known from Lower Cretaceous rocks in Laos that are in all likelihood a lateral equivalent of the Khok Kruat Formation (Hoffet, 1944; Buffetaut, 1991). Although the material from the Xinlong Formation is too scanty for systematically significant comparisons, the absence of ornithopods in the Sao Khua Formation and their presence in the Khok Kruat Formation suggests that the Xinlong Formation is closer in age to the latter.

**Ceratopsia?:** A small incomplete femur (Fig. 9e), lacking the proximal end, is generally similar to that of psittacosaurids. This group of early ceratopsians is abundantly represented in the Lower Cretaceous rocks of northern Asia, including northern and western China, Mongolia and Siberia (Averianov *et al.* 2006; Lucas, 2006), and is also known from the Khok Kruat Formation of Thailand (Buffetaut & Suteethorn, 1992; Buffetaut, Suteethorn & Khansubha, 2007) and from

beds of similar age in Laos. Its occurrence in the Xinlong Formation would not be unexpected. However, the poor quality of the available material renders its identification highly tentative.

#### 4. Stable oxygen and carbon isotope compositions of reptile apatites

Nine tooth and bone remains recovered from the Liubangcun locality were sampled and analysed for their stable oxygen and carbon isotope compositions of apatite phosphate and carbonate. Theropod tooth remains belong to the indeterminate Carcharodontosauridae and to an indeterminate spinosaurid. Two sauropod teeth have been sampled, one having a spoon-like shape and the other having a peg-like shape. Because available teeth were too fragmentary, both enamel and dentine were used for stable isotope measurement and ground into fine powder. The cortical part of a long bone of *Fusuisaurus zhaoi* was also sampled with a microdrill, as well as the coarse part of a turtle shell fragment.

Samples were prepared and their oxygen isotope compositions of the apatite phosphate ( $\delta^{18}\text{O}_p$ ) were

Table 1. Taxon and phosphatic tissue and oxygen and carbon isotope compositions of apatite phosphate and carbonate of reptile samples from the Xinlong Formation. All values have been previously published (Amiot *et al.* 2010, 2011, 2015).

Sample No.	Material	Taxon	$\delta^{18}\text{O}_{\text{PO}_4}$ (‰ VSMOW)	$\delta^{18}\text{O}_{\text{CO}_3}$ (‰ VSMOW)	$\delta^{13}\text{C}_{\text{CO}_3}$ (‰ VPDB)
NP01	Tooth bulk	Carcharodontosauridae indet.	17.3	21.2	-2.8
NP02	Tooth bulk	Carcharodontosauridae indet.	17.8	21.3	-3.6
NP03	Tooth bulk	Spinosauridae indet.	14.7	18.6	-5.8
NP04	Shell bone	Chelonia indet.	14.7	19.7	-5.0
NP05	Bone	<i>Fusuisaurus zhaoi</i>	19.0	21.8	-5.5
NP06	Tooth bulk	Theropoda indet.	17.5	18.8	-4.2
NP07	Tooth bulk	Spinosauridae indet.	16.4	18.2	-3.5
NP08	Tooth bulk	Sauropoda indet. (S)	24.5	27.7	-4.2
NP09	Tooth bulk	Sauropoda indet. (P)	20.5	24.2	-3.7

measured using a Thermo-Finnigan MAT253 at the Institute of Geology and Geophysics (Chinese Academy of Sciences, Beijing, China) following protocols detailed in Lécuyer (2004), and published as part of a larger dataset (Amiot *et al.* 2010, 2011, 2015). Prior to oxygen ( $\delta^{18}\text{O}_c$ ) and carbon ( $\delta^{13}\text{C}_c$ ) isotope measurement of apatite carbonate, samples were pre-treated following the procedure of Koch, Tuross & Fogel (1997). For each sample, a 2 mg aliquot of pre-treated powder was analysed at the Institute of Geology and Geophysics using a Thermo-Finnigan Gasbench II connected to a MAT253 mass spectrometer following a procedure adapted from Spoetl & Vennemann (2003). The measured carbon and oxygen isotopic compositions were normalized relative to the NBS-19 calcite standard, which gave a reproducibility for the carbon and oxygen isotopic compositions of apatite carbonate better than  $\pm 0.1$  ‰ and  $\pm 0.2$  ‰, respectively. Carbon and oxygen isotopic compositions are expressed as  $\delta$  values relative to V-PDB for carbon and V-SMOW for oxygen (Table 1).

The effect of diagenetic alteration on the oxygen isotope compositions of reptile apatite phosphates was assessed by Amiot *et al.* (2010, 2011, 2015); samples are considered to have kept their original  $\delta^{18}\text{O}_p$  values. Apatite carbonates are also assumed to have at least partially preserved their original stable isotope compositions based on the significant correlation existing between carbonate and phosphate  $\delta^{18}\text{O}$  values (Fig. 10).

Oxygen isotope compositions of reptile apatites range from 14.7 ‰ to 24.5 ‰. Turtles have  $\delta^{18}\text{O}$  values of *c.* 3–10 ‰ lower than theropods and sauropods; this is a result of their aquatic ecology, which results in lower transcutaneous evaporation than fully terrestrial dinosaurs (Fig. 11). It is noteworthy that teeth from the indeterminate spinosaurid have low  $\delta^{18}\text{O}_p$  values in the range of aquatic turtles. From the analysis of a larger dataset including the values discussed here, it has been shown that most spinosaurs, including the Xinlong form had semi-aquatic lifestyles, spending most of their time in water in the same way as modern hippopotamuses or crocodylians (Amiot *et al.* 2010).

Using available phosphate–water oxygen isotope fractionation equations and the relationship existing between the  $\delta^{18}\text{O}$  value of meteoric water and mean air temperature, an average air temperature of  $19 \pm 5$  °C

has been previously estimated (Amiot *et al.* 2011). Considering the low palaeolatitude of the Liubangcun locality ( $21.0 \pm 7.2$  °N), this estimate is similar to modern temperatures occurring today at similar subtropical latitudes. During the deposition of the Xinlong Formation, East Asia was submitted to a global icehouse climate with temperatures similar to present-day conditions occurring from low to middle latitudes (Amiot *et al.* 2011).

One sauropod spoon-like tooth has a  $\delta^{18}\text{O}_p$  value of 24.5 ‰. This particularly elevated value suggests that either some local drinking water sources were  $^{18}\text{O}$ -enriched relative to others, probably as a result of temporary or seasonally dry environmental conditions, or that this sauropod was obtaining most of its water from leaf water (usually  $^{18}\text{O}$ -enriched relative to local surface waters by several permils).

Carbon isotope compositions of apatites range from -5.8 ‰ to -2.8 ‰ (Table 1). Assuming an apatite-diet carbon isotope fractionation of *c.* 16 ‰ for sauropod dinosaurs (Tütken, 2011), local plants ingested by sauropods had  $\delta^{13}\text{C}$  values between -21.5 ‰ and -19.7 ‰. These values fall within the range of plants using the  $\text{C}_3$  photosynthetic pathway, but at the upper limit. Abiotic factors indirectly influence the carbon isotopic compositions of  $\text{C}_3$  plants by affecting leaf stomatal conductance which in turn constrains the magnitude of  $\text{CO}_2$  diffusion through plant epidermis (which is the main source of plant carbon). As plants growing under water stress tend to diminish their leaf stomatal conductance in order to avoid water loss, their carbon isotope compositions are comparatively  $^{13}\text{C}$  enriched. Considering the elevated  $\delta^{13}\text{C}$  values of plants ingested by sauropods, it is likely that local vegetation at the Liubangcun locality was growing in environments experiencing low amounts of precipitation or seasonal droughts, hence the extremely elevated  $\delta^{18}\text{O}_p$  value measured on the sauropod tooth. As  $\text{C}_3$  plants have  $\delta^{13}\text{C}$  values significantly correlated to mean annual precipitation (MAP; Diefendorf *et al.* 2010; Kohn, 2010), an average amount of annual precipitation of *c.*  $400 \pm 60$  mm  $\text{a}^{-1}$  has been estimated using the average  $\delta^{13}\text{C}$  value of local vegetation, itself estimated from average sauropod teeth  $\delta^{13}\text{C}$  values (Amiot *et al.* 2015). According to these climate parameters (mean annual temperature or MAT of 19 °C; MAP 400 mm  $\text{a}^{-1}$ ), this part of South China experienced subtropical arid conditions during the



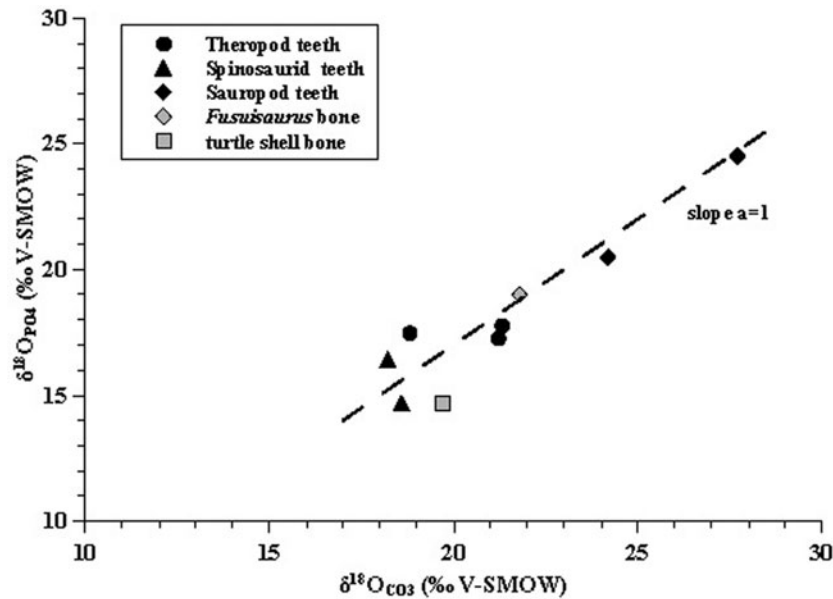


Figure 10. Oxygen isotope compositions of apatite phosphate ( $\delta^{18}\text{O}_p$ ) from studied reptile taxa plotted against their corresponding oxygen isotope composition of carbonate ( $\delta^{18}\text{O}_c$ ), along with the fitted line having a slope of 1 ( $a = 1$ ).

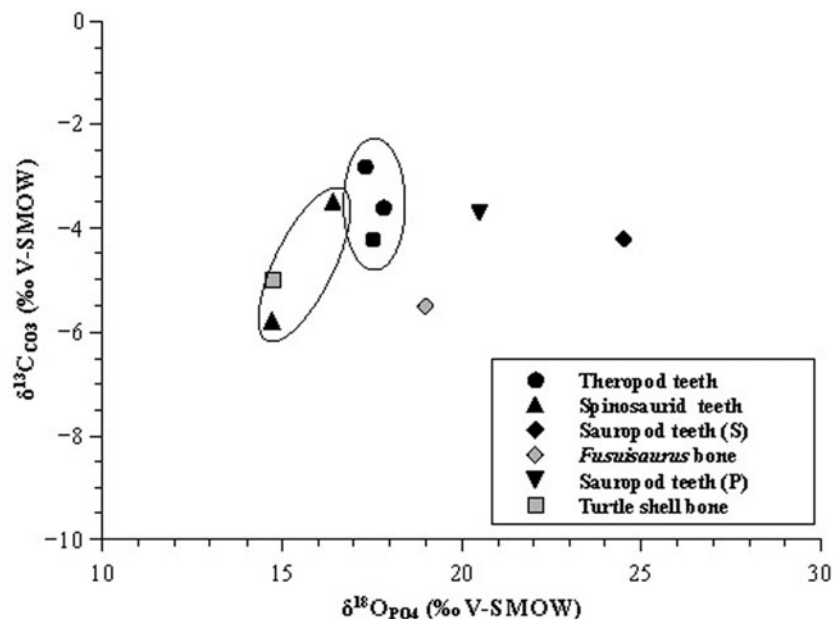


Figure 11. Oxygen isotope compositions of apatite phosphate ( $\delta^{18}\text{O}_p$ ) from studied reptile taxa plotted against their corresponding carbon isotope composition of carbonate ( $\delta^{13}\text{C}_c$ ). P – peg-like teeth; S – spoon-like teeth.

deposition of the Xinlong Formation, despite the close proximity to the ocean. Coastal mountain ranges such as the Coastal Cordillera may have acted as a barrier (rain shadow effect), preventing moisture from oceanic domains from penetrating inland and reaching this part of Guangxi (Amiot *et al.* 2015). A more extensive isotopic study of this fauna will allow a refinement of these preliminary interpretations.

##### 5. Age and palaeobiogeographical relationships of the Xinlong Formation vertebrate assemblage

Hou, Yeh & Zhao (1975) referred the ‘Napai’ Formation to Early Cretaceous time on the basis of its ver-

tebrate and bivalve fossils, and there is no reason to question that age assignment. However, a more accurate placement within the Early Cretaceous period may be possible on the basis of comparisons with other vertebrate assemblages from eastern Asia. Interestingly, comparison with well-known Early Cretaceous faunas from northern China, such as the Jehol Biota, does not reveal significant similarities as there are apparently relatively few taxa in common (*Psittacosaurus* may be an exception, but its presence in the Xinlong Formation is still poorly supported). The reasons for this lack of similarity between the Early Cretaceous faunal assemblages of NE China and those of Guangxi are many. A first point to be

considered is the different depositional environments in which the fossil-bearing formations were formed. The Jehol Biota occurs in fine-grained lacustrine sediments in which vertebrate skeletons are often exquisitely preserved. The red beds of the Xinlong Formation are fluvial deposits with conglomerates indicative of high energy, and the vertebrate remains they contain tend to be fragmentary. Beyond taphonomic questions, the different depositional environments may partly explain faunal differences, insofar as they reflect different habitats.

Another explanation for the observed differences may be faunal provincialism. By Early Cretaceous times, the South China and North China blocks or microcontinents had been in contact for a long time (Metcalf, 2009), and there was no marine barrier between them. However, other kinds of barriers may have led to a differentiation of the vertebrate faunas of southern and northern China. Fernandez *et al.* (2009) suggested mountain ranges, such as the Qinling–Dabie orogenic belt resulting from the collision between the Sino-Korean and Yangtze cratons in central China (see Xu *et al.* 2000) as possible barriers. Climatic causes may also have played a part (as already suggested by Dong, 1993): as shown by Amiot *et al.* (2011, 2015) on the basis of isotopic evidence, NE China was apparently subjected to significantly colder climates than southern China and SE Asia.

Since faunal comparisons are difficult between the vertebrate assemblage from Guangxi and those from northern China, biostratigraphic correlations between these regions cannot provide much evidence regarding the age of the Xinlong Formation.

On the contrary, as noted in Section 3, various fossil vertebrates found in the Xinlong Formation show close affinities with forms from Early Cretaceous formations in SE Asia, notably on the Khorat Plateau of NE Thailand where the main Early Cretaceous vertebrate-bearing formations are the Sao Khua Formation, now considered as Barremian in age on the basis of bivalves (Tumpeesuwan, Sato & Nakhpadungrat, 2010), and the Khok Kruat Formation, referred to the Aptian on the basis of various biostratigraphical markers (Buffetaut *et al.* 2005) including palynomorphs (Racey & Goodall, 2009). This was already noted by Buffetaut, Suteethorn & Tong (2006) who considered that the dinosaur assemblage from the ‘Napai’ Formation was similar to that from the Sao Khua Formation, but noted that the ornithopods from Guangxi mentioned by Dong (1979) had no counterpart in the Sao Khua Formation (making the correlation uncertain). As described in Section 3, however, several vertebrate groups from the Xinlong Formation show interesting similarities to those from the Khok Kruat Formation. These resemblances can be summarized as follows:

- Chondrichthyes: although *Heteroptychodus* has a longer stratigraphic range, the taxa *Hybodus aequitridentatus*, *Acrorhizodus khoratensis* and *Khoratodus foreyi* were previously restricted to the

Khok Kruat Formation. Their presence in the Xinlong Formation strongly supports an identical age for both formations.

- Testudines: both the adocid *Shachemys* and the carretochelyid *Kizylkumemys* occur in both the Xinlong Formation and the Khok Kruat Formation. *Kizylkumemys* is also known from the Sao Khua Formation, but *Shachemys* is not. This strongly suggests that the Xinlong and Khok Kruat formations are coeval.
- Dinosauria: among Theropoda, both Spinosauridae and Carcharodontosauridae occur both in Guangxi and in Thailand. In Thailand, both families are known from the Sao Khua Formation (Buffetaut & Ingavat, 1986; Buffetaut & Suteethorn, 2012) as well as from the Khok Kruat Formation (Buffetaut *et al.* 2005; Azuma *et al.* 2011). However, a significant difference between the dinosaur faunas from these formations is that ornithischian dinosaurs have never been reported from the Sao Khua Formation, while they are represented in the Khok Kruat Formation by both psittacosaurids (Buffetaut & Suteethorn, 1992; Buffetaut, Suteethorn & Khansubha, 2007) and hadrosauroid ornithopods (Buffetaut & Suteethorn, 2011; Shibata, Jintasakul & Azuma, 2011). Although the occurrence of psittacosaurids in the Xinlong Formation must still be regarded as tentative, ornithopods are clearly present, which supports correlation with the Khok Kruat Formation.

On the basis of the above-mentioned close similarities, it seems legitimate to consider that the vertebrate assemblages from the Xinlong and Khok Kruat formations are roughly coeval. This biostratigraphic correlation leads to the conclusion that the Xinlong Formation is, in all likelihood, Aptian in age.

From a palaeobiogeographical point of view, the above-mentioned close similarities between the vertebrates from the Xinlong Formation of Guangxi and those from the Khok Kruat Formation of NE Thailand strongly suggest that both areas were part of the same zoogeographical province during Early Cretaceous time (Fig. 12). The distance between the Khorat Plateau and the Napai Basin is *c.* 900 km today and was probably not much greater during Early Cretaceous time. Metcalfe’s palaeogeographical maps (Metcalf, 2009) show that the Indochina Block (which includes the Khorat Plateau) and the South China block were in close contact during Early Cretaceous time, and had been so since at least Late Triassic time. It is therefore not surprising that the southern part of the South China Block and the Indochina Block had the same vertebrate fauna during Aptian time. As noted above, this fauna was apparently significantly distinct from that of more northern parts of China, especially from the fossil assemblages of the Jehol Biota. Although there are several possible reasons for this, as discussed above, current evidence suggests the existence of a distinct SE Asian zoogeographical province, which included both SE Asia proper and parts of South

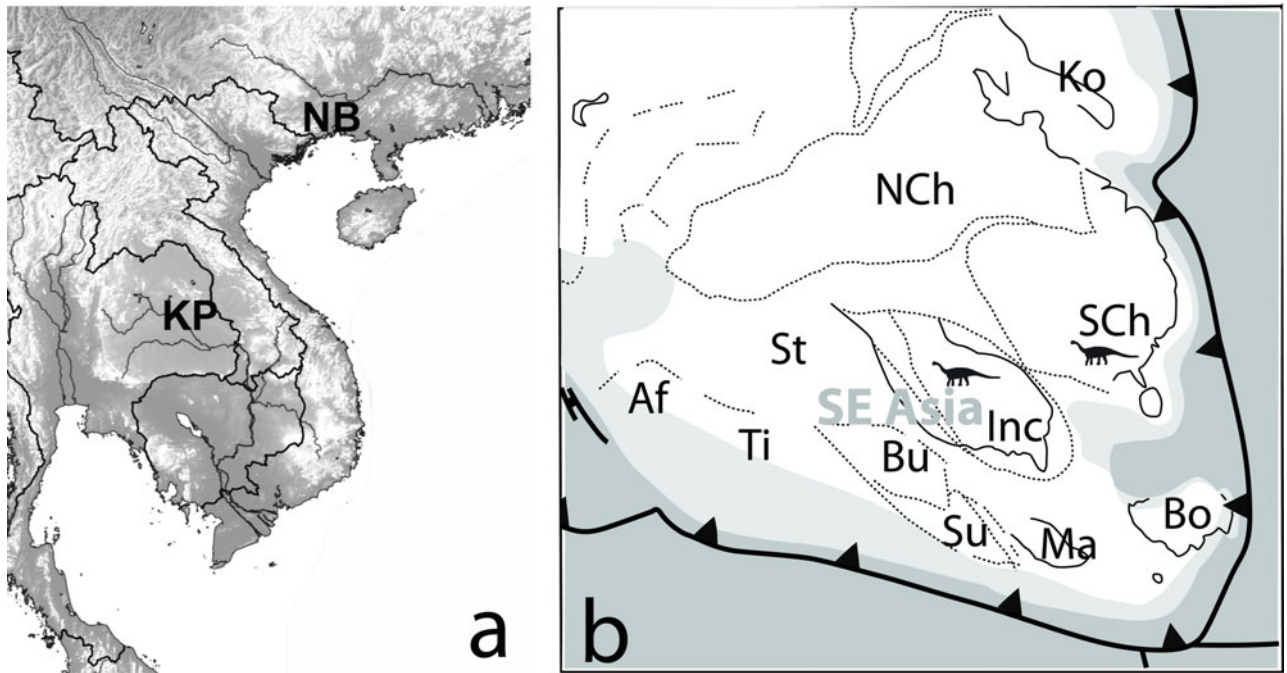


Figure 12. (Colour online) Geography and palaeogeography. (a) Present locations of the Khorat Plateau (KP) and the Napai Basin (NB). (b) Palaeogeographical map of eastern Asia for the mid-Cretaceous period, modified after Vrielynck & Bouysse (2001). The dinosaur silhouettes show the locations of the Khorat Plateau and the Napai Basin. Af – Afghanistan; Bo – Borneo; Bu – Burma; Inc – Indochina; Ko – Korea; Ma – Malaysia; NCh – North China; SCh – South China; St – Shan–Thai; Su – Sumatra; Ti – Tibet.

China, during Early Cretaceous time. It should be noted that in a review of the Early Cretaceous dinosaur faunas of China, Dong (1993) already suggested that distinct northern (*Psittacosaurus* fauna) and southern provinces could be distinguished, the relatively poorly known southern province (including the Guangxi localities) being characterized by the absence of psittacosaurids. Finds of psittacosaurids in Thailand and Laos, and possibly in Guangxi, show that this group was present in the southern region as we envision it, but it seems to have been less abundant there than in the northern parts of China. Such a regional provincialism has also been suggested on the basis of the distribution of sinamiid fishes, which are known in several Early Cretaceous eastern Asian localities and in the Barremian Sao Khua Formation in Thailand (Cavin *et al.* 2007). Where the northern boundary of that southern province was located remains uncertain. Comparisons between the Early Cretaceous southern assemblages and those from central China may provide interesting evidence. The occurrence of the turtle *Kizylkumemys*, originally described from Central Asia, is also interesting and suggests that more comparisons with other vertebrate assemblages should be performed. As noted above, some higher-level groups of vertebrates occurring in the Xinlong Formation, such as carcharodontosaurs and iguanodonts, had a wide distribution during Early Cretaceous time in Asia; however, biogeographical comparisons should be made at a lower taxonomic level to be significant, and the material from Guangxi is sometimes too fragmentary to make this possible.

## 6. Conclusions

The diverse fossil assemblage from the Xinlong Formation of Guangxi is a rare instance of an Early Cretaceous (in all likelihood Aptian) vertebrate fauna from southernmost China. Recent fieldwork has confirmed the potential of this formation as a source of vertebrate fossils, and it is expected that the faunal list will become more extensive in the future as more material is unearthed. The biogeographical affinities of the Xinlong assemblage seem to be more with faunas from SE Asia, notably Thailand, than with assemblages from northern China. This suggests the possible existence of a distinct 'southern' zoogeographical region in eastern Asia during Early Cretaceous time. The causes of such a faunal provincialism are still unclear, as there were no obvious major geographical barriers between the northern and southern parts of China at that time. Differences in climate may have played a part, as suggested by geochemical evidence.

**Acknowledgements.** RA was supported by the National Basic Research Program of China grant 2012CB821900. EB's research in Guangxi is supported by CNRS. J-YM was supported by the National Natural Science Foundation of China. We thank Chaolin Huang and Shaowen Xie for their contributions in the field. The final version of the paper was improved by the useful comments of two anonymous reviewers.

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