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The dinosaur fauna of the Sao Khua Formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia

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Abstract

The most abundant and most diverse dinosaur remains hitherto found in Thailand come from the Sao Khua Formation, now considered pre-Aptian, Early Cretaceous in age. This assemblage includes theropods (the early and primitive tyrannosaurid *Siamotyrannus isanensis*; an early but relatively advanced ornithomimosaur; the enigmatic *Siamosaurus suteethorni*, and possibly another, very small theropod) and sauropods (*Phuwiangosaurus sirindhornae* and another, poorly known taxon). The Sao Khua fauna, which includes neither *Psittacosaurus* nor iguanodontids, seems to be older than any of the vertebrate assemblages from the Gobi Basin. Several of the dinosaurs from the Sao Khua Formation may be close to the origin of groups that later played an important part in the dinosaur faunas of Asia ('nemegtosaurid' sauropods) or both Asia and North America (tyrannosaurids, ornithomimids).

Keywords: Cretaceous; dinosaurs; Thailand; paleogeography; evolution

1. Introduction

Since the first discoveries in the 1970s, dinosaur remains have been found at a number of sites in several of the non-marine Mesozoic formations which constitute the Khorat Group of northeastern Thailand (see Buffetaut and Suteethorn, 1993; Buffetaut et al., 1995, for recent reviews). They include a prosauropod from the Late Triassic Nam Phong Formation, recently discovered teeth of sauropods and theropods from the probably Jurassic Phu Kradung Formation, several footprint sites in the Early Cretaceous Phra Wihan Formation, abundant skeletal remains from the Early Cretaceous Sao Khua Formation, footprints from the Early Cretaceous Phu Phan Formation, and skeletal remains of theropods, ornithopods and ceratopsians (*Psittacosaurus*) from the Aptian–Albian Khok Kruat Formartion. The great majority of the dinosaurs hitherto found in Thailand come from the red clays and sandstones of the Sao Khua Formation, and this assemblage, notably because of its age, is of considerable importance for our understanding of the early stages of dinosaur evolution in Asia during the Cretaceous. The purpose of the present paper is to review what is currently known of the dinosaurs from the Sao Khua Formation, and to discuss their more general significance in this context.

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2. Age and depositional environment of the Sao Khua Formation

The Sao Khua Formation, which crops out in many parts of the Khorat Plateau of northeastern Thailand, was defined by Ward and Bunnag (1964, p. 15) "for the section of rocks between the restricted Phra Vihan and the Phu Phan Formations in the drainage area of the Huai Sao Khua", an intermittent stream between the cities of Udon Thani and Nong Bua Lamphu. As for all formations of the Khorat Group, accurate dating proved difficult because of the scarcity of stratigraphically useful fossils. Ward and Bunnag (1964), following fossil identifications by Japanese palaeontologists, considered the Sao Khua Formation as Jurassic, probably Liassic, in age. A Jurassic age was subsequently accepted by most workers, although a Late Jurassic age was generally thought more likely than a Liassic one (see reviews in Sattayarak, 1983, and Racey et al., 1994, 1996).

When vertebrate remains began to be discovered in larger numbers in the Sao Khua Formation, a Middle or Late Jurassic age seemed likely. The first discoveries revealed the occurrence of sauropod dinosaurs, which were thought to show resemblances with the Late Jurassic *Camarasaurus* (Ingavat and Taquet, 1978). The occurrence of the crocodilian genus *Goniopholis* (Buffetaut and Ingavat, 1983) which in Europe is known from both the Upper Jurassic and the Lower Cretaceous, was also in agreement with a Late Jurassic age. When the vertebrates from the Sao Khua Formation became better known, however, problems began to arise, notably because, contrary to what could logically be expected for palaeobiogeographical reasons, the abundant sauropod remains from the Sao Khua Formation bore little resemblance to the increasingly well known sauropods from the Middle Jurassic Xiashaximiao Formation and the Late Jurassic Shanshaximiao Formation of China. The discovery of a relatively advanced ornithomimosaur in the Sao Khua Formation was also unexpected in a supposedly Jurassic Formation.

Racey et al. (1994, 1996) have proposed a far-reaching reinterpretation of the ages of the Mesozoic non-marine formations of northeastern Thailand, largely based on palynological studies. According to their results, a large part of the Khorat Group in fact belongs to the Lower Cretaceous (an interpretation already suggested by Piyasin, 1985). The Phra Wihan Formation contains Early Cretaceous palynomorphs, suggesting a Berriasian to Barremian age (Racey et al., 1994, 1996), and the overlying Sao Khua Formation is necessarily Early Cretaceous, too. This is confirmed by fission track dating on detrital zircons from the Phra Wihan Formation which indicate an Early Cretaceous age (Bristow et al., 1994). The recent discovery of Early Cretaceous palynomorphs (A. Racey, pers. commun.) in a sample of Sao Khua sediments collected by the authors of the present paper from levels overlying the dinosaur site at Wat Sakawan is in agreement with this conclusion, and bivalves from the Sao Khua Formation apparently confirm an Early Cretaceous age (Meesook et al., 1995). The age of the Sao Khua Formation is further constrained by the dating of the Khok Kruat Formation, which overlies the Phu Phan Formation, which itself overlies the Sao Khua Formation. The Khok Kruat Formation has yielded the Early Cretaceous dinosaur *Psittacosaurus* (Buffetaut et al., 1989; Buffetaut and Suteethorn, 1992) and a freshwater shark, *Thaiodus ruchae*, which is otherwise known only from the Aptian–Albian of Tibet (Cappetta et al., 1990). The Khok Kruat Formation is therefore referred to the Aptian–Albian (an age partly confirmed by the occurrence of Albian–Cenomanian palynomorphs in the overlying Maha Sarakham Formation: Sattayarak et al., 1991). The Sao Khua Formation can therefore safely be placed in the Lower Cretaceous. Its exact age is still somewhat uncertain: it is probably younger than Berriasian and older than Aptian.

The depositional environment of the Sao Khua Formation has also been the subject of controversy. Ward and Bunnag (1964) considered that the rocks of the Khorat Group were essentially non-marine, and that marine ingressions had been rare. However, Kobayashi et al. (1963), on the basis of invertebrate and vertebrate fossils, proposed a marine depositional environment. The idea of marine ingressions in the Sao Khua Formation was taken up by Hahn (1982), who, on the basis of several pelecypod horizons, concluded that several marine ingressions from the Jurassic sea of western Thailand had taken place during the deposition of the Sao Khua Formation.

The bivalves found in the Sao Khua Formation are in fact non-marine (A. Meesook, pers. commun.), and the purported teeth of marine reptiles (identified as belonging to an ichthyosaur and a plesiosaur) reported by Kobayashi et al. (1963) certainly belong to continental forms: the so-called 'ichthyosaur' tooth apparently belongs to the enigmatic dinosaur *Siamosaurus*, and the 'plesiosaur' tooth is in all likelihood a crocodilian tooth. There is therefore no palaeontological evidence for marine ingressions in the Sao Khua Formation. Mouret et al. (1993) have interpreted the depositional environment of the Sao Khua Formation as "a very extensive flood plain having low energy meandering rivers". Racey et al. (1996, p. 26) came to a very similar conclusion, describing the sandstones and mudstones of the Sao Khua Formation as having been "deposited in low-energy, meandering fluvial channels and extensive floodplains which were modified by pedogenesis". The vertebrate fauna from the Sao Khua Formation, which includes only freshwater and terrestrial forms (freshwater hybodont sharks, turtles, the freshwater crocodilian *Goniopholis* and various dinosaurs) is in agreement with these recent reconstructions.

3. The dinosaurs from the Sao Khua Formation

The first dinosaur bone to be reported from the Sao Khua Formation, the distal end of a sauropod femur, was found at Phu Wiang (Khon Kaen Province) in 1976 by Mr Sutham Yaemniyom, of the Department of Mineral Resources (Ingavat et al., 1978; Ingavat and Taquet, 1978). Since then, the number of known dinosaur localities in the Sao Khua Formation has increased considerably (see Martin, 1995, for a partial list). We present here a revised list, with comments, of the dinosaurs currently known from the Sao Khua Formation.

3.1. Theropoda

Theropod remains, mostly in the form of isolated teeth, are not uncommon in the Sao Khua Formation, and are even quite abundant at some localities, but associated or articulated remains are not common. Nevertheless, several types of theropods have been recognized.

Tyrannosauridae. One of the best theropod specimens hitherto found in the Sao Khua Formation is a partial skeleton, consisting of the pelvis, the sacrum, part of the tail and a few dorsal vertebrae (Fig. 1), from site PW9 at Phu Wiang. It was described by Buffetaut et al. (1996) as a new genus and species of tyrannosaurid, *Siamotyrannus isanensis*. Blade-like, compressed, serrated theropod teeth are often found in the Sao Khua Formation, sometimes associated with sauropod skeletons, as at Phu Wiang (Buffetaut and Suteethorn, 1989) and Wat Sakawan (Suteethorn et al., 1995), which in all like-

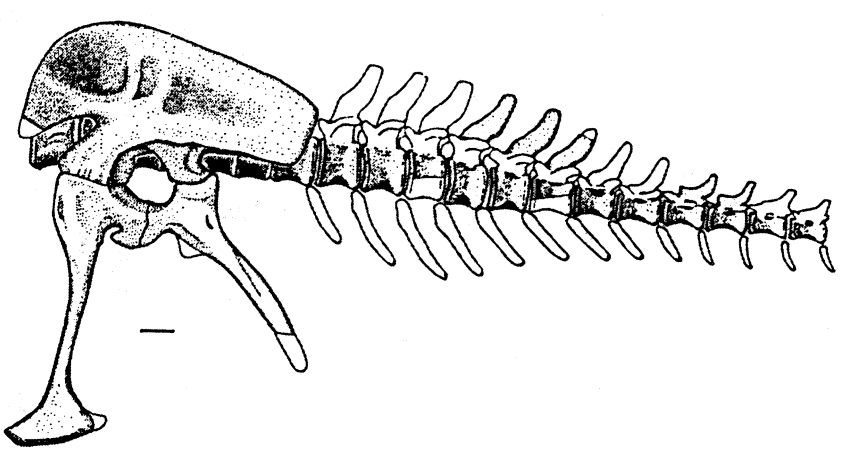

Fig. 1. Reconstruction of the pelvis, sacrum and anterior portion of the tail of the early and primitive tyrannosaurid *Siamotyrannus isanensis*, from the Sao Khua Formation at Phu Wiang, northeastern Thailand. This specimen shows a mixture of primitive characters and derived tyrannosaurid features. Scale bar 10 cm. After Buffetaut et al. (1996).

lihood indicates predation or scavenging. It is likely that many of these teeth belong to *Siamotyrannus*, which reached a length of about 6.5 m, but in the absence of good skull material, this is difficult to prove. A well-preserved tibia found at Phu Wiang, together with a partial sacrum resembling the type of *Siamotyrannus isanensis*, exhibits tyrannosaurid features and very probably belongs to this taxon. A maxilla fragment containing compressed teeth, also from Phu Wiang, may also belong to *Siamotyrannus*, but it is very incomplete. The significance of *Siamotyrannus isanensis* is that it is both the oldest and the most primitive known tyrannosaur (Buffetaut et al., 1996). The type specimen combines derived tyrannosaurid features (incipient subhorizontal shelf on the ilium, anteriorly developed distal 'boot' on the pubis, muscle insertion scar on the ischium etc.) with primitive ones (obturator 'hook' on the pubis, slender neurapophyses on the caudals etc.), and it can be considered as the sister-group to all other tyrannosaurs. The as yet undescribed tibia also shows the features to be expected in an early tyrannosaurid, for instance in the shape and extent of the astragalar facet. *Siamotyrannus* pre-dates the oldest hitherto known tyrannosaurids, from the Cenomanian of Central Asia and western North America, by some 20 million years, and its occurrence in the Lower Cretaceous of Thailand, at a time when tyrannosaurs were apparently not present outside Asia, suggests that the family may have appeared in Asia, and later dispersed to North America.

Ornithomimosauria. This group of theropods is known essentially from site PW5 at Phu Wiang. Fairly abundant material, consisting only of postcranial elements (vertebrae and bones of the hind limb), has been collected there, and will allow the erection of a new taxon, to be described in detail elsewhere. One of the most interesting features of this 'ostrich-dinosaur' is the structure of its metatarsus, which exhibits a fairly advanced 'arctometatarsalian' condition, to use a term of Holtz (1994): the third metatarsal is triangular in cross-section along most of its length, and its proximal end is strongly 'pinched' between the expanded proximal ends of the second and fourth metatarsals (Fig. 2). In these features, the ornithomimosaur from Thailand is more advanced than the primitive ornithomimosaurs from Mongolia, *Harpymimus okladnikovi* (Aptian–Albian) and

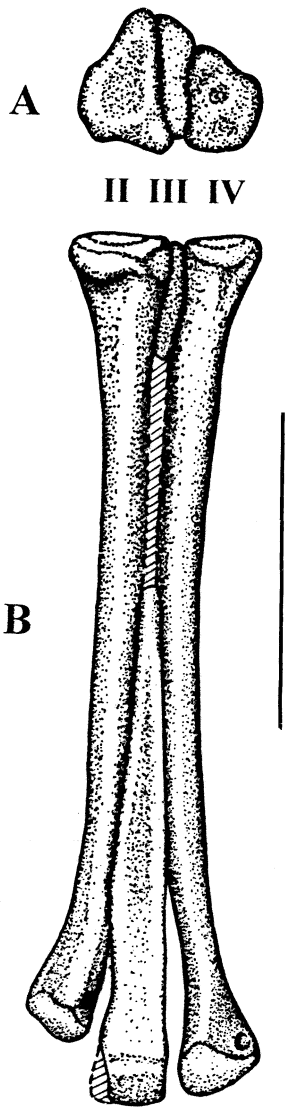

Fig. 2. Reconstruction of the left metatarsus of a new ornithomimosaur from the Sao Khua Formation at Phu Wiang, in proximal (A) and anterior (B) views. The third metatarsal is triangular in cross-section distally, and reduced to a sliver of bone between the second and fourth metatarsals proximally. However, its proximal end is still visible in anterior view. Scale bar 5 cm. Drawing by Haiyan Tong.

Garudimimus brevipes (Cenomanian–Turonian), in which the third metatarsal is less compressed and does not show a triangular cross-section (Barsbold, 1981; Barsbold and Perle, 1984). However, unlike more advanced forms included in the Ornithomimi-

dae by Barsbold and Osmolska (1990), the proximal end of the third metatarsal of the Thai form is still visible in anterior view as a thin sliver of bone between the proximal ends of the second and fourth metatarsals. In this respect, the Thai ornithomimosaur is more primitive than even the early ornithomimid *Archaeornithomimus*, from the Cenomanian of Inner Mongolia (Gilmore, 1933; Smith and Galton, 1990). Another primitive feature of the Thai form is the relative shortness of the metatarsus relative to the tibia. The Thai ornithomimosaur is thus more advanced than the primitive Mongolian forms, although they are geologically younger, but less advanced than the Late Cretaceous Ornithomimidae. It shows that relatively advanced ornithomimosaurs (at least in their foot structure) were already present in Asia very early in the Cretaceous, which may indicate that advanced ornithomimosaurs first evolved in Asia, before they spread to North America.

Spinosauridae? Very peculiar teeth from the Sao Khua Formation at Phu Wiang have been described by Buffetaut and Ingavat (1986) as *Siamosaurus suteethorni*. They have a tall, rather straight and only slightly compressed crown covered with numerous well marked striations, and their carinae are not serrated. Although they superficially resemble crocodilian teeth, they do not show the usual curvature, and the shape of the crown is more reminiscent of that of theropod dinosaurs, despite the low degree of compression. They have been tentatively referred to the family Spinosauridae, in which the teeth are not markedly compressed, and the carinae, at least in *Spinosaurus aegyptiacus*, are not serrated (Stromer, 1915). However, it should be admitted that the numerous striations on the teeth of *Siamosaurus* are different from the slight fluting seen on some *Spinosaurus* teeth. Isolated teeth of *Siamosaurus* are frequently found at many vertebrate localities in the Sao Khua Formation, sometimes, as at Wat Sakawan, in association with sauropod remains, which suggests predation or scavenging. However, the shape of the teeth rather suggests a piscivorous diet. Unfortunately, however, no skeletal material referrable to *Siamosaurus* has yet been found, and the exact affinities of this enigmatic animal therefore remain uncertain.

Other theropods. Small theropod limb bones, notably including a tibia, were described by Buffetaut and Ingavat (1984) and referred to a *Compsognathus*-like theropod. A few additional teeth and postcranial elements of small theropods have since then been found at several localities in the Sao Khua Formation, but beyond indicating that small or very small forms were present, they do not allow very precise identifications.

3.2. Sauropoda

Sauropod remains are probably the most frequently found dinosaur fossils in the Sao Khua Formation (a fact which is certainly linked to their large size and massiveness). The first dinosaur bone to be described from Thailand (Ingavat et al., 1978; Ingavat and Taquet, 1978) was the distal end of a femur from Phu Wiang, which did not allow a precise identification. Comparisons were made with the femur of *Camarasaurus*, but subsequent discoveries have shown that there is no real evidence of that genus in the Sao Khua Formation. Mentions of possible resemblances with *Omeisaurus* (Buffetaut and Suteethorn, 1989) have also proved unfounded. Following the description of abundant sauropod material from Phu Wiang and Phu Pha Ngo (Kalasin Province) by Martin (1995), the situation has been much clarified, and the exceptionally productive new sauropod locality at Wat Sakawan (Kalasin Province; see Suteethorn et al., 1995) is providing a large amount of new evidence about that group. However, the material from Wat Sakawan is still being excavated and prepared, so that some of the remarks below are necessarily preliminary.

The best known sauropod from the Sao Khua Formation is *Phuwiangosaurus sirindhornae*, described on the basis of an incomplete skeleton from locality Phu Wiang 1 at Phu Wiang by Martin et al. (1994). Material from many other sites, including Phu Pha Ngo and Wat Sakawan, has been referred to *Phuwiangosaurus*, and there is no doubt that our knowledge of this form will be much increased when nearly complete skeletons from Wat Sakawan are described.

Phuwiangosaurus sirindhornae was a mid-sized sauropod (reaching a length of some 15 to 20 m). The original diagnosis was based only on postcranial material. Among the most important distinguishing features of this taxon are the shape of the anterior

cervical vertebrae, which have a low and broad neural arch, and are compressed dorsoventrally, and the wide bifurcation of the neural spines of the posterior cervicals. In these respects, *Phuwiangosaurus sirindhornae* differs markedly from the Jurassic sauropods from China placed in the family Euhelopodidae (*Euhelopus*, *Omeisaurus*, *Mamenchisaurus*), in which the anterior cervicals are compressed laterally, and the bifurcation of the posterior cervicals is very shallow. The position of the fourth trochanter of the femur also separates *Phuwiangosaurus* from the Euhelopodidae. Despite some resemblances with the Camarasauridae, there are many differences in the dorsal vertebrae and the girdles which preclude inclusion in that family. Generally, it was concluded (Martin et al., 1994, p. 1091) that "*Phuwiangosaurus sirindhornae* does not show close similarities with any sauropod family already described". The newly discovered skeletons of *Phuwiangosaurus sirindhornae* from Wat Sakawan (Suteethorn et al., 1995) have already provided additional data about this animal and its possible relationships. In particular, teeth and a few skull remains referrable to this taxon have been found. The skull remains include premaxillae and a partial maxilla, which are quite unlike those of *Camarasaurus.* The teeth are slender, with a cylindrical root and a curved and lanceolate crown, with a convex labial surface and a concave or flat lingual surface. They are very different from the broader, more or less spoon-shaped teeth of the Camarasauridae, Brachiosauridae and Euhelopodidae. They closely resemble the teeth of *Nemegtosaurus mongoliensis*, from the Upper Cretaceous of Mongolia (Nowinski, 1971), and there may be fairly close relationships between *Phuwiangosaurus* and *Nemegtosaurus* (Fig. 3). This is difficult to demonstrate at the moment, for the simple reason that *Nemegtosaurus* (as well as the probably related *Quaesitosaurus*, also from the Upper Cretaceous of Mongolia: see Kurzanov and Bannikov, 1983) is known only from its skull, whereas *Phuwiangosaurus* is known mainly (but no longer exclusively) from its postcranial skeleton. The Cretaceous sauropods of Asia are still relatively poorly known, and there are few specimens with which *Phuwiangosaurus* can be compared in a useful way. There seem to be very few resemblances with the enigmatic *Opisthocoelicaudia*, known only from a postcranial skeleton from the

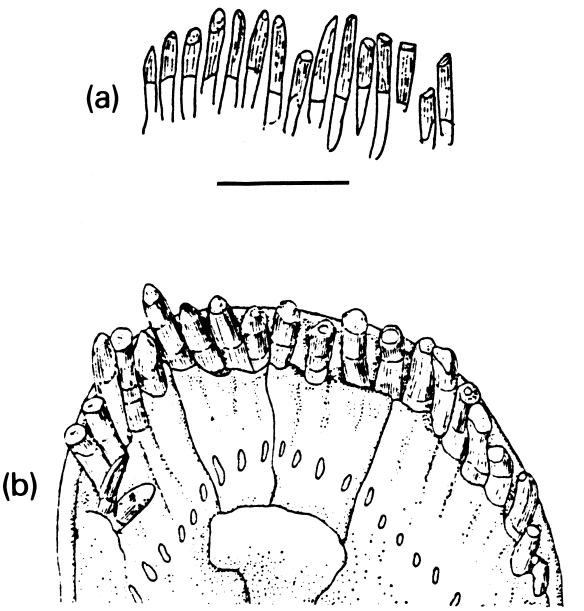

Fig. 3. (a) A group of teeth referrable to the sauropod *Phuwiangosaurus*, found in the Sao Khua Formation at Wat Sakawan. Although the jaw bones were not preserved, the teeth, possibly from the upper jaw, have retained their original position. (b) The upper teeth of *Nemegtosaurus mongoliensis*, from the Upper Cretaceous of Mongolia, for comparison (after Nowinski, 1971). Scale bar 5 cm.

Upper Cretaceous of Mongolia (Borsuk-Bialynika, 1977). Potentially interesting comparisons could be made with the sauropod skeleton from the Upper Cretaceous of Shanxi, China, recently reported by Pang et al. (1995) as a titanosaurid. To judge from its amphicoelous caudal vertebrae, this animal is certainly not a titanosaurid, and its teeth are described as being similar to those of *Nemegtosaurus mongoliensis*. Better knowledge of it may shed some light on the actual diversity of the Late Cretaceous sauropods of Asia, and on possible relationships with the Early Cretaceous forms from Thailand. The very poorly known sauropods from the late Early Cretaceous of Laos, contrary to the opinion of Hoffet (1942), are certainly not titanosaurids (Buffetaut, 1991; Taquet et al., 1992); they are somewhat younger than the Thai forms from the Sao Khua Formation, because the dinosaur-bearing formation in Laos appears to an equivalent of the Khok Kruat Formation of Thailand (Buffetaut, 1991), and comparisons with *Phuwiangosaurus* would be interesting. At the present time,

dental evidence suggests that *Phuwiangosaurus* may be close to the ancestry of *Nemegtosaurus* and related Late Cretaceous forms (the 'Nemegtosauridae' of Upchurch, 1994).

Thanks to the discovery of disarticulated juvenile bones at several sites in the Phu Wiang hills, some data are available on the ontogeny of *Phuwiangosaurus* (Martin, 1994). In some aspects of their anatomy (simpler pleurocoels and neural arches of vertebrae, well marked remains of a lesser trochanter on the femur, etc.), juveniles appear to be more reminiscent of primitive sauropods than adults of the same taxon.

Although most of the sauropod specimens found at Wat Sakawan appear to belong to *Phuwiangosaurus*, some clearly do not. They include a jaw fragment containing large spoon-shaped teeth resembling those of brachiosaurids, and a large elongated humerus which is also reminiscent of brachiosaurids. A more detailed description of this material will be needed, however, before the occurrence of a true brachiosaurid in the Sao Khua Formation can be confirmed.

4. Conclusions: the general character of the Sao Khua dinosaur fauna and its place in dinosaur history

From this brief review of the dinosaurs from the Sao Khua Formation, some conclusions can be drawn concerning its general composition and its broader significance.

Although the Sao Khua dinosaur assemblage is the most abundant and diverse dinosaur fauna heretofore discovered in South-East Asia, it is still incompletely known. The number of taxa hitherto identified is still rather small by comparison with other, better known dinosaur faunas, and there is little doubt that continued research in the Sao Khua Formation will enlarge it in the future. A peculiarity worth mentioning, however, is the dearth of ornithischian remains among the dinosaurs collected from the Sao Khua Formation. Although hundreds of bones have now been recovered from the Sao Khua Formation, no clearly identifiable ornithischian remains have yet been found. This does not necessarily mean that ornithischians were completely absent from the Sao Khua fauna, but it certainly suggests that they were not abundant, and were at least outnumbered by saurischians (especially sauropods), or that an unusual taphofacies is being sampled. This is in sharp contrast with Early Cretaceous assemblages in other parts of the world (those from the European Wealden, for instance, or from Niger in Africa), in which ornithischians, especially ornithopods, are abundant. It also contrasts with later dinosaur assemblages from Asia. In Thailand, the Khok Kruat Formation, the age of which is probably Aptian–Albian (Cappetta et al., 1990; Racey et al., 1994, 1996), has yielded, besides theropods, remains of the primitive ceratopsian *Psittacosaurus* (Buffetaut et al., 1989; Buffetaut and Suteethorn, 1992) and of iguanodontid ornithopods. Ornithopods are also known from beds apparently equivalent to the Khok Kruat Formation in Laos (Hoffet, 1944; Buffetaut, 1991; Taquet et al., 1992).

In the Gobi Basin, which has one of the best Cretaceous vertebrate records in Asia (Jerzykiewicz and Russell, 1991), the Tsagantsabian 'Age' of Jerzykiewicz and Russell (1991), which may be Valanginian to late Neocomian, and the Shinkhudukian 'Age', which may be Aptian, have yielded relatively few dinosaurs, including poorly known theropods and sauropods, and *Psittacosaurus*. Iguanodontids first appear in the Gobi Basin in the Khukhtekian 'Age', which may be Aptian–Albian in age. Comparisons with South-East Asian data suggest that the Khok Kruat Formation may be of roughly the same age as the 'Khukhtekian', and that the Sao Khua Formation, which has not yielded *Psittacosaurus*, may be older than the Tsagantsabian. However, the difficulty of correlating non-marine formations in Asia on the basis of fossil vertebrates is illustrated by the fact that in Japan iguanodontid remains are known from the upper part of the Itoshiro Subgroup, which, on the basis of marine fossils from underlying and overlying formations, is later than Oxfordian and earlier than Late Barremian to Aptian, the iguanodontid-bearing formations being considered as probably 'Early Neocomian' in age (Hasegawa et al., 1995). This would suggest that iguanodontids appeared in Japan earlier than in either the Gobi Basin or South-East Asia, which is problematic if one accepts that they were immigrants from Europe.

Be that as it may, the Sao Khua dinosaur assemblage appears to be earlier than any of those containing iguanodontids in the Gobi Basin, and probably earlier than those containing *Psittacosaurus*. Very few localities in Asia have yielded a dinosaur assemblage similar to that from the Sao Khua Formation. A possible exception may be the Napan Basin of Guangxi (south China), where Early Cretaceous vertebrates have been described by Hou et al. (1975). Besides a supposed brachiosaurid (considered a 'euhelopodine' by Dong, 1992), the Napan Formation has yielded compressed theropod teeth resembling those from the Sao Khua Formation, as well as supposed pliosaurid teeth which in fact resemble the teeth identified as *Siamosaurus suteethorni* from the Sao Khua Formation. Although the evidence is still slender, the Napan assemblage may prove to be similar to that from the Sao Khua Formation.

Beyond the correlation problems posed by the comparison of the Sao Khua dinosaur assemblage with those from other Early Cretaceous formations in Asia, the broader issue of the significance of this assemblage for dinosaur history in Asia (and elsewhere) is worth addressing. Several of the dinosaurs found in the Sao Khua Formation apparently are early and more or less primitive representatives of groups which later came to occupy a prominent position in dinosaur faunas. This is fairly clear in the case of *Siamotyrannus isanensis*, which is both the oldest and the most primitive known tyrannosaurid. Considering that no tyrannosaurids have been reported from rocks as old as the Sao Khua Formation in other parts of the world, it seems legitimate to suggest that tyrannosaurids evolved in Asia during the Early Cretaceous, eventually to become the dominant large theropods in Asia in the Late Cretaceous, and to disperse to North America probably at the end of the Early Cretaceous or the beginning of the Late Cretaceous. The ornithomimosaur from the Sao Khua Formation may be interpreted along similar lines. Although putative ornithomimosaurs have been reported from the Upper Triassic of North America (Chatterjee, 1993) and the Upper Jurassic of Europe (Brokenshire and Clarke, 1993), the real significance of these finds is uncertain, as is the attribution of *Elaphrosaurus*, from the Upper Jurassic of East Africa, to the ornithomimosaurs. The supposed ornithomimosaur *Timimus hermani* from the Albian of Australia (Rich and Vickers-Rich, 1994) cannot be compared with the Thai form, since it is based on a femur, but in any case it is later in age than the latter. The Sao Khua ornithomimosaur, as mentioned above, is more advanced in its metatarsal structure than the later Mongolian *Harpymimus* and *Garudimimus*. This points to an early diversification of the ornithomimosaurs, and the Thai form may be considered an early representative of the 'advanced' ornithomimosaurs (the Ornithomimidae), which became widespread both in Asia and in North America during the Late Cretaceous. This again points to Asia as the possible 'cradle' of a group of theropods which later played an important role in Late Cretaceous Asiamerican faunas.

The case of the Sao Khua sauropods, especially *Phuwiangosaurus*, is more uncertain, because the Late Cretaceous sauropods of Asia are still relatively poorly known. However, as mentioned above, dental evidence suggests possible links between *Phuwiangosaurus* and the Nemegtosauridae (and the newly reported sauropod from Shanxi, which may be a nemegtosaurid). A better knowledge of both the cranial anatomy of *Phuwiangosaurus* and the post-cranial anatomy of the Nemegtosauridae is needed, however, before this hypothesis can be tested more safely. In any case, there is no evidence that *Phuwiangosaurus*-like (or *Nemegtosaurus*-like) sauropods ever reached North America, where the only known Late Cretaceous sauropod is the titanosaurid *Alamosaurus*, a probable South American immigrant (Lucas and Hunt, 1989).

Finally, the possible part played in the evolutionary history of Asian (and North American) dinosaurs by some of the forms belonging to the Sao Khua assemblage should be replaced in the broader context of the palaeobiogeographical history of Asia. Various lines of geological and paleontological evidence indicate that the South-East Asian blocks came into contact with 'mainland Asia' at the latest early in the Mesozoic, or earlier (see Metcalfe, 1996). In the Jurassic and Cretaceous, South-East Asia was part of the same general bioprovince as central, eastern and northern Asia. As pointed out by Russell (1993, 1995), there is evidence of an isolation of central and eastern Asia (by seaways across central Eurasia and Beringia) during part of the Mesozoic, possibly from the end of the Liassic to the Aptian. The

Sao Khua dinosaurs would then be representatives of a late stage of endemism of Asian faunas, which ended when connections became established again with North America and Europe during the Aptian–Albian. A result of this re-establishment of land connections with other northern land masses probably was the dispersal into Asia of several of the groups of vertebrates listed by Russell (1993), including such dinosaurs as the Iguanodontidae (see, however, the remarks above about the early age of iguanodontid teeth from Japan). In view of recent discoveries in the Sao Khua Formation, however, some of the groups listed by Russell (1993) as immigrants into Asia may in fact have dispersed *from* Asia to other parts of the world (notably North America) at the end of the Early Cretaceous. This applies, in particular, to the Ornithomimidae. On the other hand, Russell's opinion that the Tyrannosauridae originated in Asia (Russell, 1993) is supported by the discovery of *Siamotyrannus* in the Sao Khua Formation.

Because they apparently antedate most other known Cretaceous vertebrate-bearing formations in Asia, the Sao Khua Formation and its faunal assemblage are of obvious importance for our understanding of the beginning of the Cretaceous radiation of dinosaurs and other land vertebrates, not only in Asia but also in other parts of the world, which were later subjected to faunal interchange with Asia (such as North America). As more and more vertebrate localities are discovered in the Sao Khua Formation of Thailand, there is no doubt that new important data will come to light concerning this important episode in the history of Mesozoic terrestrial faunas.

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