THE LOWER JAW OF *SUNOSUCHUS THAILANDICUS*, A MESOSUCHIAN CROCODILIAN FROM THE JURASSIC OF THAILAND

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ABSTRACT. A nearly complete lower jaw is described of the longirostrine mesosuchian crocodilian *Sunosuchus thailandicus* Buffetaut and Ingavat (1980), from the Phu Kradung Formation (early Jurassic) of north-eastern Thailand, and the affinities of the genus are discussed. The jaw is large and robust, with a long symphysis, and each dentary contains about thirty teeth. Despite the unusually elongated mandibular symphysis the genus is referred to the Goniopholididae rather than to the Pholidosauridae, on the basis of the skull characters present in the Chinese species *S. miaoi* Young (1948). *Sunosuchus*, however, is in some respects morphologically intermediate between the Goniopholididae and the Pholidosauridae.

IN 1979 the posterior part of the right ramus of the lower jaw of a large crocodilian was collected from the Jurassic Phu Kradung Formation by Mr. Nares Sattayarak (Department of Mineral Resources, Bangkok), near the town of Nong Bua Lam Phu in north-eastern Thailand. The specimen was subsequently described by us (Buffetaut and Ingavat 1980) and referred to a new species of the genus *Sunosuchus* Young 1948, *S. thailandicus*. In November 1980 a Thai–French party visited the locality under the guidance of Mr. Sattayarak, and could excavate most of the remaining parts of the mandible of the same individual. The purpose of this paper is to describe the lower jaw of *S. thailandicus* on the basis of the nearly complete specimen now available, and to discuss the affinities of *Sunosuchus* more fully than was possible in 1980.

GEOLOGICAL SETTING

The specimen was found in a road-cut at km 80+800 on the highway between Udon Thani and Nong Bua Lam Phu. It was embedded in a reddish claystone containing calcareous nodules which give it a conglomeratic appearance, belonging to the Phu Kradung Formation. The Phu Kradung Formation belongs to the lower part of the Khorat Group (see Ramingwong 1978, for a review of the Khorat Group). Although it was first considered to be largely Triassic (Ward and Bunnag 1964), the Phu Kradung Formation is now usually referred to the early Jurassic (Hahn 1982), which is in accordance with recent magnetostratigraphic data (Bunopas 1981; Maranate 1982). Recent discoveries of land vertebrates in the Khorat Group (Buffetaut 1982*a*) have allowed a better dating of its formations, and these biostratigraphic data are in agreement with an early Jurassic age for the Phu Kradung Formation (Buffetaut and Ingavat, in press), although very few vertebrate fossils have been found in this formation itself. The best specimen discovered so far is the crocodilian jaw described in this paper, and it does not provide accurate biostratigraphic information (except that it has to be younger than the Triassic). At the moment, it is still impossible to refer the Phu Kradung Formation to any definite stage of the early Jurassic.

The Khorat Group, which occupies a vast area of north-eastern Thailand, is interpreted as an essentially freshwater molasse deposit resulting from the erosion of mountains created by the collision of the Thai-Chan, Indochina, and South China blocks (Indosinian orogeny) sometime in the middle or late Triassic (Bunopas 1981). The Phu Kradung Formation, which contains

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non-marine bivalves, is supposed to have been deposited in a fluvio-lacustrine environment (Hahn 1982). Teeth from this formation which have been referred to marine reptiles (Kobayashi *et al.* 1963; Ward and Bunnag 1964) in all likelihood actually belong to crocodilians (Buffetaut and Ingavat 1980), and cannot be used as evidence of marine influences.

PRESERVATION OF THE SPECIMEN

The lower jaw of *S. thailandicus* from Nong Bua Lam Phu is kept in the collections of the Department of Mineral Resources, Bangkok, under no. TF 1370. When found, the specimen was already broken within the sediment, and had been further damaged by roots, especially in its posterior parts. The dentaries were separated along the symphyseal suture. Many teeth are missing, and their alveoli are filled with matrix; in some of them the tips of replacement teeth are visible. All the erupted teeth still preserved in their alveoli are broken; a number of tooth fragments were found in the sediment around the jaw, but only a few could be fitted back to it. The edges of the alveolar openings are often poorly preserved, so that in some parts of the dentaries it is difficult to count the alveoli. The left ramus of the mandible is broken at the level of the most posterior teeth, and roots have damaged this region, which is now difficult to reconstruct. On the right side, a section comprising the back part of the symphysis (posterior to the seventeenth tooth) and the anterior part of the ramus could not be found (see Pl. 25) despite a thorough search of the outcrop, which also failed to reveal any other skeletal elements of this crocodilian.

DESCRIPTION

The mandibular symphysis is long, reaching the level of the twenty-fifth tooth, and represents about 42% of the total length of the lower jaw, but it is also robust and relatively wide, with an anterior spoon-shaped expansion followed by a constriction (Pl. 25, figs. 1, 2). More posteriorly, the sides of the symphysis diverge only slightly towards the rear. In lateral view (Pl. 25, fig. 3) the toothed part of the jaw is seen to be slightly curved, its dorsal side being concave and its ventral side convex. Posterior to the symphysis, the mandibular rami diverge gradually. The medial side of the left ramus makes an angle of 30° with the longitudinal axis of the symphysis. The *fenestra mandibularis externa* is elongated and both its ends are pointed.

Measurements

Total length of lower jaw (as reconstructed)	1140 mm
Length of symphysis (dorsally)	475 mm
Maximum height of symphysis (at the level of the twenty-second tooth)	56 mm
Maximum width of left dentary (at the level of the fourth tooth)	80 mm
Length of splenial symphysis	170 mm

Dentary. The dentaries are elongated and joined together at the symphysis for a considerable part of their length. Twenty-eight alveoli are visible on the left dentary, the posterior part of which is damaged, and it is likely that there were actually thirty teeth in each dentary. Anteriorly, the dentaries are widened to form the above-mentioned spoon-shaped expansion, the dorsal surface of which is slightly concave transversally and convex longitudinally. The maximum width of the symphysis is at the level of the fourth alveoli, the edges of which are projecting laterally. Posterior to the expansion, the jaw becomes narrower up

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EXPLANATION OF PLATE 25

Figs. 1–5. Lower jaw of *Sunosuchus thailandicus* Buffetaut and Ingavat 1980, from the early Jurassic Phu Kradung Formation near Nong Bua Lam Phu, north-eastern Thailand, Collection of the Department of Mineral Resources, Bangkok, no. TF 1370 (holotype). 1, dorsal view. 2, ventral view of symphysis and left ramus. 3, left lateral view. 4, lateral view of anterior part of right dentary. 5, medial view of anterior part of left dentary. All figs. ×½. Photographs by C. Abrial.

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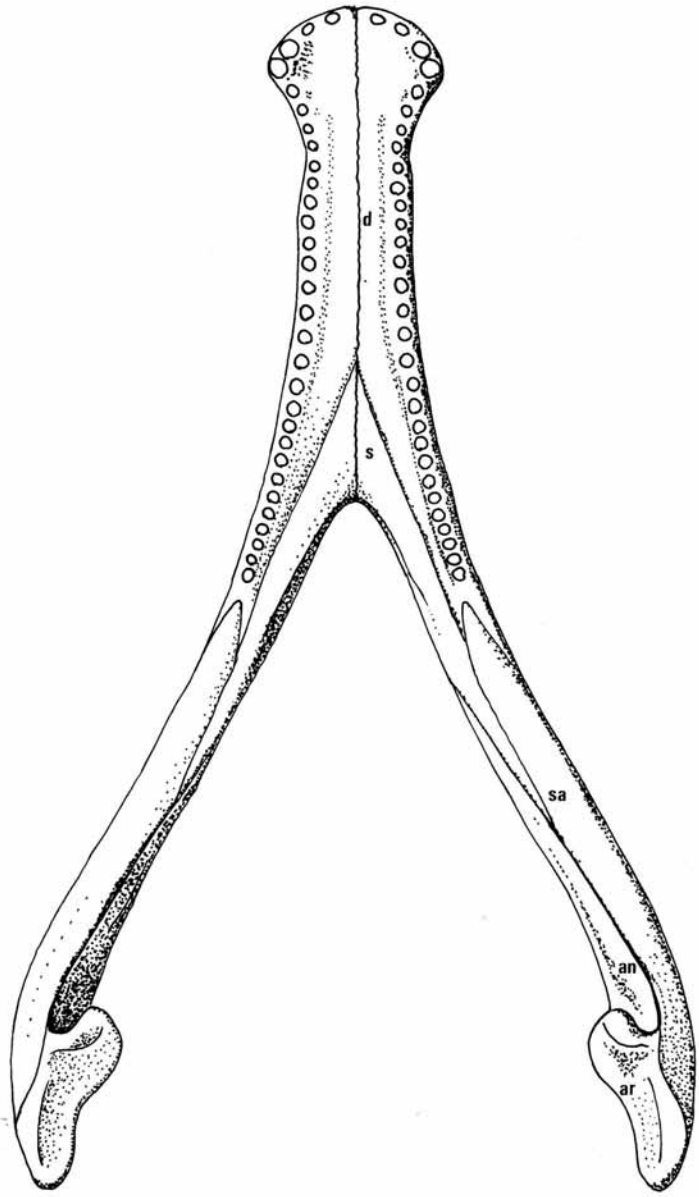
to the level of the seventh tooth, the symphysis being narrowest at the level of the interval between the seventh and eighth teeth. Further posteriorly, the symphysis becomes slightly wider again. The two most anterior alveoli (with diameters of 12 and 15 mm respectively) open upwards and towards the front. At this level, the anterior edge of the symphysis is regularly rounded. The third and fourth alveoli are very large (diameters: 20 and 23 mm) and contiguous; they open upwards and outwards. The fifth alveolus is much smaller (diameter: 10 mm) and separated from the fourth by a fairly long space (20 mm). More posteriorly, the diameters of the alveoli are difficult to measure accurately because their edges are not perfectly preserved. Up to the ninth alveolus, the alveoli are small, with diameters between 10 and 13 mm, and separated by short spaces (5 to 10 mm). The lateral edges of the alveoli protrude in dorsal view, more so on the right side than on the left, a condition which may well be abnormal. Further posteriorly, the alveoli are almost contiguous, separated by spaces only a few millimetres long. Posterior to the end of the symphysis, the walls between the alveoli are not very distinct, which gives the impression that the teeth were set in a groove. The diameter of the teeth does not seem to decrease much towards the rear. In lateral view, on the left side (Pl. 25, fig. 3), the lateral edge of the alveolar row is regularly curved, with the concavity facing upwards. On the right side (Pl. 25, fig. 4), the outline is more irregular. Medial to the tooth rows, the buccal floor is nearly flat, sloping only slightly from the midline towards the sides. There is no sagittal ridge, and only slight longitudinal depressions on both sides. From the level of the seventeenth alveolus rearwards, a weak ridge is visible immediately medial to the tooth rows. At the level of the sixteenth alveolus on the right side, and medial to it, there is a distinct rounded pit, with no symmetrical depression on the left side. Generally speaking, the teeth on the right side show a more irregular implantation, which may be pathological. The medial face of the dentaries is a sutural surface (Pl. 25, fig. 5) longitudinally crossed by the Meckelian canal, which ends anteriorly at the level of the sixth tooth. Grooves and ridges diverge on both sides of this canal. The ventrolateral surfaces of the dentaries are ornamented with irregular deep grooves, which become more loosely arranged anteriorly, where their longitudinal orientation disappears. Just below the tooth rows, a series of vascular foramina is visible.

The teeth are poorly preserved. They are strong, conical, and slightly recurved. There are very stout recurved fangs in the third and fourth alveoli. The apex of the teeth is rarely preserved. However, in the seventeenth alveolus of the left dentary, the rounded tip of an unworn replacement tooth is visible, with irregular ridges and wrinkled carinae. The teeth bear numerous fine ridges, separated by grooves with a concave floor. The carinae are poorly marked.

Splenial. The splenials taper to a point between the dentaries, thus taking part in the mandibular symphysis. Ventrally, the right splenial is seen to reach the level of the thirteenth tooth. Dorsally, the splenial was apparently somewhat shorter; to judge from the poorly preserved anterodorsal end of the left splenial, it reached the level of the seventeenth or eighteenth tooth. In posterior view, the left splenial shows a deep pit overhung by the posterodorsal part of the bone. Posteriorly, in the jaw rami, each splenial forms a kind of low ridge medial to the tooth row. Still further back, the splenial becomes a relatively thin bony plate adhering to the more lateral bones of the jaw and reaching the anterior extremity of the *fenestra mandibularis externa*, but these regions are poorly preserved and few details can be seen.

Mandibular rami. In the posterior parts of the mandibular rami, the sutures between the bones are usually difficult to trace, so that it is not convenient to describe each bone separately. On the lateral surface, the dentary is fork-shaped posteriorly and thus forms the anterior border of the *fenestra mandibularis externa*. Along the ventral edge of this opening, it tapers to an elongated point. More ventrally, the anterior end of the angular also forms a point, below the posterior end of the dentary. Above the *fenestra mandibularis externa*, the suture line between the surangular and the dentary is poorly visible. The *fenestra mandibularis externa* is roofed over by the surangular, which forms a smooth bony plate, convex dorsally and concave ventrally. The ventral limit of the *fenestra* is a more robust bony bar formed by the angular; its ventrolateral surface is covered with grooves, while the medial and the concave dorsal surfaces are smooth. Posterior to the *fenestra mandibularis externa*, the surangular and the angular meet along a hardly discernible suture to form, on the lateral side, a vast bony surface ornamented with deep irregular pits separated by strong ridges. This surface is limited dorsally by a distinct ridge borne by the surangular. This bone does not take part in the glenoid surface for articulation with the quadrate. The glenoid surface is formed by the articular alone; it is large, tongue-shaped, with a strong rounded medial expansion, which overhangs the medial surface of the bone. The retroarticular process is moderately long (170 mm on the left side), not much recurved, with a slight upward concavity. It is built mainly by the articular, the angular and the surangular being included in it along part of its length only, on the lateral side.



TEXT-FIG. 1. Reconstruction of the lower jaw of *Sunosuchus thailandicus*, based on specimen TF 1370 (holotype), in the collection of the Department of Mineral Resources, Bangkok. Dorsal view. Abbreviations: an, angular; ar, articular; d, dentary; s, splenial; sa, surangular. $\times \frac{1}{6}$.

AFFINITIES OF *SUNOSUCHUS THAILANDICUS*

The additional data now available about the mandible of the Nong Bua Lam Phu crocodilian justify a further discussion of its affinities (Buffetaut and Ingavat 1980).

Affinities with Sunosuchus miaoi. The type species of the genus *Sunosuchus* is *S. miaoi* Young 1948, based on various remains including an incomplete skull and lower jaw from the Jurassic Hokou series of Kansu, in north-central China (see Young 1948, Buffetaut and Ingavat 1980). Comparisons between *S. miaoi* and *S. thailandicus* are relatively difficult, because most of the mandibular symphysis (the anterior part) of the Chinese specimen is missing, while nothing is known about the skull of the Thai form. However, the parts known in both specimens are very similar. The resemblances in the general shape of the mandibular rami and of the *fenestra mandibularis externa*, and in the morphology of the teeth, have already been mentioned in our previous paper. It now appears that the posterior part of the symphysis is also similar in both forms, but so little is preserved of the symphyseal region in the Chinese fossil that this comparison is not very revealing. In any case, knowledge of the complete lower jaw of the Thai crocodilian by no means precludes its inclusion in the genus *Sunosuchus*. Distinction from the Chinese form at the species level is justified by size and proportional differences (Buffetaut and Ingavat 1980).

Affinities of the genus Sunosuchus. The discovery that *S. thailandicus* is a very long-snouted crocodilian prompts a new discussion of the systematic position of the genus *Sunosuchus*. Young (1948) classified *S. miaoi* among the Pholidosauridae because he assumed that its snout was long and relatively narrow. Although this was not exactly obvious on the basis of the Chinese specimen, the discovery of the jaw from Thailand now shows that Young was right in considering *Sunosuchus* as a longirostrine crocodilian. In 1980 we defended the view that *Sunosuchus* should be included in the Goniopholididae, because of several features of the skull of *S. miaoi*, viz. small supratemporal fenestrae, anterior palatal openings, and the possible presence of maxillary depressions. Although, as we already pointed out, some Goniopholididae had relatively long snouts, the very long mandibular symphysis of *S. thailandicus* is at first sight more reminiscent of the consistently long-snouted Pholidosauridae (although it is rather different from *Pholidosaurus* itself, in which the jaws are much more slender). As mentioned above, the mandibular symphysis of *S. thailandicus* reaches the level of the twenty-fifth tooth, while it reaches the level of the sixth or seventh alveoli in *Goniopholis*, and that of the eleventh tooth in *Vectisuchus leptognathus*, a relatively long-snouted goniopholidid from the Wealden of England (Buffetaut and Hutt 1981). The shape of the symphysis of *S. thailandicus*, and especially of its anterior end, is also reminiscent of some pholidosaurids, notably the very large *Sarcosuchus*, from the lower Cretaceous of Niger and Brazil (see Buffetaut and Taquet 1977) in which, incidentally, the symphysis reaches at least the level of the twenty-third tooth. Although the rather conspicuous constriction at the level of the interval between the seventh and eighth teeth in *S. thailandicus* is not so marked in *Sarcosuchus*, in both instances there is a noticeable anterior expansion, the widest part of which corresponds to the large third and fourth alveoli. However, some short-snouted Goniopholididae, such as *Goniopholis crassidens* from the Purbeck and Wealden of England, are also very similar to *S. thailandicus* in this respect, although they have a short symphysis (see the lower jaw figured by Owen 1878, pl. I). The main difficulty about assessing the affinities and systematic position of *Sunosuchus* is that the Goniopholididae and the Pholidosauridae are two closely related mesosuchian families. Actually, the question is whether *Sunosuchus* should be considered as a primitive pholidosaurid, with small supratemporal fenestrae, or as a specialized long-snouted goniopholidid, and in this respect the length of the symphysis is probably not of prime importance, all the more so that elongation of the jaws is known to have occurred independently in many crocodilian lineages. There remains the already mentioned skull characters that we used (Buffetaut and Ingavat 1980) to support the inclusion of *Sunosuchus* in the family Goniopholididae. The presence of a maxillary depression in the posterior part of the maxillae (about the definition and significance of this feature, see Buffetaut 1982*b*) would be important evidence in favour of this inclusion, but it needs to be checked on the actual

specimen whether the depression shown on Young's figures is really natural, and not an artefact of preservation. Maxillary depressions are known only in the Goniopholididae. Anterior palatal openings in the palatines and maxillae, like those of *S. miaoi*, have been reported only in some North American Goniopholididae (Mook 1967; Langston 1973) of the late Jurassic, and this may also be a character restricted to some goniopholidids. However, these openings may actually represent a primitive condition retained from Triassic crocodilians in which the palate was not as well developed as in the Mesosuchia (Buffetaut 1982*b*). In this case they may have also been present in primitive representatives of several mesosuchian families, including possibly the Pholidosauridae. The problem cannot be solved at the moment for lack of relevant evidence (it should be remembered that extremely little is known about the early representatives of most families of freshwater or terrestrial Mesosuchia prior to the late Jurassic; see Buffetaut 1982*b*). As to the small size of the supratemporal fossae, it is also a primitive feature for all Mesosuchia. The question is whether a pholidosaurid-like crocodilian with small supratemporal fossae should be included in the Pholidosauridae.

In the absence of data about some crucial parts of the skull, such as the premaxillae, which are hook-shaped in the Pholidosauridae (Buffetaut 1982*b*), it is obviously difficult to reach a definite conclusion about the systematic position of *Sunosuchus*. We think the best attitude at the moment is to consider it as a long-snouted, specialized goniopholidid, while keeping in mind that the Pholidosauridae probably have their origin among the Goniopholididae (Buffetaut 1982*b*), and that *Sunosuchus* is in some ways morphologically intermediate between these two families.

A NOTE ON PALAEOBIOGEOGRAPHY

There is little to add to the remarks on the palaeobiogeographical significance of *S. thailandicus* which were made in our 1980 paper. On the basis of its morphology and of the depositional environment of both the Phu Kradung Formation in Thailand and the Hokou series in China, *Sunosuchus* can be considered as a presumably piscivorous freshwater crocodilian, which should be used as a continental faunal element in palaeobiogeographical reconstructions. In the context of the hypothesis of the northward drift of South-East Asia and its subsequent collision with mainland Asia (see Ridd 1980), the occurrence of the genus *Sunosuchus* in Thailand and in China (and, so far, nowhere else) does suggest that in the Jurassic the fauna of north-eastern Thailand already had Laurasian affinities. Recent palaeontological discoveries in Thailand actually indicate that colonization of north-eastern Thailand by Laurasian continental vertebrates had already taken place earlier: the late Triassic, probably Norian, vertebrate fauna from the Huai Hin Lat Formation, which includes lungfishes, stegocephalian amphibians, turtles, and phytosaurs, shows striking Laurasian affinities (review in Buffetaut 1982*a*). This in turn indicates that collision of the Indochina block (which includes north-eastern Thailand) with South China occurred no later than the late Triassic.

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