A NEW SPECIES OF THE ORNITHISCHIAN DINOSAUR *PSITTACOSAURUS* FROM THE EARLY CRETACEOUS OF THAILAND

by ERIC BUFFETAUT *and* VARAVUDH SUTEETHORN

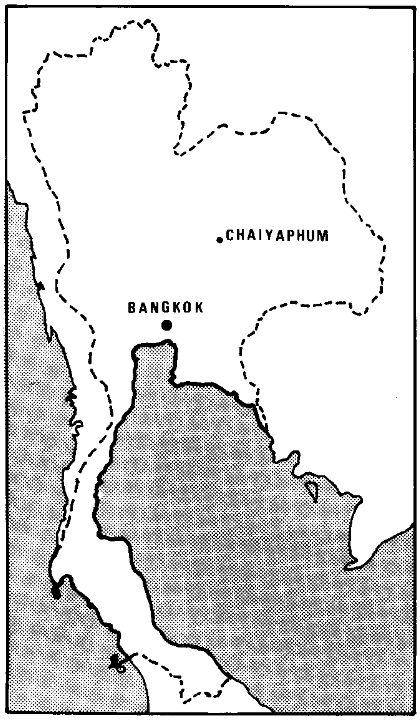
ABSTRACT. Dinosaur jaw remains from the Early Cretaceous Khok Kruat Formation of northeastern Thailand, including a well-preserved dentary and a maxilla fragment, are described as belonging to a new species of the primitive ceratopian *Psittacosaurus*, *P. sattayaraki*. It differs from previously described species of *Psittacosaurus* from Mongolia and China in the morphology of its dentary. The Khok Kruat Formation is referred to the Aptian–Albian on the basis of palaeontological evidence, and this supports the hypothesis that faunal assemblages containing *Psittacosaurus* in other parts of Asia are late Early Cretaceous in age. This occurrence in the Early Cretaceous of the Indochina Block indicates that by that time the microcontinent had become accreted to mainland Asia.

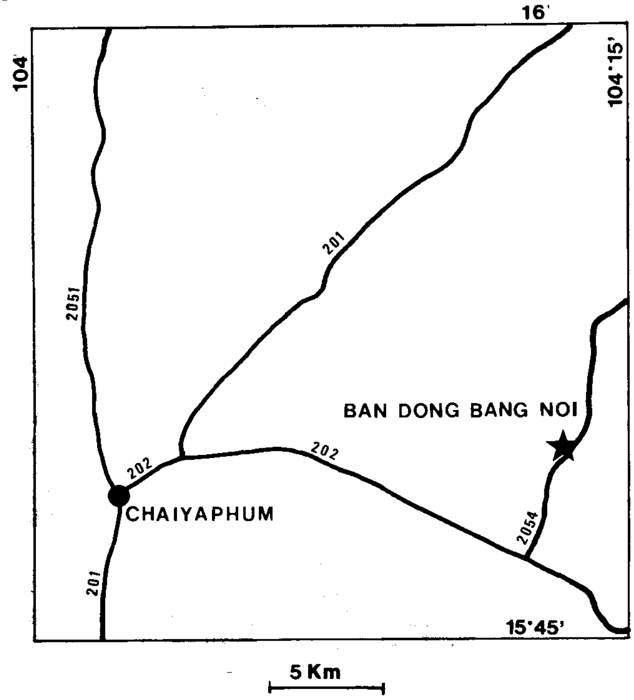
A FEW years ago Mr Nares Sattayarak of the Mineral Fuels Division of the Thai Department of Mineral Resources discovered a small jaw in the Khok Kruat Formation in the vicinity of the city of Chaiyaphum, in the northeastern part of Thailand. This was identified as the dentary of a small ornithischian dinosaur. During a subsequent visit to the locality, we found an additional jaw fragment, possibly belonging to the same individual. This material was described as belonging to the primitive ceratopian *Psittacosaurus* in a preliminary note (Buffetaut, Sattayarak and Suteethorn 1989). The purpose of the present paper is to describe the Thai *Psittacosaurus* in greater detail and to examine its systematic position more accurately, which leads us to erect a new species for its reception. In addition, we discuss the age of the locality and, more generally, the stratigraphical and geographical distribution of *Psittacosaurus*.

GEOLOGICAL SETTING

The specimens described below were found in an outcrop of red sandstones along a road at Ban Dong Bang Noi, some 20 km east of Chaiyaphum, in Chaiyaphum Province, on the Khorat Plateau of northeastern Thailand (Text-fig. 1). They occurred at the junction between a bed of fine-grained red sandstones and a thin layer of more conglomeratic sediment. These red beds belong to the Khok Kruat Formation, which itself belongs to the upper part of the Khorat Group, the thick succession of Mesozoic non-marine rocks which forms the northeastern part of Thailand. The Khok Kruat Formation consists of fluviatile red sandstones and conglomerates, reaching a thickness of several hundred metres. The name Khok Kruat Formation was first introduced by Ward and Bunnag (1964); they correlated it with 'Upper Indosinian' rocks in Laos and showed it in their correlation chart as ranging in age from basal Cretaceous to the Campanian–Maastrichtian boundary. The alternative name 'Ban Na Yo Formation' was used by Japanese geologists (e.g. Iwai *et al.* 1966). Molluscs from Ban Na Yo were considered as Early Cretaceous in age by Kobayashi (1964), although he later referred them to the Late Cretaceous (Kobayashi 1968). Although there is general agreement as to the Cretaceous age of the Khok Kruat Formation, it has been assigned various positions within that system (see the review by Sattayarak, 1983). Some of the fossil vertebrates found in the Formation (Buffetaut and Ingavat 1986) have turned out to be biostratigraphically useful. The occurrence of *Psittacosaurus* is in agreement with an Early Cretaceous age (see below). The peculiar hybodont shark *Thaiodus ruchae*, described from the same formation by Cappetta,

[Palaeontology, Vol. 35, Part 4, 1992, pp. 801–812.]





TEXT-FIG. 1. Maps showing the location of Chaiyaphum in northeastern Thailand and of the *Psittacosaurus sattayaraki* locality in the Khok Kruat Formation at Ban Dong Bang Noi, Chaiyaphum Province.

Buffetaut and Suteethorn (1990), is known from deltaic beds of the middle part of the Takena Formation of southern Tibet, which also contain Aptian–Albian orbitolinids (Cappetta *et al.* 1990). An Aptian–Albian age is thus likely for the Khok Kruat Formation, which may be correlated with the dinosaur-bearing beds of southern Laos (Buffetaut 1991).

Although the only identifiable vertebrate remains from the Ban Dong Bang Noi outcrop are the *Psittacosaurus* remains described below, other localities in the Khok Kruat Formation have yielded various vertebrate fossils (Buffetaut and Ingavat 1986). The quarries in the vicinity of Ban Khok Kruat, near the city of Nakhon Ratchasima (also known as Khorat), in particular, have yielded teeth of the hybodont shark *Thaiodus ruchae*, a *Lepidotes*-like actinopterygian fish (represented by isolated scales and a fairly complete specimen now at the Science Museum, Bangkok), ornamented turtle plates reminiscent of trionychids, crocodilian teeth of different shapes (some slender and pointed, others stout and blunt) apparently belonging to different taxa, and scanty remains of theropod dinosaurs (including teeth and fragmentary bones).

SYSTEMATIC PALAEONTOLOGY

Subclass DINOSAURIA Owen, 1842
Order ORNITHISCHIA Seeley, 1887
Suborder CERATOPSIA Marsh, 1890
Family PSITTACOSAURIDAE Osborn, 1923
Genus PSITTACOSAURUS Osborn, 1923

Psittacosaurus sattayaraki, sp. nov.

Text-figs 2–3

Derivation of name. In honour of Nares Sattayarak, who discovered the type specimen.

Holotype. Right dentary TF 2449*a* (Text-figs 2C–E, 3; palaeontological collection of the Department of Mineral Resources, Bangkok).

Hypodigm. Maxilla fragment TF 2449*b* (Text-fig. 2A–B).

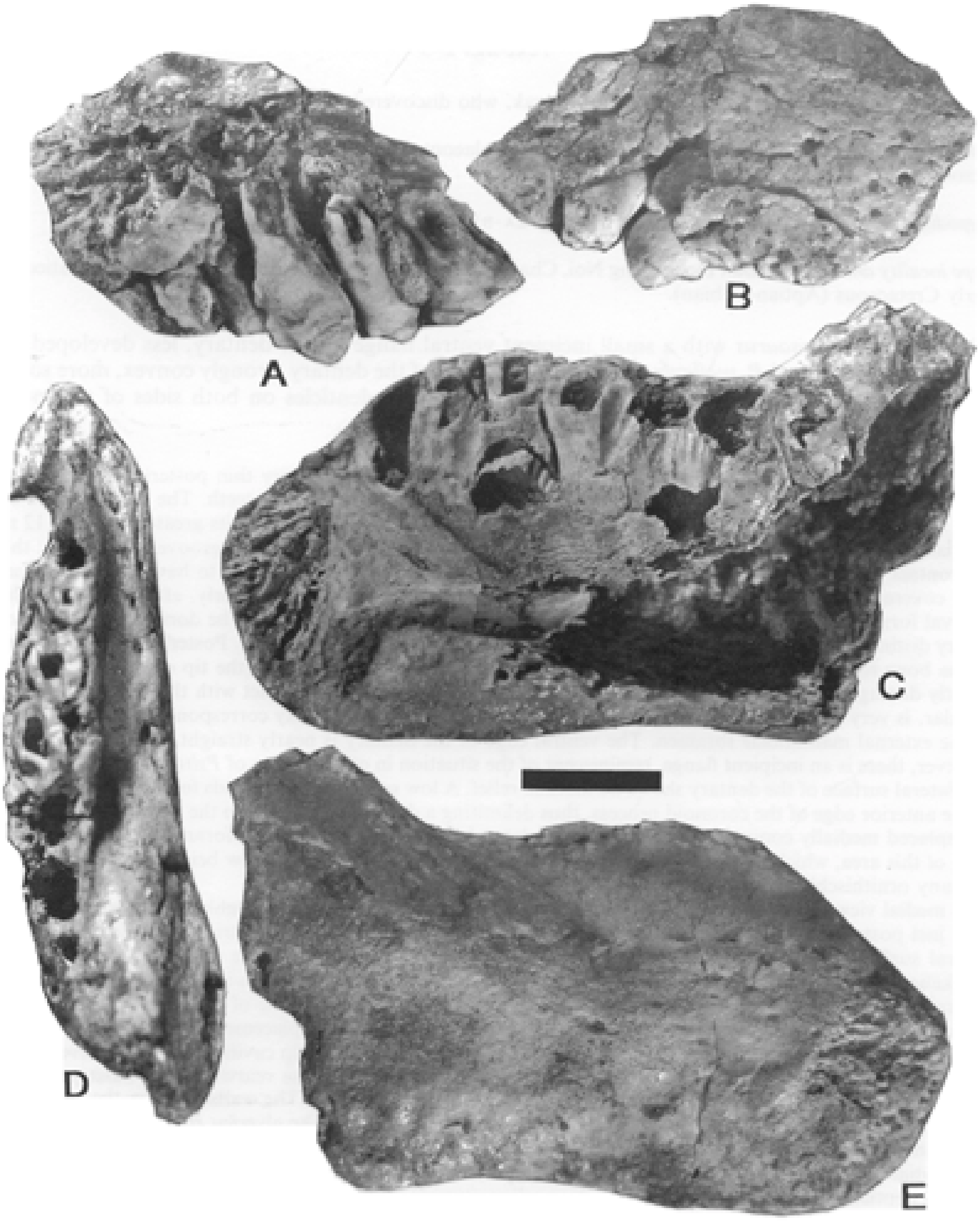
Type locality and horizon. Ban Dong Bang Noi, Chaiyaphum Province, Thailand; Khok Kruat Formation, late Early Cretaceous (Aptian–Albian).

Diagnosis. Psittacosaurus with a small incipient ventral flange on the dentary, less developed than in *P. mongoliensis* and *P. meileyingensis*. Alveolar edge of the dentary strongly convex, more so than in other species of *Psittacosaurus*. Dentary teeth with five denticles on both sides of the median primary ridge.

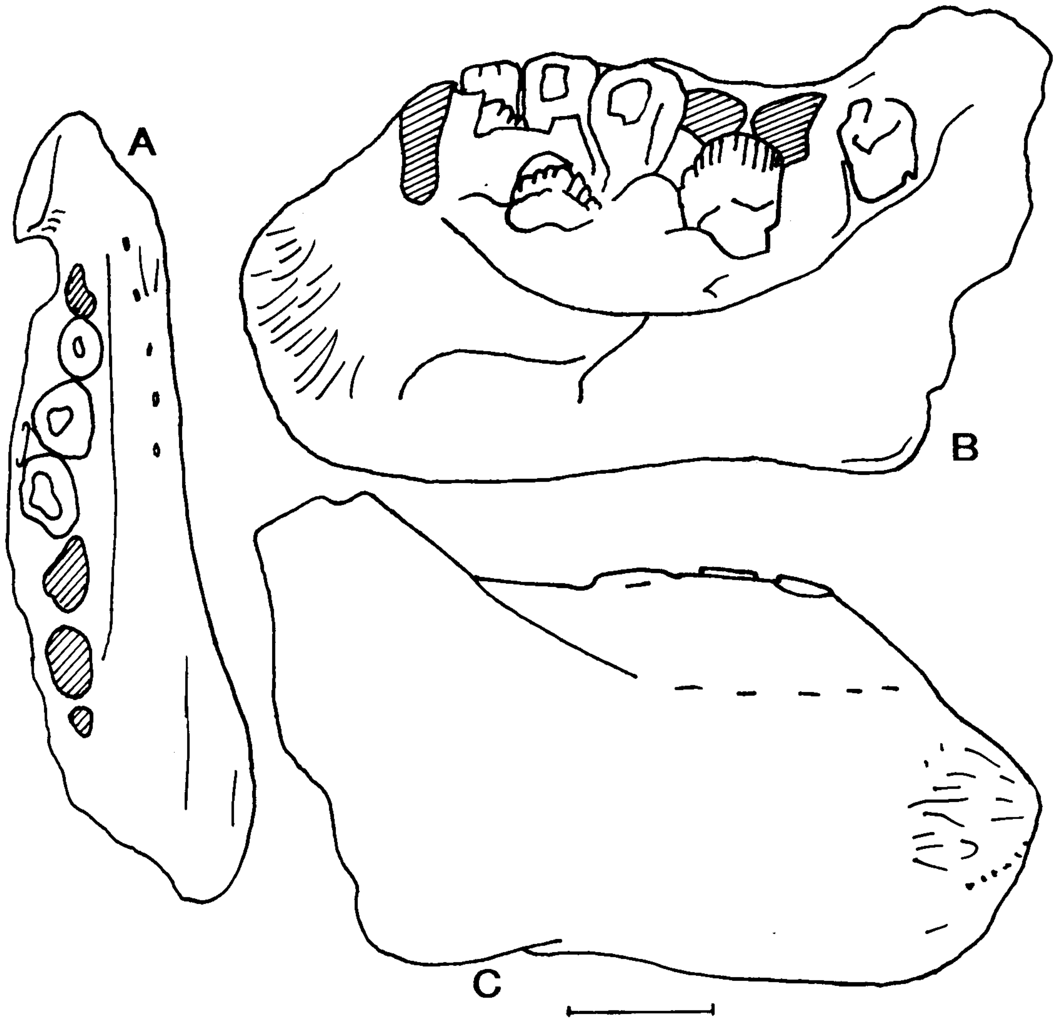
Description. The right dentary (Text-figs 2C–E, 3) is nearly complete; its very thin posterior edge is slightly damaged, as are the inner walls of the alveoli which thus expose replacement teeth. The length of the bone is 53 mm, its maximum height (at the level of the coronoid process) 31 mm, and its greatest breadth 12 mm. The lateral surface of the blunt anterior end is roughened, bearing irregular short grooves and ridges; this is the contact area for the predentary bone, which, as usual in *Psittacosaurus*, seems to have been large and to have covered a sizeable portion of the anterior end of the dentary. More posteriorly, after a short toothless interval forming a rounded groove, the lateral edge of the alveolar row (forming the dorsal edge of the bone) is very distinctly convex in its anterior part, and slightly concave more posteriorly. Posteriorly, the dorsal edge of the bone rises at a 45° angle, to form the well-developed coronoid process (the tip of which seems to be slightly damaged). The posterior edge of the bone, corresponding to the contact with the surangular and the angular, is very thin and has suffered some damage. A small notch in it may correspond to the anterior part of the external mandibular foramen. The ventral edge of the dentary is nearly straight. In its posterior part, however, there is an incipient flange, reminiscent of the situation in other species of *Psittacosaurus* (see below). The lateral surface of the dentary shows no marked relief. A low smooth ridge extends forward in prolongation of the anterior edge of the coronoid process, thus delimiting a dorsal area, lateral to the alveolar border, which is displaced medially compared to the rest of the lateral surface. A row of small foramina marks the ventral limit of this area, which apparently corresponds to the cheek region (the tooth row being displaced inward, as in many ornithischians).

In medial view, the dentary shows a very large Meckelian groove, which is roughly triangular in shape and ends just posterior to the symphyseal area. The latter consists of a more or less triangular, deeply furrowed, sutural surface for union with the left dentary. Between the symphysis and the alveolar region, above the Meckelian groove, there is a narrow concave area. The alveolar region forms an incipient dental battery, the ventral limit of which follows a regular curve ending posteriorly at the base of the coronoid process. The damaged medial wall of the alveoli exposes several fairly well-preserved replacement teeth. The crowns of the three functional teeth still present in alveoli are broken, revealing large pulp cavities. There are seven alveoli, which increase in diameter from the first to the fourth, and then decrease rearward; the most posterior is smallest, and placed medial to the anterior part of the coronoid process. The walls between the alveoli must have been poorly ossified, since the alveoli now appear to be confluent. The alveolar row is straight; its length is 31 mm. Crowns of replacement teeth are visible in the second, third and fifth alveoli. As in all psittacosaurs, the medial face of the crown bears a bulbous median primary ridge. On each side of this median ridge, there are five denticles, continued downward by descending secondary ridges. These do not extend below the upper half of the crown. There is no sharp distinction between the crown and the root: the crown tapers downward and merges gradually into the more or less cylindrical root. The labial face of the dentary teeth cannot be observed.

The maxilla fragment (Text-fig. 2A–B) is small and poorly preserved. Because of this, although originally identified as part of a left maxilla (Buffetaut *et al.* 1989), its original position is not easy to determine, and it may be from the right side of the skull. Five teeth are still attached to the jawbone, and one loose replacement tooth is also present in the alveolus for the smallest tooth. The bone as preserved shows a fairly marked



TEXT-FIG. 2. *Psittacosaurus sattayaraki*, sp. nov. from the Khok Kruat Formation (Aptian–Albian) of Ban Dong Bang Noi, Chaiyaphum Province, northeastern Thailand. A–B, TF 2449*b*, maxilla fragment in medial and lateral views. C–E, TF 2449*a* (holotype), right dentary in medial, dorsal and lateral views. Both specimens belong to the Palaeontological Collection of the Department of Mineral Resources, Bangkok. Scale bar represents 10 mm.



TEXT-FIG. 3. *Psittacosaurus sattayaraki*, sp. nov. TF 2449*a*, right dentary in dorsal (A), medial (B) and lateral (C) views. Scale bar represents 10 mm.

curvature in its dorsal part, which may correspond to the distinct angle between the alveolar region and the dorsal part of the maxilla generally observed in *Psittacosaurus* (the inward displacement of the tooth row being linked with the occurrence of a cheek pouch). The inner surface of the maxilla is very poorly preserved, and the roots of the teeth are clearly visible. The functional teeth are either broken or worn. As in the dentary teeth, the crown gradually tapers into the cylindrical root. The crowns are set at an angle to the axis of the roots, as already described in *Psittacosaurus meileyingensis* by Sereno, Cheng and Rao (1988). The crowns are too worn or broken to show any details. Only the above-mentioned loose replacement tooth shows a relatively strong primary ridge and a few additional denticles on both sides of it.

Discussion. The jaw fragments found at Ban Dong Bang Noi clearly belong to *Psittacosaurus*, as shown by the shape of the relatively deep and short dentary and the morphology of the teeth, with their bulbous primary ridge and secondary denticles. They may well belong to the same individual, although this is not possible to demonstrate conclusively. Both fragments have been prepared in formic acid, which has revealed a number of fine details. The holotype is the better specimen, and it is this which provides the diagnostic characters.

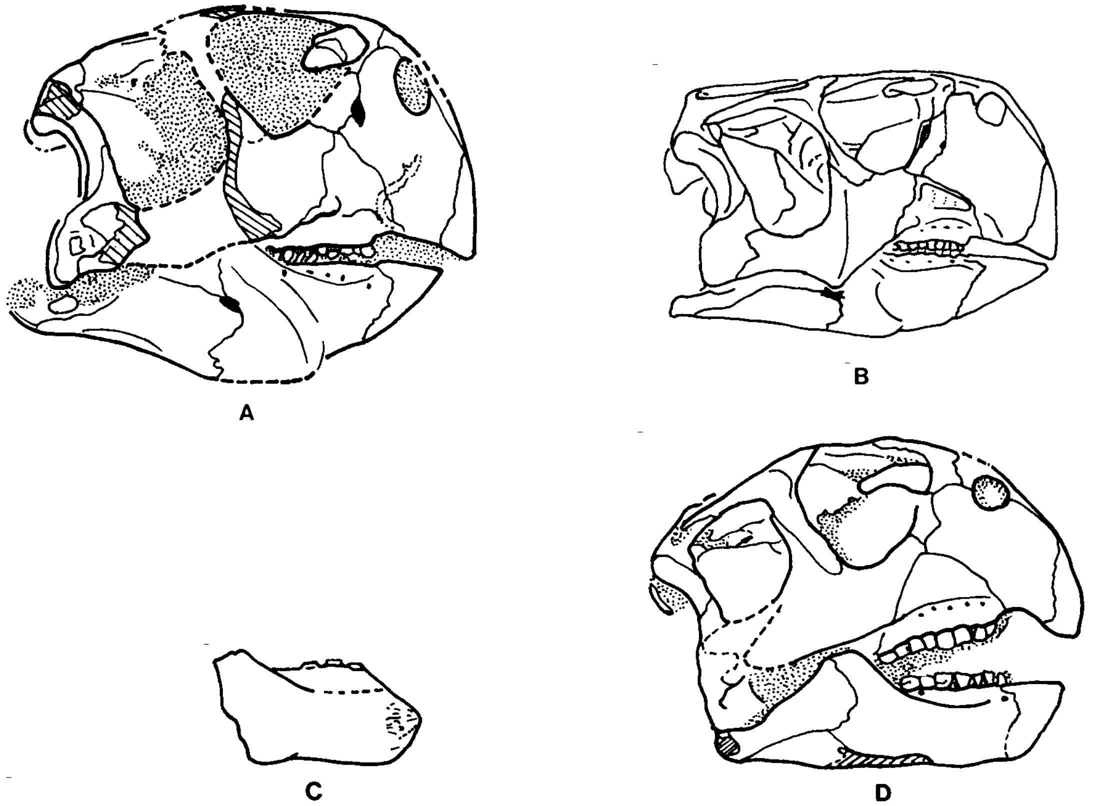
Comparison with other species of the genus is made difficult since only the dentary is well enough preserved; the many cranial features which have been used to separate species of *Psittacosaurus* are not available. Nevertheless, the dentary and lower teeth from Ban Dong Bang Noi show a combination of characters which we consider separate them from previously described species.

Comparisons have been made on the basis of descriptions of the best-known Mongolian and Chinese species of *Psittacosaurus*: *P. mongoliensis*, *P. meileyingensis*, *P. sinensis* and its probable synonym *P. youngi* (see Sereno 1990*b*), and *P. xinjiangensis*. In addition, casts of *Psittacosaurus mongoliensis* and *P. youngi* at the Natural History Museum, London, were also used for comparative purposes. Following Sereno (1990*a*, 1990*b*), *Protiguanodon mongoliensis* Osborn, 1923, *Psittacosaurus osborni* Young, 1932 and *P. tingi* Young, 1932 are considered as junior synonyms of *Psittacosaurus mongoliensis*. The material from Siberia recorded by Rozhdestvensky (1955) has not yet been described in detail, so that no meaningful comparison can be made, but this find has been referred to *Psittacosaurus mongoliensis* Osborn. Comparison with *Psittacosaurus guyangensis*, described by Cheng (1983) from Inner Mongolia (and a possible synonym of *P. mongoliensis* according to Sereno 1990*b*), in which the jaws are incompletely known, has also been attempted.

A first and possibly important point is whether the Thai material belongs to a fully-grown or juvenile individual. Ontogenetic changes in *Psittacosaurus* have been documented by Coombs (1982) on the basis of juvenile specimens from Mongolia in the American Museum of Natural History (AMNH 6535 and AMNH 6536), but no juvenile features are listed for the dentary, which does not seem to have undergone very notable morphological changes during growth. Dentary TF 2449*a* is about twice the size of that of AMNH 6536 and three times the size of that of AMNH 6535. It is about two-thirds the size of that of the type of *Psittacosaurus mongoliensis* described from Mongolia by Osborn (1923), and about the size of that of the type of *Psittacosaurus youngi* from Shandong described by Chao (1962) and of that of the type of *Psittacosaurus meileyingensis* from Liaoning described by Sereno *et al.* (1988). These comparisons suggest that the type of *Psittacosaurus sattayaraki* does not belong to a particularly young individual. An estimate based on the skeletal restorations published by Osborn (1924) suggests a total body length of about 1 m for *Psittacosaurus sattayaraki*. This is about 25 per cent less than that of *Psittacosaurus mongoliensis* as reconstructed by Osborn (1924), but considerably more than the body lengths calculated by Coombs (1982) for AMNH 6536 (390 mm) and AMNH 6535 (265 mm). Curiously enough, however, Coombs (1982) mentions that in the very small skulls from Mongolia, 'the predentary and dentary bones are fused together', which was certainly not the case in TF 2449*a*, in which the predentary has separated from the dentary at the level of the unfused sutural region (and is lost).

The number of dentary teeth may also be of some relevance to the question of the individual age of TF 2449*a*, because the number increased during growth in *Psittacosaurus* as pointed out by Sereno (1990*a*, 1990*b*). According to Sereno (1990*a*), 'tooth count increases during growth from as few as five to as many as twelve in *P. mongoliensis*. Adult tooth count varies from eight to twelve among psittacosaurid species'. The presence of seven alveoli in TF 2449*a* may suggest that it does not belong to a fully-grown individual. In any case, as pointed out by Sereno (1990*b*, p. 203), 'a slight difference in tooth count from that of a type specimen, obviously, should not be used to distinguish a new species of psittacosaur, particularly in the absence of other age criteria'.

Whether the two main characters used to define *Psittacosaurus sattayaraki* (i.e. degree of development of a ventral flange on the dentary and curvature of the alveolar edge) are affected by ontogenetic change is difficult to ascertain, because the very young individuals described by Coombs (1982) apparently do not show the regions in question very clearly. Coombs's figures do not suggest a marked curvature of the alveolar edge, and his description mentions a straight ventral margin, which seems to imply the absence of a flange. Flange development seems to be quite variable from species to species, with a very strong flange (associated with a marked ridge on the lateral face of the dentary) in *Psittacosaurus meileyingensis* and no flange in *Psittacosaurus sinensis* and *P. youngi*, although the type specimens of all three species are of about the same size. This suggests that flange development was not primarily size-related and that the degree of development of the flange can indeed be used as a differential character. As to the outline of the alveolar edge, it is usually much less convex than in *Psittacosaurus sattayaraki*, whatever the size of the bone, except in some specimens of *P. mongoliensis* in which some curvature is observable.



TEXT-FIG. 4. A comparison of the holotype of *Psittacosaurus sattayaraki* (C) with skulls and lower jaws of other species of *Psittacosaurus*: *P. meileyingensis* (A), *P. mongoliensis* (B) and *P. youngi* (D). A-B, D after Sereno 1990*b*. Not to scale.

The main differences between *Psittacosaurus sattayaraki* and the other species of *Psittacosaurus* mentioned above are the following (see also Text-fig. 4):

Psittacosaurus mongoliensis Osborn, 1923 has a larger number of dentary teeth in adult individuals than *Psittacosaurus sattayaraki*; however, as mentioned above, an increase in tooth number during growth has been reported in *Psittacosaurus* and this difference may not be significant, since the type of *P. mongoliensis* is larger than that of *P. sattayaraki*. The ventral flange of the dentary is more developed in *Psittacosaurus mongoliensis* than in *P. sattayaraki*, in which it is incipient.

Psittacosaurus meileyingensis Sereno *et al.*, 1988 from Liaoning (North China) clearly differs from *P. sattayaraki* by the strong development of its ventral flange, associated with the presence of a marked ridge on the lateral surface of the dentary. Although there are nine dentary teeth instead of the seven in *Psittacosaurus sattayaraki* this difference may not be of great significance, although the types of *P. sattayaraki* and *P. meileyingensis* are of roughly the same size.

In *Psittacosaurus sinensis* Young, 1958 from Shandong, there is no indication of a ventral flange on the dentary, and the convexity of the alveolar edge is less marked than in *Psittacosaurus sattayaraki*.

Psittacosaurus youngi Chao, 1962 from the same formation in Shandong as *P. sinensis*, may well be a junior synonym of the latter (Sereno 1990*b*). There are eight dentary teeth, no ventral flange, and a nearly straight alveolar edge, compared to the markedly convex one seen in *Psittacosaurus sattayaraki*.

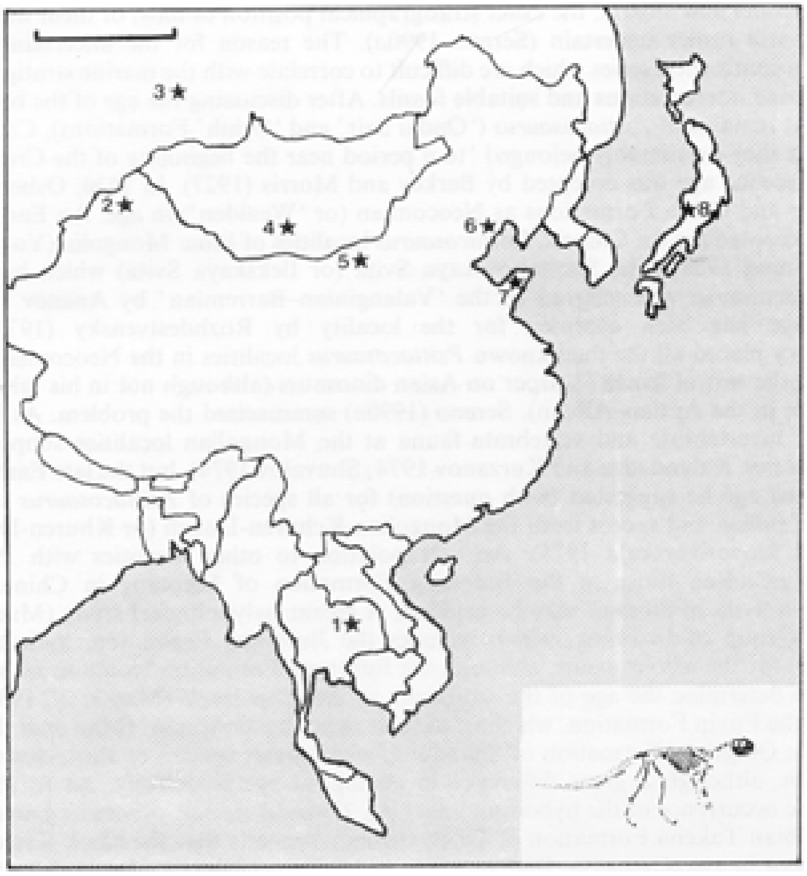
Psittacosaurus xinjiangensis Sereno and Chao, 1988 from Xinjiang has a lower jaw which is poorly known. However, it seems that there was no ventral flange on the dentary. A single dentary tooth was reported, and it differs from those of other species of *Psittacosaurus*, including *P. sattayaraki*, in having more denticles, i.e. ten on each side of the primary ridge.

Psittacosaurus guyangensis Cheng, 1983 from Inner Mongolia includes a relatively complete maxilla with an associated incomplete lower jaw. Many characters of the mandible, such as the development of a ventral flange, cannot be observed. The alveolar edge may have been convex, but apparently less so than in *Psittacosaurus sattayaraki*. The number of dentary teeth is unclear. An unworn lower tooth figured by Cheng shows, on the lingual side, a bulbous median ridge flanked by four secondary denticles on each side, instead of the five in *P. sattayaraki* and most other species of the genus. An exception is *P. xinjiangensis*, but such a minor variation is probably not significant (Sereno 1990*b*, who argued that *Psittacosaurus guyangensis* is not distinguishable from *P. mongoliensis*).

It thus appears that the form from Thailand differs from all reasonably well-defined species of *Psittacosaurus* by at least some characters of its dentary (notably the development of the ventral flange and/or the curvature of the alveolar edge), and that its separation at the species level is justified. As pointed out by Sereno (1990*a*), little is known about psittacosaurid interrelationships, and the incomplete nature of the available material of *Psittacosaurus sattayaraki* clearly makes it especially difficult to define its relationships with other species of the genus. If a greater development of the ventral flange is considered as a derived character, *Psittacosaurus sattayaraki* appears to be more primitive than *P. meileyingensis*. Its ventral flange is also smaller than that of *Psittacosaurus mongoliensis*, although it somewhat resembles the latter in the curvature of the dorsal edge of the dentary. *Psittacosaurus sinensis* and *P. youngi* may appear less derived than *P. sattayaraki* in the absence of a ventral flange; they also differ from it in having a straighter alveolar edge. *Psittacosaurus xinjiangensis* also seems to lack a ventral flange, and differs from *P. sattayaraki* in the great number of denticles on its lower teeth, but the polarity of the latter character is uncertain. The closest resemblances of *Psittacosaurus sattayaraki* seem to be with *P. mongoliensis*; more complete material could lead to a revision of this tentative interpretation.

THE DISTRIBUTION OF *PSITTACOSAURUS* IN TIME AND SPACE

Psittacosaurus remains were first discovered in Outer Mongolia by the American Museum of Natural History Central Asiatic Expedition of 1922 (Andrews 1932). A large amount of additional material was later collected at various Mongolian localities, notably by Soviet–Mongolian expeditions (see Kalandadze and Kurzanov 1974). In China, psittacosaurs have been found in Inner Mongolia (Young 1932; Bohlin 1953; Cheng 1983), Shandong (Young 1958; Chao 1962), Xinjiang (Sereno and Chao 1988) and Liaoning (Sereno *et al.* 1988). There is also a report from the Gorno-Altayaskaya Autonomous Region in Western Siberia (Rozhdestvensky 1955, 1960, 1973). Poorly preserved limb bones from the Kitadani Formation of Japan were referred to 'Psittacosauridae gen. et sp. indet.' by Dong *et al.* (1990; see also Manabe and Hasegawa 1991). The southernmost locality was in Shandong, at a latitude of about 37°N (with the Japanese one farther east at roughly the same latitude). As already pointed out (Buffetaut, Sattayarak and Suteethorn 1989), the discovery of *Psittacosaurus* in Thailand thus greatly extends the geographical range of the genus (the Thai locality, at about 16°N, is some 3000 km distant from the Shandong locality: Text-fig. 5). The geographical distribution of *Psittacosaurus*, as known today, partly parallels that of other groups



TEXT-FIG. 5. The distribution of psittacosaurid localities (stars) in Asia. 1, *Psittacosaurus sattayaraki*, northeastern Thailand (this paper); 2, *Psittacosaurus xinjiangensis*, Xinjiang, China (Sereno and Chao 1988), 3, *Psittacosaurus mongoliensis*, Kuznetz Basin, Siberia (Rozhdestvensky 1955, 1960); 4, *Psittacosaurus mongoliensis*, Gobi Desert, Outer Mongolia (Osborn 1923; Shuvalov 1974); 5, *Psittacosaurus mongoliensis* (including *P. osborni*, *P. tingi*, *P. guyangensis*), Inner Mongolia, China (Young 1932; Bohlin 1953; Cheng 1983); 6, *Psittacosaurus meileyingensis* and *P. mongoliensis*, Liaoning, China (Sereno *et al.* 1988); 7, *Psittacosaurus sinensis* and its possible synonym *P. youngi*, Shandong, China (Young 1958; Chao 1962); 8, Psittacosauridae gen. et sp. indet., Honshu, Japan (Dong *et al.* 1990; Manabe and Hasegawa 1991). Scale bar: 1000 km.

of non-marine organisms in the Cretaceous of Asia, in particular the bivalves *Trigonioides* and *Plicatounio*, which have been reported from the Khok Kruat Formation in Thailand (Kobayashi 1964) and also occur in Mongolia, northwestern China and Manchuria, as well as the Lena Basin in Siberia, and Japan (Kobayashi 1968).

From a palaeobiogeographical point of view, the Thai locality is important because of its location on the Indochina block or microcontinent. The occurrence of *Psittacosaurus* there indicates that in the Early Cretaceous this block had strong faunal affinities with more northern parts of Asia, including the Siberian, Junggar and North China blocks. This in turn leads to the conclusion that by Early Cretaceous times the assembly of Indochina to mainland Asia was already realized (Buffetaut, Sattayarak and Suteethorn 1989), contrary to what is shown on some palaeogeographical reconstructions (Tarling 1988), but in accordance with others (Besse and Courtillot 1988).

Although there is general agreement as to the Early Cretaceous age of the *Psittacosaurus* localities in Mongolia, China and Siberia, the exact stratigraphical position of most of them within the Early Cretaceous is still rather uncertain (Sereno 1990*a*). The reason for the uncertainty is that the localities are in continental series which are difficult to correlate with the marine stratigraphical scale for lack of marine intercalations and suitable fossils. After discussing the age of the beds which had yielded the first remains of *Psittacosaurus* ('Ondai Sair' and 'Oshih' Formations), Cockerell (1924) concluded that they presumably belonged 'to a period near the beginning of the Cretaceous', and an Early Cretaceous age was accepted by Berkey and Morris (1927). In 1930, Osborn considered the Ondai Sair and Oshih Formations as Neocomian (or 'Wealden') in age. An Early Cretaceous age was also accepted for the Chinese *Psittacosaurus* localities of Inner Mongolia (Young 1932) and Shandong (Young 1958). The Shestakovskaya Svita (or Ilekskaya Svita) which has yielded the Siberian *Psittacosaurus* was referred to the 'Valanginian–Barremian' by Ananev (1958), and a Neocomian age has been accepted for the locality by Rozhdestvensky (1973). In 1974, Rozhdestvensky placed all the then known *Psittacosaurus* localities in the Neocomian, an opinion he repeated in the text of his 1977 paper on Asian dinosaurs (although not in his table 1, in which he placed them in the Aptian–Albian). Sereno (1990*a*) summarized the problem. As he remarked, the associated invertebrate and vertebrate fauna at the Mongolian localities supports an Early Cretaceous age (see Kalandadze and Kurzanov 1974; Shuvalov 1974), but the late Early Cretaceous (Aptian–Albian) age he suggested (with question) for all species of *Psittacosaurus* is based on a single study of pollen and spores from the Mongolian Kchuren-Dukch (or Khuren-Dukh) locality (Bratzeva and Novodvorskaja 1975). An extrapolation to other localities with *Psittacosaurus mongoliensis* (including those in the Jiufotang Formation of Liaoning in China and in the Shestakovskaya Svita in Siberia) may be justified. A recent palynological study (Mao *et al.* 1990) on the Jehol Group of Liaoning, which includes the Jiufotang Formation, indicated an Early Cretaceous age for the whole group; although the Jiufotang Formation 'contains no species which can be used to determine the age of the sediments to the stage level' (Mao *et al.* 1990, p. 117), it is overlain by the Fuxin Formation, which is 'at least as young as Aptian' (Mao *et al.* 1990, p. 118). The case of the Qingshan Formation of Shandong, where other species of *Psittacosaurus* occur, is more uncertain, although a great difference in geological age is unlikely. As to *Psittacosaurus sattayaraki*, the occurrence of the hybodont selachian *Thaiodus ruchae*, otherwise known only from the Aptian–Albian Takena Formation of Tibet, strongly suggests that the Khok Kruat Formation is Aptian–Albian in age (Cappetta, Buffetaut and Suteethorn 1990; see also Buffetaut 1991). This means that *Psittacosaurus sattayaraki* is of about the same age as *P. mongoliensis*, which certainly supports Sereno's suggestion that psittacosaurs as a whole are of late Early Cretaceous age. In a brief discussion of the scanty psittacosaurid material from Japan, Manabe and Hasegawa (1991) assumed a Barremian age for the Kitadani Formation, and suggested that the Chinese faunal complex containing *Psittacosaurus* may be older than usually accepted. According to Manabe (personal communication), however, further research shows that the available evidence is not conclusive. In conclusion, the likeliest age for most psittacosaurs is late Early Cretaceous.

Acknowledgements. We thank Nares Sattayarak for collecting the first specimen of *Psittacosaurus* from Ban Dong Bang Noi and drawing our attention to this locality, Yaowalak Chaimanee for her help in the field, and Angela C. Milner (The Natural History Museum, London) for making available casts of Chinese and Mongolian specimens of *Psittacosaurus*. Paul Sereno and Makoto Manabe provided useful information, and Haiyan Tong-Buffetaut translated Chinese papers. The drawings are by Claude Briand and the photography by Claude Abrial. This work was supported by the Department of Mineral Resources (Bangkok), the Groupement Scientifique Téthys (Paris), the French Palaeontological Mission in Thailand (supported by the French Ministry of Foreign Affairs), and the Centre National de la Recherche Scientifique (Paris).

REFERENCES

ANANEV, A. 1958. Série d'Ilek. 518. *In* LIKHAREV, B. K. (ed.). *Lexique stratigraphique international, vol. ii (U.R.S.S.), fasc.* 1. C.N.R.S., Paris, 564 pp.

ANDREWS, R. C. 1932. *The new conquest of Central Asia.* American Museum of Natural History, New York, 678 pp.

BERKEY, C. P. and MORRIS, F. K. 1927. *Geology of Mongolia.* American Museum of Natural History, New York, 475 pp.

BESSE, J. and COURTILLOT, V. 1988. Paleogeographic maps of the continents bordering the Indian Ocean since the Early Jurassic. *Journal of Geophysical Research*, **93**, 11791–11808.

BOHLIN, B. 1953. Fossil reptiles from Mongolia and Kansu. *Report from the Scientific Expedition in the NW Provinces of China by Sino-Swedish Expedition.* **37**, 1–113.

BRATZEVA, T. M. and NOVODVORSKAJA, I. M. 1975. Spores and pollen from Lower Cretaceous deposits from the locality Kchuren-Dukch, MPR. *Fossil fauna and flora of Mongolia, The joint Soviet-Mongolian Palaeontological Expedition, Transactions*, **2**, 205–209. [In Russian].

BUFFETAUT, E. 1991. On the age of the Cretaceous dinosaur-bearing beds of southern Laos. *Newsletters on Stratigraphy*, **24** (1–2), 59–73.

—— and INGAVAT, R. 1986. The succession of vertebrate faunas in the continental Mesozoic of Thailand. *Bulletin of the Geological Society of Malaysia*, **19**, 167–172.

—— SATTAYARAK, N. and SUTEETHORN, V. 1989. A psittacosaurid dinosaur from the Cretaceous of Thailand and its implications for the palaeogeographical history of Asia. *Terra Nova*, **1**, 370–373.

CAPPETTA, H., BUFFETAUT, E. and SUTEETHORN, V. 1990. A new hybodont shark from the Lower Cretaceous of Thailand. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1990**, 659–666.

CHAO, S. 1962. New species of *Psittacosaurus* from Laiyang. *Vertebrata Palasiatica*, **6**, 349–360. [In Chinese].

CHENG, Z. 1983. Reptilia. Part 7. 123–136. *In* GEOLOGICAL SURVEY OF THE AUTONOMOUS REGION OF INNER MONGOLIA (ed.). *The Mesozoic stratigraphy and paleontology of Guyang coal-bearing basin, Nei Monggol Autonomous Region, China.* Geology Press, Beijing, 230 pp. [In Chinese].

COCKERELL, T. D. A. 1924. Fossils in the Ondai Sair Formation, Mongolia. *Bulletin of the American Museum of Natural History*, **51**, 129–144.

COOMBS, W. P. 1982. Juvenile specimens of the ornithischian dinosaur *Psittacosaurus. Palaeontology*, **25**, 89–107.

DONG, Z., HASEGAWA, Y. and AZUMA, Y. 1990. *The age of dinosaurs in Japan and China.* Fukui Prefectural Museum, Fukui, 65 pp. [In Japanese].

IWAI, J., ASAMA, K., VEERABURUS, M. and HONGNUSONTHI, A 1966. Stratigraphy of the so-called Khorat Series and a note on the fossil plant-bearing Palaeozoic strata in Thailand. *Geology and Palaeontology of Southeast Asia*, **2**, 179–196.

KALANDADZE, N. N. and KURZANOV, S. M. 1974. Lower Cretaceous localities of terrestrial vertebrates in Mongolia. *Mesozoic and Cenozoic faunas and biostratigraphy of Mongolia. The joint Soviet-Mongolian Paleontological Expedition, Transactions*, **1**, 288–295. [In Russian].

KOBAYASHI, T. 1964. Palaeontology of Thailand, 1916–1962. *Geology and Palaeontology of Southeast Asia*, **1**, 17–29.

—— 1968. The Cretaceous non-marine pelecypods from the Nam Phung dam site in the northeastern part of the Khorat Plateau, Thailand, with a note on the Trigonioididae. *Geology and Palaeontology of Southeast Asia*, **4**, 109–138.

MANABE, M. and HASEGAWA, Y. 1991. The Cretaceous dinosaur fauna of Japan. 41–42. *In* KIELAN-JAWOROWSKA, Z., HEINTZ, N. and NAKREM, H. A. (eds). *Fifth Symposium on Mesozoic terrestrial ecosystems and biota. Extended abstracts.* Contributions from the Paleontology Museum, University of Oslo, **364**, 72 pp.

MAO, S., YU, J. and LENTIN, J. K. 1990. Palynological interpretation of Early Cretaceous non-marine strata of northeast China. *Review of Palaeobotany and Palynology*, **65**, 115–118.

MARSH, O. C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science*, **39**, 418–426.

OSBORN, H. F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates*, **95**, 1–10.

—— 1924. *Psittacosaurus* and *Protiguanodon*: two Lower Cretaceous iguanodonts from Mongolia. *American Museum Novitates*, **127**, 1–16.

—— 1930. Ancient vertebrate life of Central Asia. 519–543 *In Livre jubilaire 1830–1930.* Société Géologique de France, Paris. **2**, 660 pp.

OWEN, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Science*, **11**, 60–204.

ROZHDESTVENSKY, A. K. 1955. New information on *Psittacosaurus*, Cretaceous ornithopods. *Voprosy Geologii Azii*, **2**, 783–788. [In Russian].

ROZHDESTVENSKY, A. K. 1960. Locality of Lower Cretaceous dinosaurs in the Kuznetz Basin. *Paleontologichesky Zhurnal*, **3**, 165. [In Russian].
—— 1973. The study of Cretaceous reptiles in Russia. *Paleontologichesky Zhurnal*, **2**, 90–99 [In Russian].
—— 1974. A history of dinosaur faunas from Asia and other continents and some problems of palaeogeography. *Mesozoic and Cenozoic faunas and biostratigraphy of Mongolia. The joint Soviet–Mongolian Paleontological Expedition. Transactions*, **1**, 107–131. [In Russian].
—— 1977. The study of dinosaurs in Asia. *Journal of the Palaeontological Society of India*, **20**, 102–119.
SATTAYARAK, N. 1983. Review of the continental Mesozoic stratigraphy of Thailand. 127–148. *In* NUTALAYA, P. (ed.). *Proceedings of the Workshop on stratigraphic correlation of Thailand and Malaysia.* Geological Society of Thailand and Geological Society of Malaysia, Bangkok, 383 pp.
SEELEY, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.
SERENO, P. 1990*a*. Psittacosauridae. 579–592. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria.* University of California Press, Berkeley, 733 pp.
—— 1990*b*. New data on parrot-beaked dinosaurs (*Psittacosaurus*). 203–210. *In* CARPENTER, K. and CURRIE, P. J. (eds). *Dinosaur systematics: perspectives and approaches.* Cambridge University Press, Cambridge, 318 pp.
—— and CHAO, S. 1988. *Psittacosaurus xinjiangensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northwestern China. *Journal of Vertebrate Paleontology*, **14**, 353–365.
—— —— CHENG, Z. and RAO, C. 1988. *Psittacosaurus meileyingensis* (Ornithischia, Ceratopsia), a new psittacosaur from the Lower Cretaceous of northeastern China. *Journal of Vertebrate Paleontology*, **14**, 366–377.
SHUVALOV, V. F. 1974. On geology and age of Khobur and Khuren-Dukh localities in Mongolia. *Mesozoic and Cenozoic faunas and biostratigraphy of Mongolia. The joint Soviet–Mongolian Paleontological Expedition. Transactions*, **1**, 296–304. [In Russian].
TARLING, D. H. 1988. Gondwanaland and the evolution of the Indian Ocean. 61–77. *In* AUDLEY-CHARLES, M. G. and HALLAM, A. (eds). Gondwana and Tethys. *Special Publications of the Geological Society, London*, **37**, 317 pp.
WARD, D. E. and BUNNAG, D. 1964. Stratigraphy of the Mesozoic Khorat Group in northeastern Thailand. *Thai Department of Mineral Resources. Report of Investigation*, **6**, 1–95.
YOUNG, C. C. 1932. On some new dinosaurs from western Suiyuan, Inner Mongolia. *Bulletin of the Geological Society of China*, **11**, 259–266.
—— 1958. The dinosaurian remains of Laiyang, Shantung. *Palaeontologia Sinica*, **16**, 1–138.

ERIC BUFFETAUT
URA 1433 du CNRS
Laboratoire de Paléontologie des Vertébrés
Case 106, 4 place Jussieu
75252 Paris Cedex 05, France

VARAVUDH SUTEETHORN
Geological Survey Division
Department of Mineral Resources
Rama VI Road
Bangkok 10 400, Thailand

Typescript received 5 December 1991
Revised typescript received 9 March 1992