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Redescription of the Mongolian Sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous Sauropod diversity

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SYNOPSIS The isolated skulls of *Nemegtosaurus mongoliensis* and *Quaesitosaurus orientalis* from the Nemegt Basin of Mongolia are among the most complete sauropod cranial remains known from the Late Cretaceous, yet their evolutionary relationships to other neosauropods have remained uncertain. Redescription of the skull of *Nemegtosaurus* identifies key features that link it and its closely related counterpart *Quaesitosaurus* to titanosaur sauropods. These include a posterolaterally orientated quadrate fossa, 'rocker'-like palatobasal contact, pterygoid with reduced quadrate flange and a novel basisphenoid–quadrate contact. Other features are exclusive to *Nemegtosaurus* and *Quaesitosaurus*, such as the presence of a symphyseal eminence on the external aspect of the premaxillae, a highly vascularised tooth bearing portion of the maxilla, an enclosed 'maxillary canal', orbital ornamentation on the postorbital, prefrontal and frontal, exclusion of the squamosal from the supratemporal fenestra and dentary teeth smaller in diameter than premaxillary and maxillary teeth.

Re-examination of Late Cretaceous sauropod distributions in the light of this well-supported phylogenetic hypothesis has important implications for their diversity at the end of the Mesozoic in Asia and elsewhere. Cretaceous Asian sauropod faunas consist solely of titanosauriforms, which probably migrated there from other landmasses during the Late Jurassic, during which time neosauropods were absent from Asia. Globally, narrow-crowned titanosaurs and rebbachisaurids radiated during the Cretaceous, but only titanosaurs survived into the latest Cretaceous. These late-surviving sauropods flourished on most continental landmasses until the end of the Maastrichtian.

KEY WORDS vertebrate palaeontology, evolution, palaeobiogeography, Mesozoic, Asia, Titanosauria

Contents

Introduction

The Central Asiatic Expeditions (1922–1930), Mongolian Palaeontological Expeditions (1946–1949), Polish–Mongolian Palaeontological Expeditions (1963–1971) and Soviet-Mongolian Palaeontological Expeditions (1969–1979) to the Gobi Desert of Mongolia discovered a wealth of fossil material that documented both the end of the age of dinosaurs and the beginning of the age of mammals in Asia (Efremov 1948; Kielan-Jaworowska & Dovchin 1968/69; Kurochkin & Barsbold 2000). These expeditions to Mongolia brought to light numerous new dinosaurs, such as ankylosaurs, ornithopods, ceratopsians and pachycephalosaurs, as well as many coelurosaurian theropods (see Benton *et al*. 2000). Subsequent studies have suggested that many Late Cretaceous Mongolian ornithischian and theropod genera are closely related to genera from similar-aged horizons in western North America, implying multiple dispersals across Beringia (Maryanska & Osmólska 1975; Russell 1993; Sereno 2000; Upchurch *et al*. 2002). Also present in the Late Cretaceous Mongolian dinosaur fauna were three sauropod genera (*Opisthocoelicaudia*, *Quaesitosaurus*, *Nemegtosaurus*) that had no hypothesised correlates in North America, despite the presence of at least one Late Cretaceous sauropod in the western USA (*Alamosaurus*: Gilmore 1922). These three Mongolian sauropod genera have received less attention than their ornithischian and theropod counterparts, despite representing some of the best preserved sauropod remains known from Late Cretaceous-aged sediments of northern (Laurasian) landmasses.

The Mongolian sauropod *Opisthocoelicaudia* was initially described as *Camarasaurus*-like (Borsuk-Bialynicka 1977; McIntosh 1990), whereas *Nemegtosaurus* and *Quaesitosaurus* were described as *Dicraeosaurus*-like (Nowinski 1971; McIntosh 1990). These designations were consistent with what was then known of the Late Jurassic Asian sauropod fauna, which included genera considered by McIntosh (1990) to be camarasaurid (*Euhelopus*) and diplodocid (*Mamenchisaurus*). Thus, Mongolia appeared to have representatives of both narrow-crowned (diplodocids, titanosaurs) and broad-crowned (camarasaurids, brachiosaurids) sauropod groups (e.g. Janensch 1929; Romer 1956; McIntosh 1990). More recently, cladistic analyses of sauropod relationships have demonstrated that broad crowns are primitive for Sauropoda (Upchurch 1995) and that narrow crowns evolved at least twice independently within the group (Salgado *et al*. 1997; Wilson & Sereno 1998). This revised context of sauropod phylogeny has produced new hypotheses for the relationships of the three Mongolian sauropods that differ from traditional views. Cladistic analyses that have included the genus agree that *Opisthocoelicaudia* is a titanosaur (e.g. Upchurch 1995, 1998; Salgado *et al*. 1997; Sanz *et al*. 1999; Curry Rogers & Forster 2001; Wilson 2002), that *Euhelopus* is either a derived titanosauriform (Wilson & Sereno 1998; Wilson 2002) or a basal neosauropod (Upchurch *et al*. 2004) distantly related to *Camarasaurus* and that *Mamenchisaurus* is a non-neosauropod (Upchurch 1995, 1998; Wilson 2002). The phylogenetic affinities of *Nemegtosaurus* and *Quaesitosaurus*, in contrast, remain unresolved.

Originally described as *Dicraeosaurus*-like, *Nemegtosaurus* and *Quaesitosaurus* alternatively have been resolved by cladistic analyses as the monophyletic sister-taxon of diplodocoids (diplodocids, dicraeosaurids and others) (Yu 1993; Upchurch 1998, 1999; Upchurch *et al*. 2002, 2004), the basal members of a clade including diplodocoids and titanosaurs (Upchurch 1995) and, most recently, as titanosaurs (Calvo 1994; Salgado & Calvo 1997; Wilson 1997; Curry Rogers & Forster 2001; Wilson 2002). Lack of consensus on the phylogenetic affinities of these taxa probably stems from ambiguity resulting from preservational distortion of the skulls, uncertainty surrounding the higher-level relationships of narrow-crowned sauropods and lack of comparative Late Cretaceous skull material. General similarities between the skulls have likewise contributed to this problem (Upchurch 1999).

Below, *Nemegtosaurus* is redescribed and features diagnosing the genus and supporting its placement within Titanosauria are identified. Based on this revision, the affinities of *Quaesitosaurus* and other Asian sauropods are reassessed and a diagnosis and definition of Nemegtosauridae are proposed. The implications of the titanosaur affinities of Nemegtosauridae for Late Cretaceous sauropod diversity in Asia and worldwide are discussed.

Institutional abbreviations

GSI, Geological Survey of India, Kolkata; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing; PIN, Russian Academy of Sciences, Moscow; PVL, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; Z. PAL, Palaeobiological Institute of the Polish Academy of Sciences, Warsaw.

Systematic palaeontology

SAUROPODA Marsh, 1878

MACRONARIA Wilson & Sereno, 1998

TITANOSAURIA Bonaparte & Coria, 1993

NEMEGTOSAURIDAE Upchurch, 1995

NEMEGTOSAURUS Nowinski, 1971

Type species. *Nemegtosaurus mongoliensis* Nowinski 1971.

Figure 1 Map of Mongolia showing the sites that produced *Nemegtosaurus mongoliensis* (Nemegt Uul), *Opisthocoelicaudia skarzynskii* (Altan Uul IV) and *Quaesitosaurus orientalis* (Shar Tsav). Locality data from (Kielan-Jaworowska 1969; Kurochkin & Barsbold 2000); Mongolia map based on Shupe *et al.* (1992). Scale bar = 500 km.

DIAGNOSIS AND OCCURRENCE. As for the species.

Nemegtosaurus mongoliensis Nowinski, 1971 (see Figs 2–16)

1971 *Nemegtosaurus mongoliensis* Nowinski: 59, figs 1–8, pls 8–14.

HOLOTYPE. Based on a nearly complete skull lacking only the dorsal margin of the narial region and portions of the mid-palate (palatines and posterior vomer), articulated with nearly complete left and right lower jaws lacking only the prearticular and articular (Z. PAL MgD-I/9).

OCCURRENCE. Nemegt Formation, Upper Cretaceous (mid-Maastrichtian; Jerzykiewicz & Russell 1991) of the Gobi Desert, Mongolia (Fig. 1).

REVISED DIAGNOSIS. *Nemegtosaurus mongoliensis* is characterised by the following autapomorphies: presence of a spur on the posterior squamosal and a conspicuous fossa surrounding the preantorbital fenestra. Other features cannot be scored in closely related taxa (i.e. *Quaesitosaurus*) and are thus ambiguous autapomorphies. These include the presence of an accessory fenestra positioned anterodorsal to the preantorbital fenestra, a jugal foramen and a coronoid foramen. For a fuller discussion of characters shared by *Nemegtosaurus* and closely related forms, see '*Nemegtosauridae*' below.

REFERRED SPECIMENS. Cranial remains of several Asian sauropods have been referred to *Nemegtosaurus* or included as members of Nemegtosauridae. First used by Upchurch (1995), Nemegtosauridae is phylogenetically defined by Upchurch *et al.* (2004: 303) as a stem-based clade including diplodocoids more closely related to *Nemegtosaurus* than to *Diplodocus*. Although this definition specifies a small clade within the phylogenetic framework supported by Upchurch *et al.* (2004), which places *Nemegtosaurus* within the Diplodocoidea, the same definition specifies a much larger group (Macronaria) under the topology supported here and elsewhere (Curry Rogers & Forster 2001; Wilson 2002). The phylogenetic definition of Nemegtosauridae is discussed in a later section (see '*Nemegtosauridae*' below). Nemegtosauridae currently includes several slender-toothed forms found in Asia.

Dong (1977) created the new species *Nemegtosaurus pachi* for a narrow-crowned tooth discovered in Upper Cretaceous strata of the Turpan Basin, Xinjiang, China. *Nemegtosaurus pachi* (IVPP V4879) resembles *N. mongoliensis* in its possession of longitudinally striated enamel near the base of the tooth (Dong 1977: pl. 2, fig. 8), but this feature is not diagnostic, as evidenced by its presence in both the narrow-crowned forms '*Titanosaurus*' *rahioliensis* (Mathur & Srivastava 1987: 564; pl. 3, fig. 6) and cf. *Alamosaurus* (Kues *et al.* 1980: figs 4–5), as well as the broad-crowned form *Mamenchisaurus sinocanadorum* (IVPP V10603; pers. obs.). For the same reason, the isolated teeth described by Dong (1997) from the Upper Cretaceous beds of the Mazongshan Area of Gansu Province, China cannot yet be referred to Nemegtosauridae.

In a reinterpretation of *Nemegtosaurus* and *Quaesitosaurus* as titanosaurs, Wilson (1997) suggested that these two genera might represent the same species. Although a close relationship between *Nemegtosaurus* and *Quaesitosaurus* is recognised here, several cranial differences support retention of separate genera (see '*Nemegtosauridae*' below).

Maryanska (2000: 458) reported a skull referable to the genus *Nemegtosaurus*. This undescribed skull is housed in the Geological Institute of the Mongolian Academy of Sciences in Ulaanbaatar. Its provenance, completeness and association with other remains have not yet been published. Thus far, however, specific features linking this new skull to *Nemegtosaurus* have not been recognised and additional comparisons are required to confirm its referral to an existing Late Cretaceous Asian genus.

Most recently, Buffetaut *et al.* (2002) interpreted new remains of the Early Cretaceous *Phuwiangosaurus* as supporting its membership in Nemegtosauridae. These include

jaw fragments and a well-preserved braincase collected from separate localities in the Sao Khua Formation (discussed in 'Relationship to other Mongolian Sauropods', below). Although Buffetaut *et al*. refer *Phuwiangosaurus* and other Early Cretaceous Asian sauropods (*Huabeisaurus*, *Mongolosaurus*) to Nemegtosauridae, they note primitive characters that differentiate them from the Late Cretaceous *Nemegtosaurus*.

Description

The following description emends and supplements that provided by Nowinski (1971), based on personal observation of the holotype (Z. PAL MgD-I/9) at the Polish Academy of Science, Warsaw. Observations of *Quaesitosaurus* are based on examination of the holotype (PIN 3906/2) at the Russian Academy of Science in Moscow.

Preservation

Nearly the entire skull of *Nemegtosaurus* is preserved; only portions of the external narial border and the middle portion of the palate have been weathered away. The skull was a single unit prior to preparation (Fig. 2), but since that time it has been separated into four pieces: an anterior skull block that includes the upper snout and anterior palate; a posterior skull block that includes braincase, posterior palate, skull roof and temporal region; and the two jaw rami. Most of the skull has been completely cleared of matrix, but matrix still fills the braincase and temporal region of the posterior skull block.

The shape of the skull has been distorted by deformation during preservation. Transverse compression is readily observed in both skull blocks. The posterior skull block has a triangular cross-section in anterior view formed by the flat skull roof and the approximated lower portions of the skull (quadratojugal and jugal). The anterior skull block bears signs of transverse compression because the midline elements of the snout have been forced past one another and the teeth have been displaced (see 'Premaxilla', below). Forward and upward shearing of the right side of the skull is evidenced by the dislocated lower jaw and crushed lateral temporal region visible in the unprepared skull (Fig. 2), as noted by Salgado & Calvo (1997), Calvo *et al*. (1998*b*) and Upchurch (1999). This deformation can be recognised in other skull elements, such as the snout bones, as discussed below. More specific comments about the preservation and distortion of each skull element is provided below.

Dermal roof complex

The dermal roof shield is made up of tooth-bearing elements (premaxilla, maxilla), median roofing elements (nasal, frontal, parietal), circumorbital elements (postorbital, prefrontal, lacrimal, jugal) and temporal elements (squamosal, quadratojugal). The skull has suffered some transverse compression, which has affected the shape of the supratemporal openings as well as the positions of the tooth-bearing elements. The cheek and eye regions of *Nemegtosaurus* are well preserved on both sides of the posterior skull block (Figs 3 & 4). Elements comprising them, in particular those of the lateral temporal region, have suffered deformation resulting from the forward shearing of the right side of the skull. This deformation has altered the shape of the various lateral skull openings on the right side, which formed the basis of Nowinski's (1971: fig. 1) skull reconstruction, the source for most comparisons (e.g. McIntosh 1990; Salgado & Calvo 1992; Upchurch 1995, 1999).

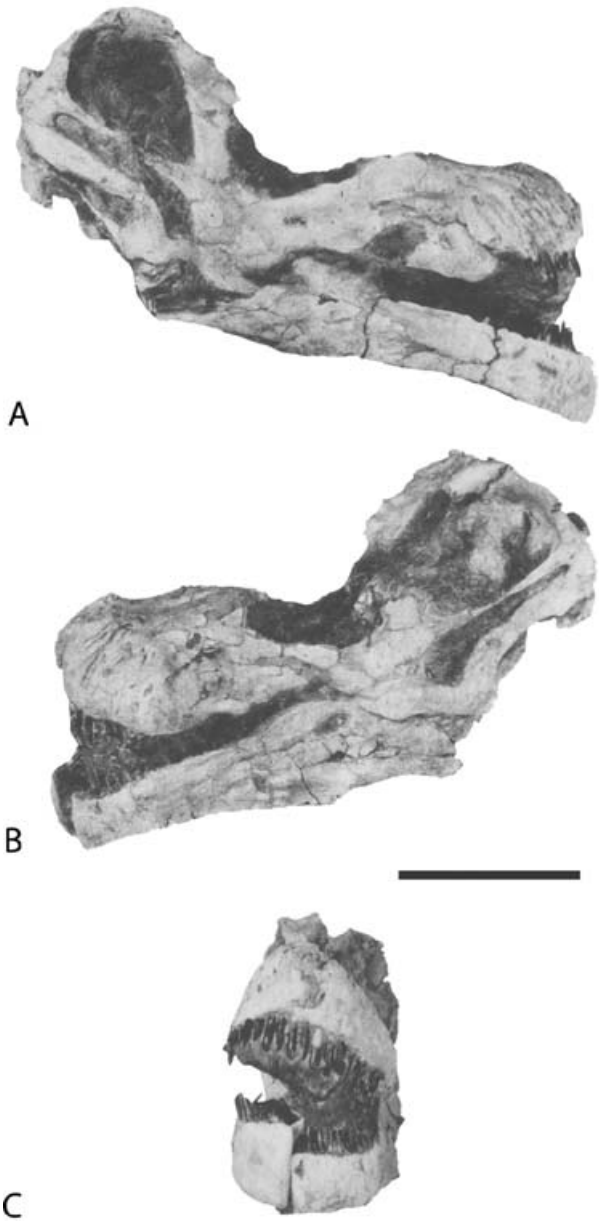

Figure 2 Skull and lower jaws of *Nemegtosaurus mongoliensis* prior to preparation in right lateral (**A**), left lateral (**B**), and anterior (**C**) views. Photographs are from Nowinski (1971: pl. 8; pl. 13, fig.2). Scale bar = 20 cm.

Premaxilla

The bodies of the right and left premaxillae are nearly completely preserved, except for an eroded area near the base of the ascending or dorsal processes. Very damaged portions of the premaxillary ascending processes are preserved in contact with the dorsal process of the maxilla. Their distal extremes and contact to the body of the premaxilla, however, are missing.

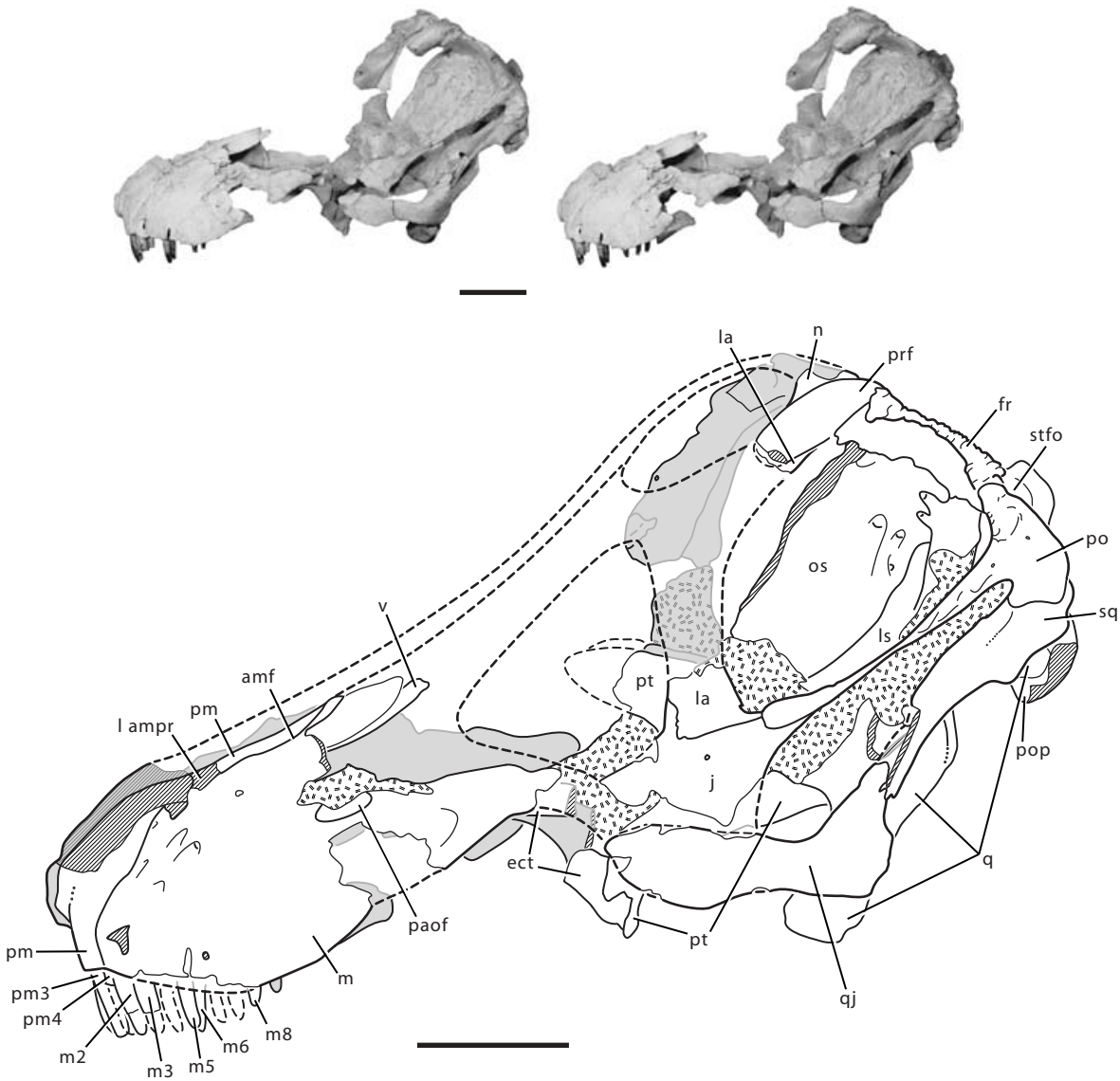

Figure 3 Stereopairs and interpretive line drawing of the prepared skull of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in left lateral view. The anterior (snout) portion of the skull has been rotated slightly out of contact with the posterior portion of the skull (compare with Figure 2). In this and other line drawings, cross-hatching indicates broken bone, pattern indicates matrix, grey tone denotes elements from the opposite side of the skull and light tone lines indicate anatomy obscured by reconstructed areas. Abbreviations used in Figures 3–15, 17, 18: **addfo**, adductor fossa; **amf**, anterior maxillary fenestra; **ampr**, anteromedial process; **an**, angular; **aof**, antorbital fenestra; **as**, articular surface (used in conjunction with other abbreviations, e.g. as **ect**); **asaf**, anterior surangular foramen; **aspr**, ascending process; **bo**, basioccipital; **bpt**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tuber; **cor**, coronoid; **d**, dentary; **den f**, dental foramen; **ect**, ectopterygoid; **eo-op**, exoccipital–opisthotic; **en**, external nares; **f**, foramen; **fm**, foramen magnum; **fo**, fossa; **fr**, frontal; **gr**, groove; **j**, jugal; **l**, left; **la**, lacrimal; **la f**, lacrimal foramen; **ls**, laterosphenoid; **ltf**, lateral temporal fenestra; **ltfo**, lateral temporal fossa; **m**, maxilla; **mgr**, Meckel's groove; **n**, nasal; **oc**, occipital condyle; **or**, ornamentation; **os**, orbitosphenoid; **p**, parietal; **pal**, palatine; **paof**, preantorbital fenestra; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **prf**, prefrontal; **psaf**, posterior surangular foramen; **pt**, pterygoid; **ptf**, post-temporal foramen; **q**, quadrate; **qfo**, quadrate fossa; **qj**, quadratojugal; **ri**, ridge; **sa**, surangular; **sh**, shelf; **so**, supraoccipital; **sp**, spur; **spl**, splenial; **sq**, squamosal; **sr**, sclerotic ring; **stf**, supratemporal fenestra; **stfo**, supratemporal fossa; **sy**, symphysis; **v**, vomer; Arabic numerals indicate tooth position; Roman numerals indicate openings for cranial nerves. Scale bars = 10 cm.

The particular arrangement of the bones and bone fragments of the snout offers some information as to the principal forces of deformation that acted on them during preservation. Due to the transverse compression of the skull, the left premaxilla has been shifted medially and interposed between the right premaxilla and its teeth (Figs 5 & 6). The first tooth on the right premaxilla has been shifted over the midline, so that it is partially bordered by the labial portion of the left premaxilla. The four teeth of the right premaxilla are likewise shifted laterally by nearly one alveolus – the fourth tooth is positioned at the junction between the premaxilla and maxilla. The forward shearing of the right side of the snout, which shifted the anteromedial process of the right maxilla to a position anterior of the left premaxillary ascending

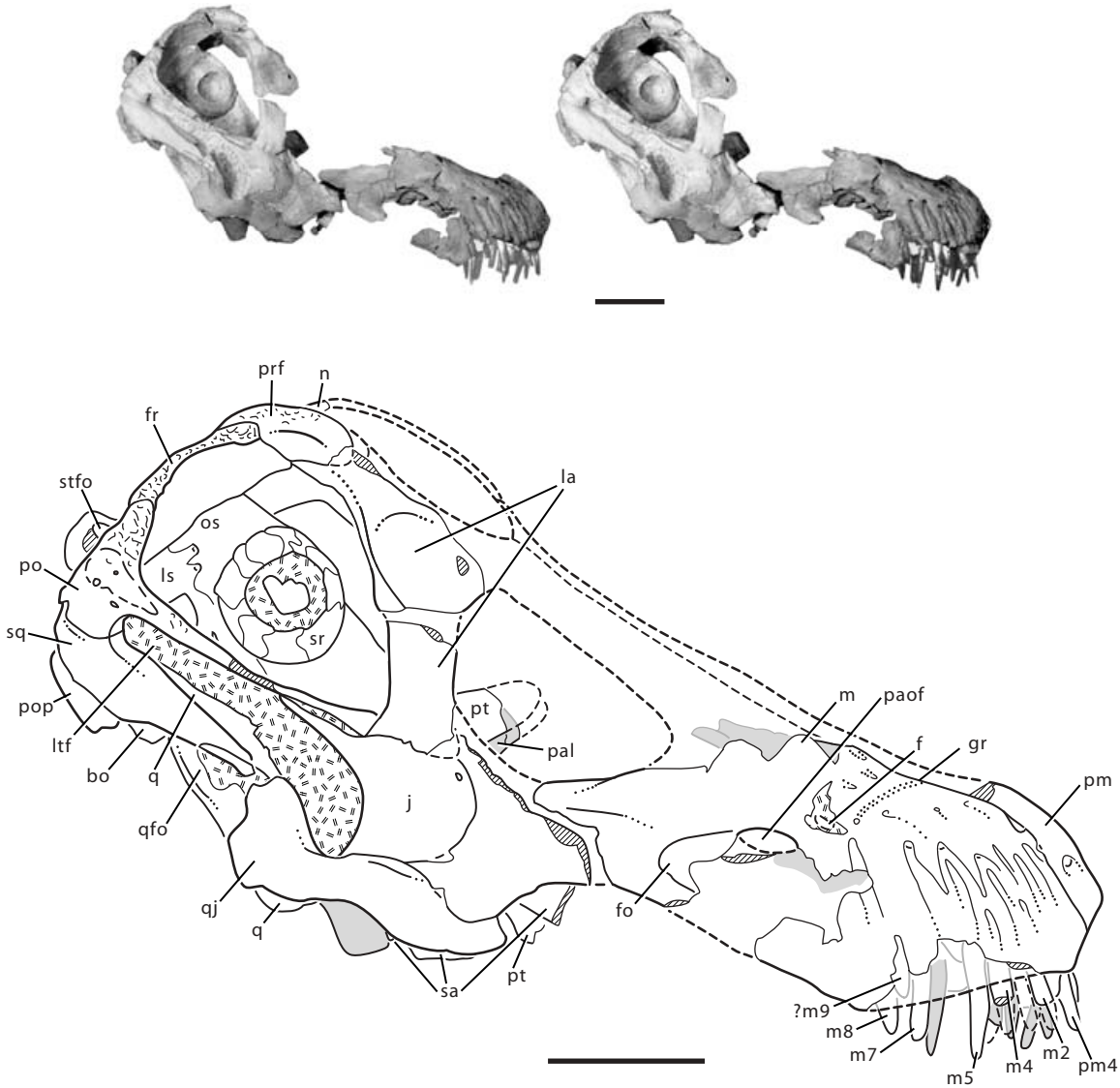

Figure 4 Stereopairs and interpretive line drawing of the prepared skull of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in right lateral view. See Figure 3 for abbreviations. Scale bars = 10 cm.

process, apparently took place after compression, because it likewise affected the left premaxilla. By virtue of its intercalation with its opposite, the left premaxilla was drawn slightly out of articulation with the body of the maxilla as the right premaxilla was sheared forward. This deformation, as well as the truncation of the dorsal process of the premaxilla creates the impression of a step in the dorsal margin of the snout in lateral view (Fig. 4), a preservational artifact that Salgado & Calvo (1997: fig. 8) incorporated into their reconstruction of *Nemegtosaurus*.

The premaxilla is triangular in anterior view, with a broad ventral (alveolar) margin and a body that tapers dorsally. Along the length of their symphyseal margin, each premaxilla bears a paramedian ridge that is approximately the breadth of one alveolus (Fig. 5). The ridge is flanked by a shallow groove formed by bone that bears a coarse, transverse orientation. Due to damage, the dorsal extent of the paramedian ridges and flanking grooves cannot be ascertained. Each premaxilla has four alveoli arranged in a fairly flat arch. Because little of their symphysis is visible, the orientation of the premaxillae relative to the axis of the skull cannot be determined with certainty. The shape of the symphyseal portion of the dentaries, however, suggest that they were nearly transversely orientated (see 'Dentary' below). The exposed portion of the medial face of the right premaxilla (Fig. 3) reveals a relatively narrow symphyseal contact, although this must be confirmed on additional specimens. A portion of the ascending process of the left premaxilla is preserved adjacent to the left maxilla. It overlaps the anteromedial process of the maxilla and partially covers an elongate opening in the maxilla (see 'Maxilla' below). The ascending process of the premaxilla is long, straight and flat. No margin of the external naris is preserved.

There are dental foramina on the medial surface of the premaxilla, corresponding to each of the four teeth. They are teardrop-shaped and increase in size laterally. Only three dental foramina on the right premaxilla are visible in ventral view, however, because the opening associated with the first

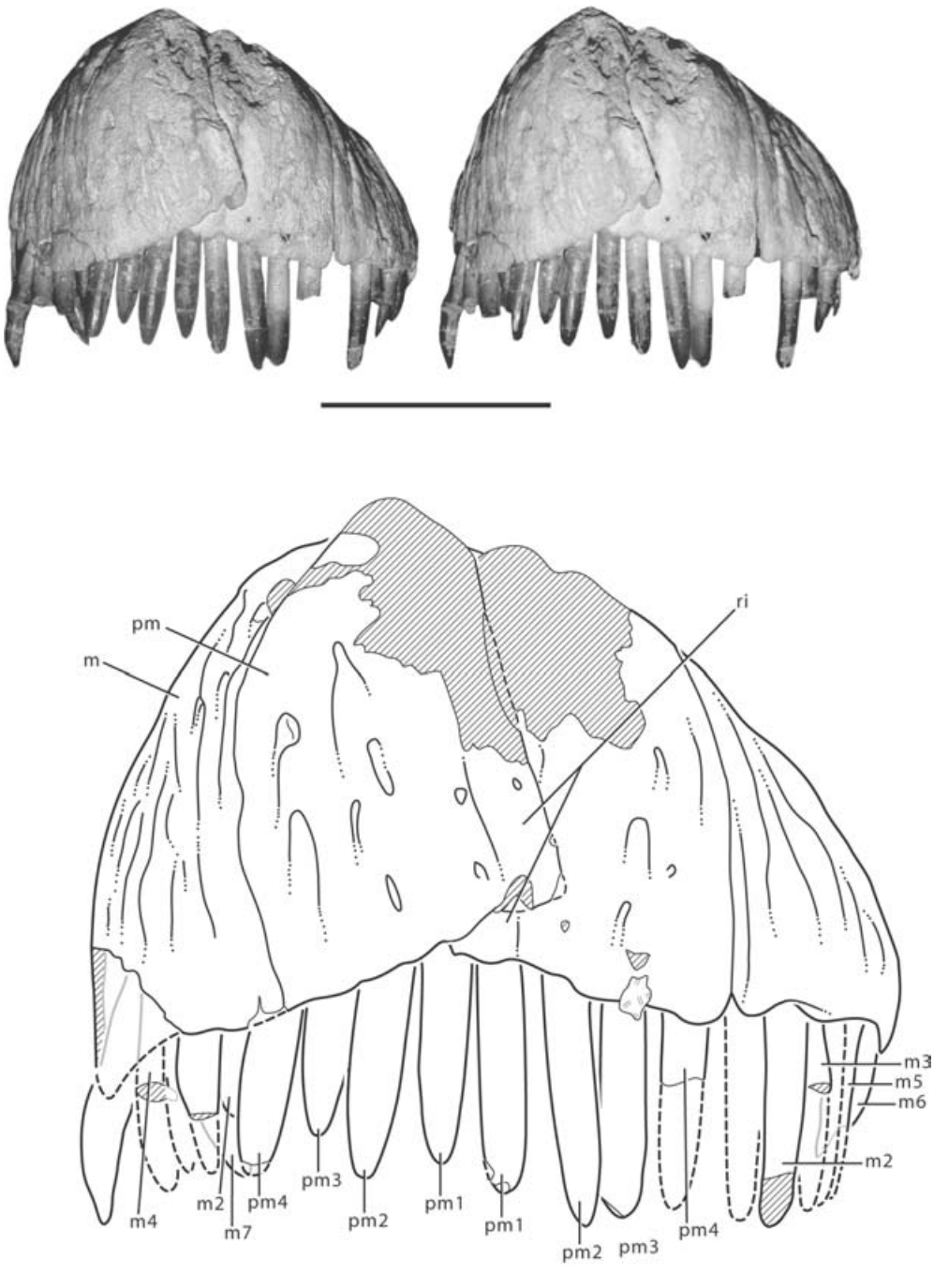

Figure 5 Stereopairs and interpretive line drawing of the snout of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in anteroventral view. The left premaxilla has been interposed between the right maxilla and its teeth by compressive forces acting during fossilisation. See Figure 3 for abbreviations. Scale bars = 10 cm.

tooth is obscured by the left premaxilla (Fig. 6). Low ridges extend toothward from the ventral margin of each dental foramen. These ridges separate shallow depressions. Close packing of the right premaxillary teeth is due to preservational compression. Those of the left side are separated by gaps of 4–6 mm (Fig. 6).

In lateral view, the body of the premaxilla has a gently rounded anterior margin (Figs 3 & 4). Unfortunately, the critical region between the body and ascending process of the premaxilla is not preserved, precluding assessment of a stepped or gradual transition between the two. No narial fossa is preserved on the preserved portion of the premaxilla, but its absence cannot be confirmed in this specimen. The bodies of the premaxilla and maxilla have gently sinuous articular margins that indicate alternating overlap between the two along their length (Figs 3 & 5). The maxilla overlaps the premaxilla near the upper and lower thirds of their contact, but the premaxilla overlaps the maxilla along the middle third. The transition between these sections is marked by a slight punctuation of what is, for the most part, a sinuous margin.

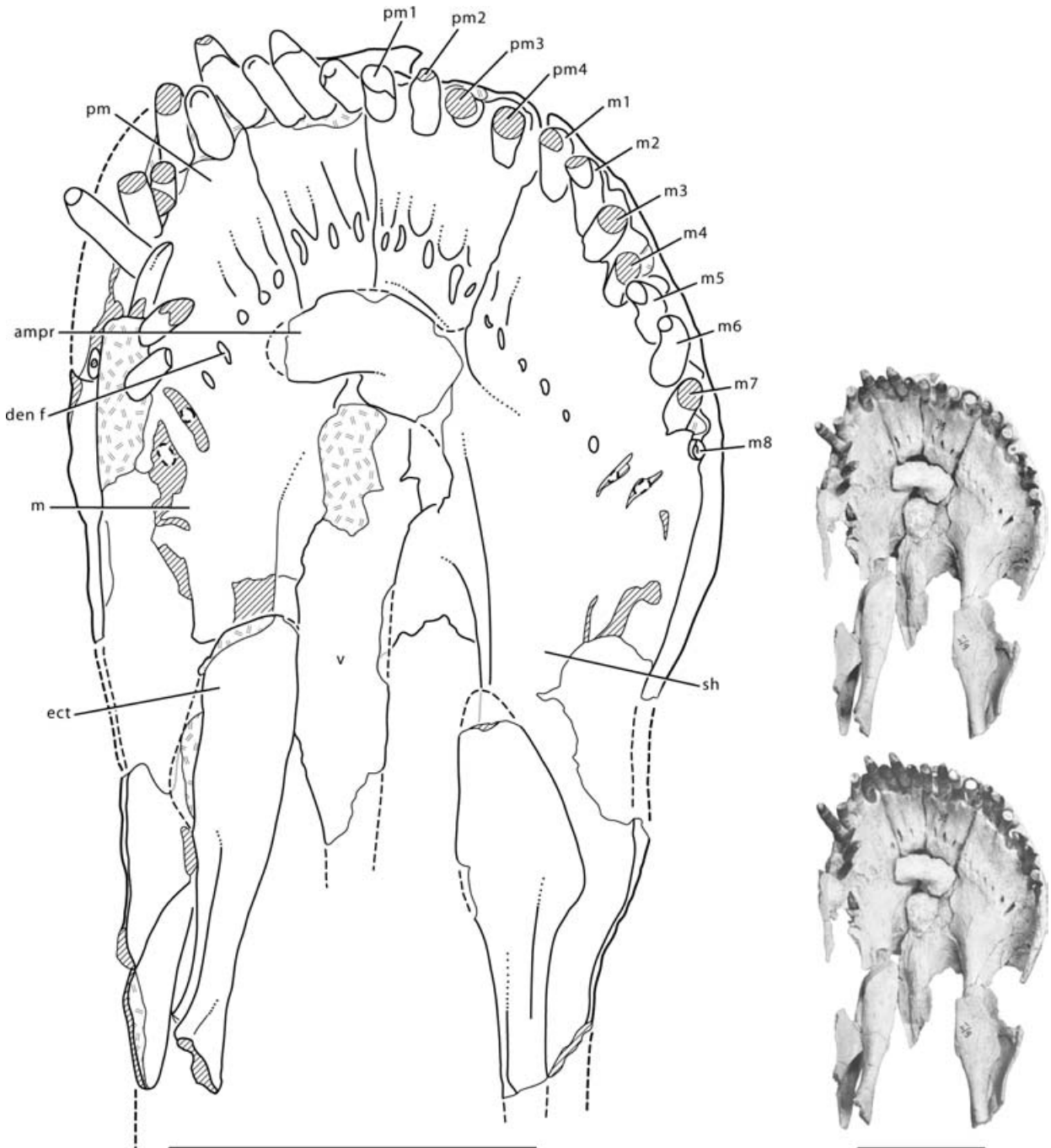

Figure 6 Stereopairs and interpretive line drawing of the snout of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in ventral view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

Maxilla

Portions of both maxillae are preserved. In general, the tooth-bearing region of the maxilla is better preserved than is the more delicate cheekward region, which is preserved only on the right side (Fig. 4). The alveolar margin of the maxilla is nearly completely preserved on the left side and enough of its post-dentigerous portion is preserved to reconstruct its shape (Figs 3 & 4). The ascending process of the maxilla is preserved up to the anterior maxillary fenestra, but absent distal to that opening. As a consequence, the shape of the two openings it borders, the external naris and antorbital fenestra, cannot be determined.

Transverse compression has approximated the right and left maxillae such that their palatal shelves are separated by only a few centimetres (Fig. 6) and forward shearing of the right side of the skull brought a portion of the right maxillary anteromedial process anterior to the left premaxillary ascending process. The left anteromedial process was detached from the remainder of the maxilla but is preserved in correct anatomical position on the palatal surface of the skull (Fig. 6). Nowinski (1971: 65), however, associated the left maxillary anteromedial process with the adjacent vomer and described them together as a 'T-shaped vomer'. As noted by Upchurch (1999), the crossbar belongs to the maxilla (see 'Vomer',

below) and it closely resembles that of *Quaesitosaurus* (see Fig. 17).

The maxillary tooth row terminates anterior to the preserved portion of the antorbital fenestra, whose anterior limit cannot be determined. Despite this incompleteness, *Nemegtosaurus* did not possess the anteroposteriorly elongate antorbital fenestra that characterises *Rapetosaurus* (Curry Rogers & Forster 2004). The tooth row probably terminated anterior to the antorbital fenestra, a feature also present in diplodocoids (Upchurch 1998, 1999; Wilson 2002). There are eight teeth preserved on the left side and either eight or nine on the right. The uncertainty stems from damage in the posterior region of the snout (Fig. 6). Nowinski (1971: table 1) and McIntosh (1990: 393) listed maxillary tooth counts of eight, but there appears to be one missing tooth from the left side. Nine maxillary teeth and four premaxillary teeth would match the dentary tooth count, which is 13 (Nowinski 1971: 70; see 'Dentary' below). Eight teeth were preserved in association with the *Rapetosaurus* maxilla and Curry Rogers & Forster (2004) estimated that there would have been a total of 12–14 maxillary teeth. With four premaxillary teeth, which are standard in all sauropods, this estimate implies a 5–8 tooth mismatch between the 16–18 upper teeth and the 11 lower teeth in *Rapetosaurus*. The dentary of the titanosaur *Malawisaurus* bears 15 alveoli (Jacobs *et al*. 1993), implying a maxillary tooth count of 11 if there were four premaxillary teeth and equal numbers of upper and lower teeth. In this context, the reduced maxillary tooth count in *Nemegtosaurus*, *Quaesitosaurus* (see Fig. 17) and *Rapetosaurus* may be a diagnostic feature, but more titanosaur tooth counts are needed. The entire tooth-bearing portion of the maxilla is coursed by deep vascular grooves that run towards the alveolar margin of the jaw. Some of these grooves anastamose distally. Nearly all of these openings are positioned ventral to the anterior maxillary foramen and anterior to the last tooth. This highly vascularised region of the snout is delimited by a shallow transverse groove (Figs 3 & 4). A highly vascularised anterior maxilla is also present in *Diplodocus* (Wilson & Sereno 1998: fig. 6B); less pronounced neurovascular grooves are present in the maxillae of *Apatosaurus* (Berman & McIntosh 1978: fig. 7A) and *Dicraeosaurus* (Janensch 1935–1936: fig. 108). *Quaesitosaurus* (PIN 3906/2) also bears a highly vascularised snout, but this feature cannot be determined in other titanosaurs because complete maxillae have not yet been described.

Just posterior to the tooth row and to the transverse groove is an enlarged oval depression that spans nearly 10 cm along its anteroposterior axis. Within this depression are two openings, which Nowinski (1971: fig. 2) termed 'infraorbital fenestrae'. Madsen *et al*. (1995: 9) regarded them as anterior maxillary fenestrae, but Upchurch (1999: 112, fig. 2) regarded them as preantorbital fenestrae. The larger, more posteriorly positioned opening exits from a space enclosed by the medial portion of the maxilla, which is here termed the 'palatal canal'. I consider this to be the preantorbital opening and the much smaller, more anteriorly placed opening to be an accessory foramen. The palatal canal is triangular in cross-section, with its base formed by the palatal shelf and its sides formed by medial and lateral aspects of the maxilla. The lateral wall of the canal is extremely thin (1–2 mm) near the exit of the preantorbital fenestra. The medial wall of the canal is thicker and apparently contiguous with the maxillary ascending and anteromedial processes. In most sauropods, the anteromedial process is tab-like and medially orientated, whereas the ascending process is elongate and posterodorsally oriented. In *Nemegtosaurus*, however, these two processes are merged into a single, medial sheet of bone that underlies the ascending process of the premaxilla. An elongate opening enters the palatal canal at the junction of these processes and the body of the maxilla. This large opening (45 mm long, 10 mm wide) was referred to as the 'intermaxillary foramen' by Nowinski (1971: fig. 1) and as the 'subnarial foramen' by Upchurch (1999: 111, fig. 2). Unlike the subnarial foramen, which passes between the premaxilla and maxilla in saurischians (Sereno & Novas 1993), the opening in *Nemegtosaurus* enters the maxilla via the palatal canal. I regard this opening as the anterior maxillary foramen, based on topological correspondence with that opening in other sauropodomorphs (*Plateosaurus*, *Camarasaurus*, Wilson & Sereno 1998: figs 5A, 7C; *Brachiosaurus*, Janensch 1935–1936: fig. 42). The subnarial foramen may have been located just below the anterior maxillary foramen, to which it was linked by a short groove. However, only the maxillary portion of such an opening is preserved; position of the subnarial foramen must be confirmed in other specimens. It is not known whether the subnarial foramen in *Nemegtosaurus* is reduced in size, lost, or modified.

In lateral view, the ventral margin of the maxilla is arched immediately posterior to the tooth row (Figs 3 & 4). The curve of the post-dentigerous maxilla appears smooth and it is both longer and more arched than in other sauropods. At its posterior extreme, the maxilla overlaps the jugal along a margin that is roughly concave posteriorly. The elongate ventral process of the maxilla extends below the jugal, which does not contribute to the ventral margin of the skull. Although it appears that the maxilla contacted the quadratojugal, the nature and extent of this contact cannot be determined because the latter has been shifted forward and out of place. The posterior maxilla is much deeper than, and less arched than, the corresponding portion of the *Rapetosaurus* maxilla, which may be autapomorphic in these regards (Curry Rogers & Forster 2004: figs 1, 3–4).

Nasal

Portions of the right and left nasals are preserved along their contacts with the prefrontal and frontal (Fig. 7). Nearly the entirety of the nasal ventrolateral process is preserved on the left side of the skull. Its distalmost tip, however, is missing and may have extended further alongside the prefrontal (Fig. 8). The midline contact of the nasals – and thus part of the margin of the external naris – has not been preserved (Fig. 7), but small portions of the right and left anterior process offers some information on the three-dimensional orientation of the naris (Figs 3 & 4).

The ventrolateral process of the nasal is tongue-like and dorsoventrally deep. At its distal extreme, the ventrolateral process of the nasal contacts the anteromedial surface of the lacrimal, which separates it from the prefrontal. It has a smooth internal surface that represents the posterolateral margin of the external naris, which was retracted to a position between the prefrontals, as reconstructed by Nowinski (1971: fig. 2) and Upchurch (1999: fig. 6D). The size and shape of the external naris, however, was not preserved. Nowinski (1971: 66) stated his uncertainty about the presence of an internarial bar, but reconstructed confluent external nares

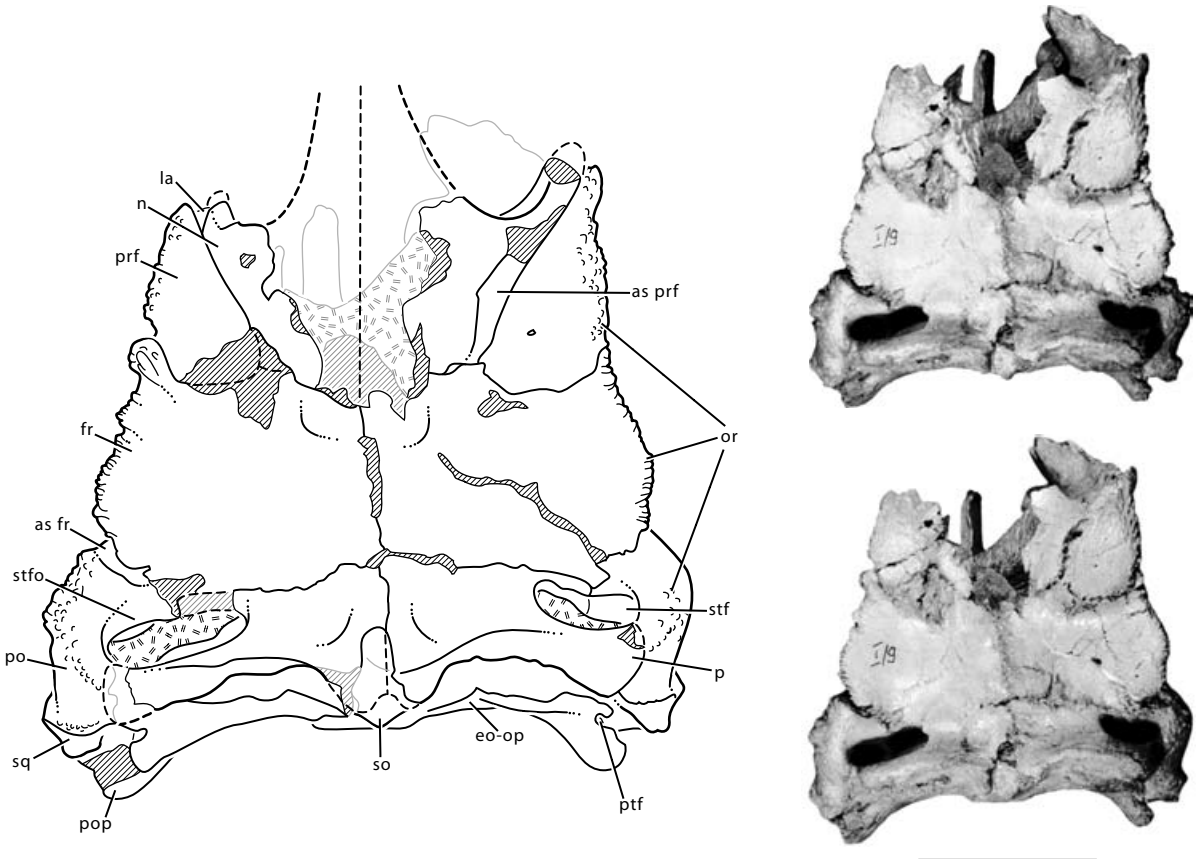

Figure 7 Stereopairs and interpretive line drawing of the posterior portion of the skull of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in dorsal view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

(1971: fig. 2). Upchurch (1995) scored the external nares as confluent and dorsally facing, but more recently (1999: 111) has stated that neither can be determined. Curry Rogers & Forster (2004: 127) regarded the external nares of *Nemegtosaurus* as fully retracted and confluent, in agreement with the presumed condition in *Rapetosaurus*. The anterior process of the nasal is poorly preserved in *Nemegtosaurus*, but nonetheless indicates a broad internarial bar (>4 cm) that would have tapered anteriorly. In lateral view, the anterior process diverges from the lateral process, indicating that the external nares were somewhat laterally orientated (Figs 3 & 4 and see Fig. 16).

Posteriorly, the nasal overlaps the frontal, which is extremely thin at its anterior extreme. Nearly half of this contact has been preserved on the right side, but slightly less is preserved on the left. From this limited evidence, it appears that the frontal–nasal contact was angled slightly posteromedially, as suggested by Nowinski (1971: 65), but better specimens are required to confirm this.

Frontal

The frontals are completely preserved on both right and left sides, but the right side has been slightly compressed transversely and the left has been damaged in the region of its prefrontal articulation (Fig. 7).

An interdigitated suture clearly separates right and left frontals, which are each transversely elongate and together hexagonal in dorsal view. The lateral margin of the frontal is concave where it flanks the prefrontal but convex at its greatest breadth near mid-length (Fig. 7). Its orbital margin bears roughened ornamentation that continues anteriorly and posteriorly on the prefrontal and postorbital, respectively (Figs 7 & 8).

The frontal is positioned between the nasal and parietal along the midline and between the prefrontal and postorbital along the orbital margin of the skull. As discussed above, the frontal–nasal contact is not well preserved, but the frontals appear to have been concave forward in dorsal view. Although the frontals are fairly flat transversely, a shallow but marked anteromedial depression is present near their contact with the nasals, as in *Saltasaurus* (PVL 4017-162) and *Quaesitosaurus* (PIN 3906/2). The paramedian doming present on the frontals of *Rapetosaurus* (Curry Rogers & Forster 2004: fig. 13) is not present in *Nemegtosaurus*. The prefrontal–frontal articulation is also concave forward, but asymmetrically so, with a greater forward excursion on the orbital margin (Fig. 7). The parietal–frontal contact is relatively straight but angled slightly posterolaterally. The suture is interdigitated and was probably a butt-joint, as in other sauropods. Although at its lateral extreme the frontal approaches the supratemporal opening, it does not participate in the supratemporal fossa. The frontal–postorbital contact is vertical and planar, but orientated anterolaterally rather than posterolaterally.

Ventrally, the frontal contacts elements of the lateral wall of the braincase. Its suture with the orbitosphenoid

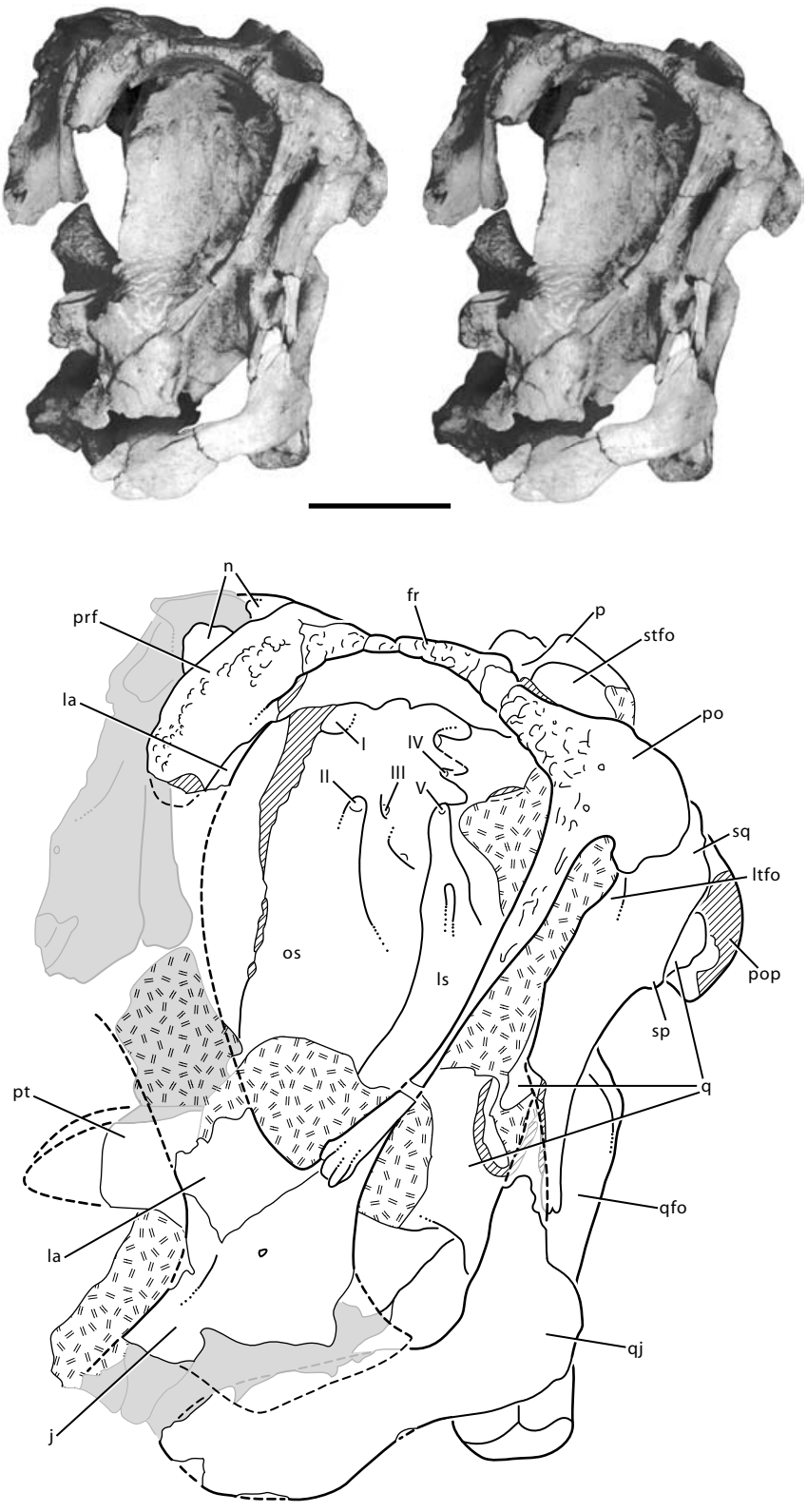

Figure 8 Stereopairs and interpretive line drawing of the posterior portion of the skull of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in left lateral view. See Figure 3 for abbreviations. Scale bars = 10 cm.

anteriorly is interdigitated, whereas that with the laterosphenoid appears smooth. A well defined ridge projects anterolaterally from the underside of the frontal at the anterior extreme of its orbitosphenoid contact. Present in many sauropods, this ridge separates the lateral, orbital portion of the skull from its medial, narial portion.

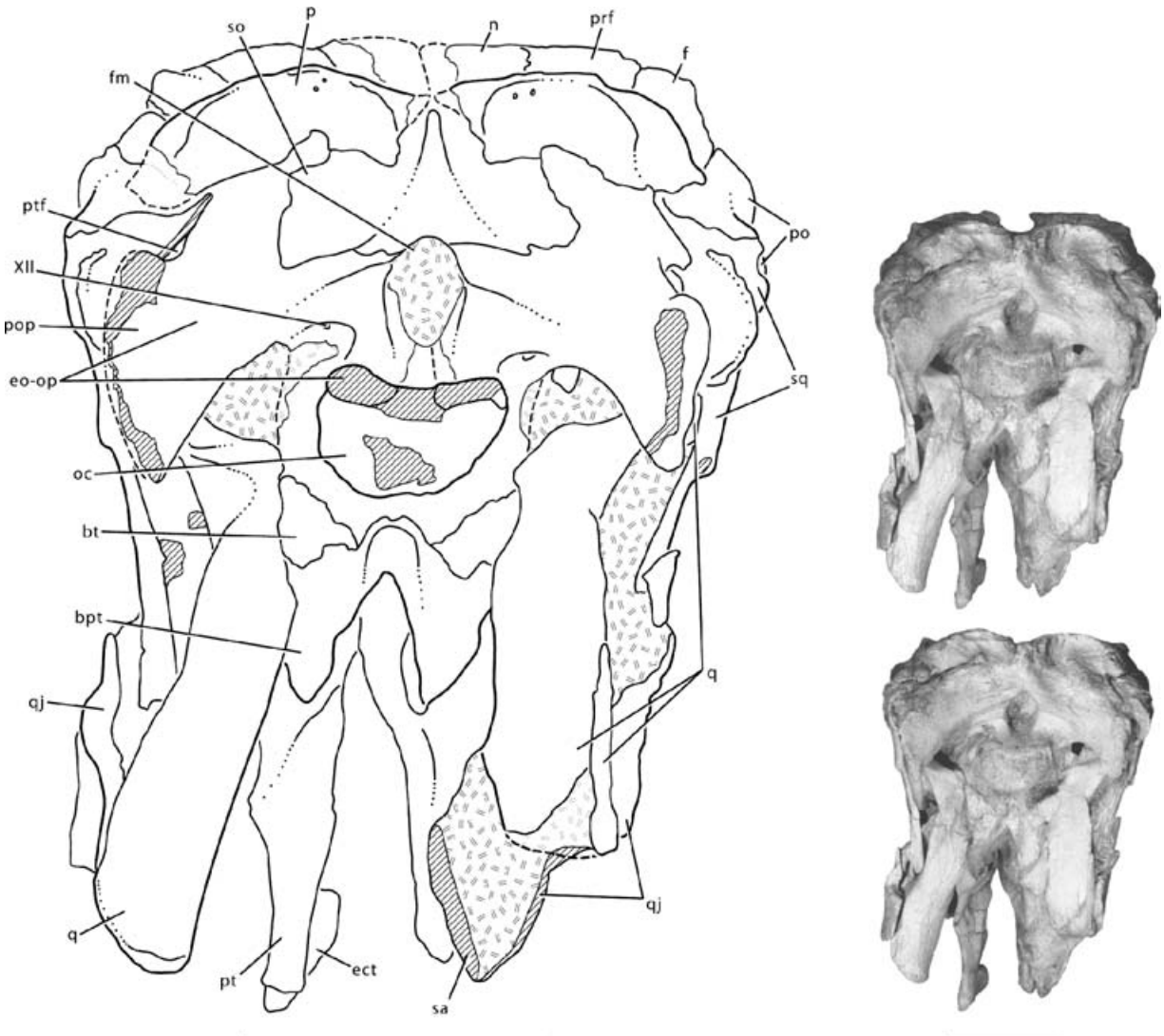

Figure 9 Stereopairs and interpretive line drawing of the posterior portion of the skull of *Nemegtosaurus mongoliensis* (Z. PAL MgD-I/9) in posterior view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

Parietal

The parietals are nearly completely preserved, except for a median gap near their contact with the supraoccipital. As the posteriormost element of the skull roof, the parietal has a broad exposure both dorsally and posteriorly (Figs 7 & 9).

In dorsal view, the anterior and posterior margins of the parietal are roughly parallel to one another. No parietal or postparietal openings are present (contra Nowinski 1971: fig. 2). The parietal has a short, flat midline suture and two lateral processes that contact the postorbital in front of and behind the supratemporal fenestra. The anterior lateral process is shorter and narrower than the longer and thicker posterior process. This double contact excludes the squamosal from the margin of the supratemporal fenestra (Nowinski 1971; Upchurch 1995). *Rapetosaurus* does not have a well developed anterior lateral process and the frontal appears to have bordered the supratemporal fenestra (Curry Rogers & Forster 2004: figs 2, 15C). Anteriorly, the parietal is flat transversely, but posteriorly it is raised so that the posterior wall of the supratemporal opening is visible in lateral view although the opening itself is not (Fig. 8). The supratemporal fenestra is elliptical, with its long axis canted 10–15° posterior of the transverse axis of the skull. Right and left openings are separated from the midline of the skull by a distance surpassing the greatest diameter of each.

In posterior (occipital) view, the parietal is sandwiched between the supraoccipital, postorbital, exoccipital–opisthotic and squamosal (Fig. 9). The well developed occipital fossa on the posterior parietal is bounded by a raised ridge of bone. The parietal is strap-shaped in posterior view, and its greatest height is less than that of the foramen magnum. The parietal has a broad, flat contact with the postorbital laterally and is contacted by a narrow isthmus of the squamosal just ventral to this. By virtue of these contacts, the parietal is excluded from the margin of the post-temporal fenestra.

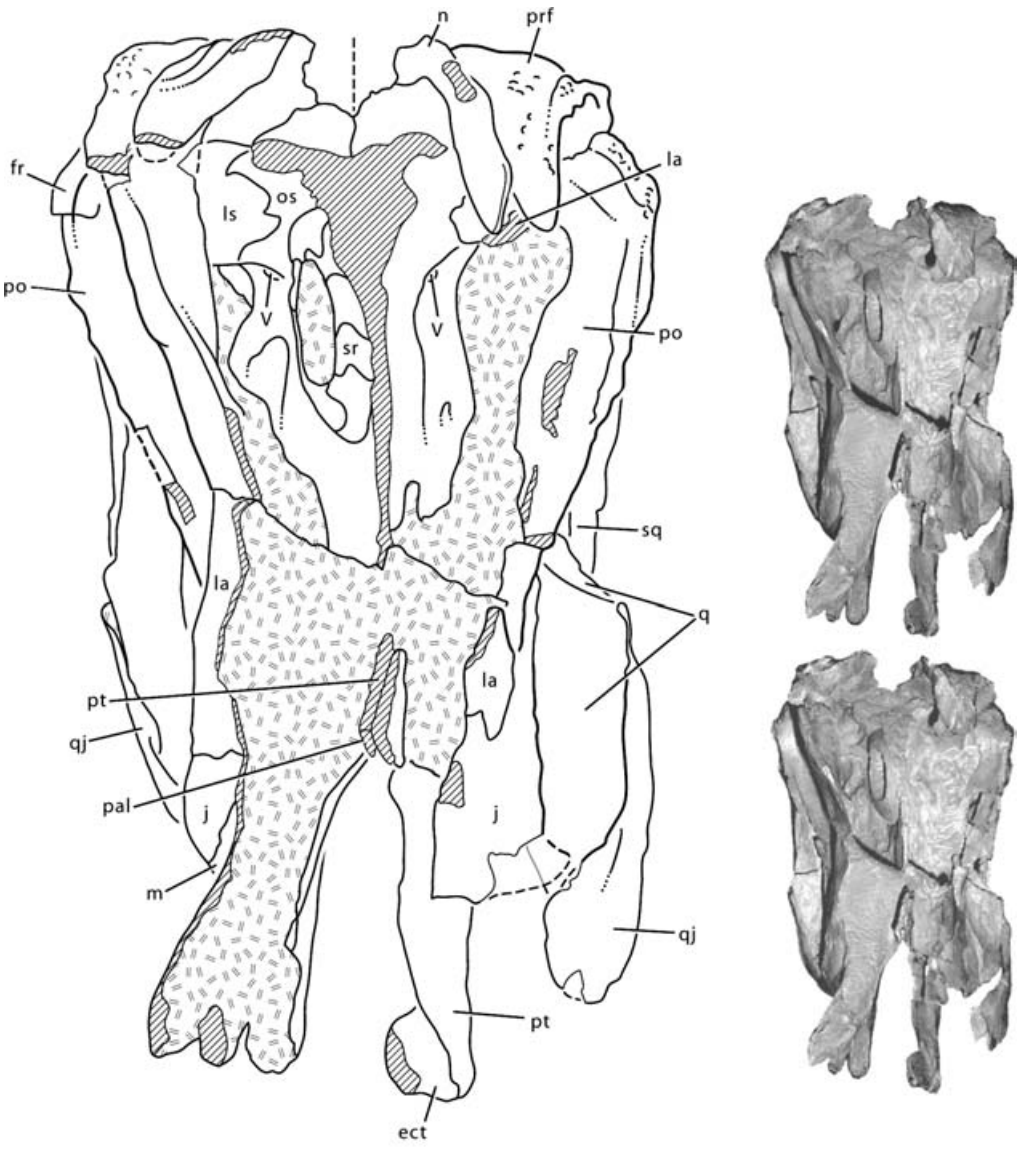

Figure 10 Stereopairs and interpretive line drawing of the posterior portion of the skull of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in anterior view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

Postorbital

The postorbitals are complete on both sides of the skull (Figs 3 & 4). As a result of the transverse compression that has bent inwards their ventral processes (Fig. 10), both postorbitals have been pulled out of articulation with the frontals (Fig. 7). The right postorbital has suffered additional crushing, which has artificially reduced the size of the right supratemporal fenestra. The left appears undistorted.

The postorbital is T-shaped in lateral view, with an elongate ventral process and relatively short anterior and posterior processes (Fig. 8). The anterior process is approximately half as deep as the posterior process, giving the postorbital the appearance of a percussion hammer. The anterior process of the postorbital contacts the frontal and parietal medially, separating the orbit from the supratemporal fenestra. The anterior process is heavily ornamented, especially near its contact with the frontal (Figs 7 & 8), as in *Quaesitosaurus* (PIN 3906/2). It meets the frontal in a deep, vertical suture that is directed anterolaterally. The posterior process of the postorbital is dorsoventrally deep and contacts the anterior process of the squamosal laterally (Fig. 8) and the lateral processes of the parietal dorsally (Fig. 7). The posterior process separates the supratemporal and lateral temporal fenestrae. Its articulation with the squamosal is planar, near vertical and orientated transversely. This condition differs from the tongue-and-groove postorbital–squamosal articulation of other dinosaurs. Although the postorbital is unknown in *Rapetosaurus*, the presence of a triangular notch on the lateral aspect of the squamosal suggests it had a typical postorbital–squamosal contact (Curry Rogers & Forster 2004: fig. 18). In dorsal view, the posterior process of the postorbital contacts both termini of the C-shaped portion of the parietal, forming the lateral margin of the supratemporal opening (Fig. 7). A shallow supratemporal fossa is present on the postorbital.

There is no orbital ornamentation on the posterior process of the postorbital.

The ventral process of the postorbital, which separates the lateral temporal fenestra from the orbit, is slightly concave along its orbital margin. The ventral process is narrow anteroposteriorly and broad transversely towards its proximal end. The ventral process narrows transversely towards its distal end, where its anteroposterior breadth exceeds its transverse breadth. The ventral process bears ornamentation near its junction with the anterior and posterior processes, but this texture disappears near its midlength (Fig. 8). The distal end of the ventral process bears a rounded margin, which contacts the posterodorsal process of the jugal. As evidenced by the matrix separating it from the jugal on the right side, the postorbital has been displaced anteriorly out of articulation (Fig. 4). The postorbital–jugal contact is better preserved on the left side, where it appears that the postorbital contacted the lacrimal to exclude the jugal from the margin of the orbit (Figs 3 & 8).

Prefrontal

The prefrontal is complete on the right side and nearly so on the left, which lacks only its distal tip (Figs 7 & 10). Both prefrontals have been damaged somewhat near their connection to the frontal.

The prefrontal is tongue-shaped and downwardly curving. It contacts the frontal posteriorly, the nasal medially and the lacrimal anteroventrally. The prefrontal forms the anterodorsal margin of the orbit and is marked by heavy ornamentation in that region (Fig. 8). In contrast to the ridge-like ornamentation of the frontal, the prefrontal orbital ornamentation consists of numerous small, pointed projections. The prefrontal of *Rapetosaurus* bears much more subtle ornamentation near its contact with the frontal (Curry Rogers & Forster 2004: fig. 11).

Posteriorly, the prefrontal is embraced by an embayment in the frontal (Fig. 7). The posterior margin of the prefrontal is smooth and lacks the posteromedially orientated 'hook' characteristic of diplodocids (Upchurch 1998; Wilson 2002). The anterior process of the nasal parallels the prefrontal and excludes it from the margin of the external naris (Fig. 7). The prefrontal and nasal were separated by the lacrimal anteriorly. The prefrontal overlaps the lateral surface of the lacrimal on a well developed articular facet that is bounded by a low lip.

Lacrimal

The right lacrimal is nearly complete except for a narrow interval at midlength that was lost during preparation of the specimen (see Figs 2(A) and 4). A small portion of the proximal left lacrimal is preserved adjacent to the nasal and a small piece of the distal end is present in articulation with the jugal (Figs 3 & 8).

The lacrimal is a nearly vertical element that separates the orbit from the antorbital fenestra. It bears no ornamentation, unlike other elements bordering the orbit (namely the prefrontal, frontal & postorbital). The lacrimal has a posterior projection that separates the nasal and prefrontal. The lacrimal is broad anteroposteriorly in lateral view and its base rests on the lateral surface of the jugal. The proximal lacrimal, which bears a lacrimal canal whose anterior exit is visible medially (Fig. 8), is approximately twice as broad transversely as anteroposteriorly. A shallow groove is present on the medial aspect of the lacrimal. The posterior ridge that defines this groove is a continuation of the ventral ridge on the frontal, which separates the orbital and nasal cavities. The anterior process of the lacrimal is incomplete but appears to have been well developed in *Nemegtosaurus*. It does not appear to have been as elongate as that of *Rapetosaurus*, which may be autapomorphic (Curry Rogers & Forster 2004: fig. 7).

Nowinski (1971: fig. 2) reconstructed the lacrimal on the margin of the external naris, as did both Upchurch (1999: fig. 2B) and Curry Rogers & Forster (2004: 126). However, the lateral process of the nasal and the dorsal process of the maxilla are not completely preserved and it cannot yet be determined whether they contacted to exclude the lacrimal from the external naris. I have conservatively reconstructed a nasal–maxilla contact as is present in other sauropods (Figs 3 & 4 and see Fig. 16).

Jugal

The jugal is well preserved on both sides of the skull, lacking only portions of its antorbital margin and its posterior process (Figs 3, 4 & 8). The medial aspect of both the left and right jugal is covered by matrix. The jugal connects temporal, circumorbital and tooth bearing elements of the skull and, in doing so, approaches or borders the margins the lateral temporal fenestra, orbit and antorbital fenestra.

The jugal is a large, flat element marked by a posterior embayment that represents the anteroventral margin of the lateral temporal fenestra. On either side of this embayment extend processes of unequal length, the longer of which projects posterodorsally along the posterior surface of the postorbital. The shorter, posteroventral process is not completely preserved on either side, but its brevity can be confirmed from its overlap facet on the anterior process of the quadratojugal (Fig. 8). One foramen opens on the jugal, just below its contact with the lacrimal. This opening is preserved on both sides of the skull of *Nemegtosaurus* (Figs 3 & 4). This opening is absent in *Rapetosaurus* (Curry Rogers & Forster 2004: fig. 6), and its presence cannot be confirmed in *Quaesitosaurus*, which does not preserve a jugal.

Anteriorly, the jugal is overlapped by the maxilla. As mentioned above, the bone in the cheek region is extremely thin, but it appears that the maxilla did not exclude the jugal from the antorbital fenestra, contra reconstructions by Nowinski (1971: fig. 1) and Salgado & Calvo (1997: fig. 8). The jugal of *Rapetosaurus* maintains short orbital and antorbital margins (Curry Rogers & Forster 2004:125–126).

Squamosal

The squamosal is nearly completely preserved on both sides, lacking only the distal terminus of its ventral process (Figs 3, 4 & 8). The medial aspect of both the left and right squamosal is obscured by matrix. The left squamosal has been disarticulated from the quadrate head and its ventral process has been displaced medially to a position within the quadrate fossa, along with a piece of the quadrate (Fig. 9). The right squamosal is also deformed, having been levered forward with the forward shearing of the right side of the skull. Consequently, the squamosal ventral process has been pushed into the lateral temporal fenestra. Deformation has artificially reduced the angle of the apex of the lateral temporal fenestra on both sides.

The squamosal forms the posterodorsal corner of the skull, contacting the skull roof, occipital and temporal elements. The squamosal is triradiate, with an elongate ventral process, an abbreviate anterior process and a narrow, medially-directed occipital process. The anterior process of the squamosal contacts the postorbital to form the temporal bar, which separates the lateral temporal and supratemporal fenestrae. The postorbital–squamosal contact is vertical and flat, which differs from the tongue-and-groove articulation of other dinosaurs. Although it forms part of the temporal bar, the squamosal does not enter the margin of the supratemporal fenestra, which is enclosed solely by the parietal and postorbital. This condition is shared by *Quaesitosaurus* (PIN 3906/2) but is not present in *Rapetosaurus* (Curry Rogers & Forster 2004: 134).

The posterior aspect of the squamosal bears a medially-directed occipital process that separates the lateral portions of the parietal and exoccipital–opisthotic, excluding the former from the border of the post-temporal fenestra (Fig. 9). The posterior surface of the squamosal is overlapped by the paroccipital process, a contact that is marked by a sharply defined facet bounded by a ridge. The squamosal ridge and those of the postorbital and parietal bound a shallow occipital fossa. The occipital process of the squamosal wraps around the posterior aspect of the quadrate head, which is visible posteriorly (Fig. 9). In addition to the squamosal, the quadrate is supported posteriorly by the paroccipital process. The nature of the squamosal–quadrate articulation cannot be assessed in this specimen because this region has not yet been prepared, but it probably resembled that of other saurischians, in which the squamosal has a well developed socket that receives the convex head of the quadrate.

The ventral process of the squamosal forms much of the posterior margin of the lateral temporal fenestra and a shallow lateral temporal fossa is preserved on its anterior aspect (Fig. 8). In lateral view the ventral process is concave posteriorly, which results in an anteriorly-broadening lateral temporal fenestra. The ventral process is not completely preserved on either side, but it probably contacted the posterior quadratojugal, based on the relationship between these bones preserved on the left side (Fig. 8). A squamosal–quadratojugal contact was suggested by Nowinski (1971) and Upchurch (1999), but Madsen *et al*. (1995) concluded that they did not contact. Together, the ventral process of the squamosal and the dorsal process of the quadratojugal form the lateral boundary of a broad quadrate fossa (Fig. 9), as indicated by Nowinski (1971: 67). A small 'spur' is present on the posterior surface of the ventral process, near the base of the three-bone junction involving the paroccipital process and the quadrate (Fig. 8). This spur is unknown elsewhere in Sauropoda and may represent an autapomophy of *Nemegtosaurus*.

Quadratojugal

The quadratojugal has been crushed forwards on both sides, the right side more so than the left (Figs 2–4). Nevertheless, the body and anterior process of the quadratojugal are well preserved on both sides. Its dorsal process has been damaged on the right side, but is better preserved on the left (Fig. 8). The left quadratojugal is not obscured by other skull elements and provides most of the valuable characters of this element.

The quadratojugal forms the ventrolateral corner of the skull and of the lateral temporal fenestra. Like the squamosal, it overlies the quadrate. The quadratojugal–quadrate contact is marked by a surface of roughened bone on the distolateral quadrate. In lateral view, the posterior portion of the quadratojugal is rounded and projects beyond the dorsal process. The bone in this region bears weak transverse striae that can be seen on both right and left sides. Preserved portions of the dorsal process of the quadratojugal indicate that it was elongate and probably contacted the anterior surface of the squamosal, but the shape of the element and the nature of its contact with the quadrate and squamosal is not certain (Figs 3 & 4). The body and dorsal process of the quadratojugal form the ventrolateral boundary of the quadrate fossa.

The anterior process of the quadratojugal is tongue-shaped, with a slightly convex dorsal margin and a sinuous ventral margin (Fig. 8), as in *Quaesitosaurus* (Kurzanov & Bannikov 1983: fig. 1). This condition is present but less pronounced in *Diplodocus*, which also bears an elongate anterior process (Wilson & Sereno 1998: fig. 6A). The dorsal margin of the anterior process of the quadratojugal is overlapped by the jugal, a contact is marked by a distinct facet that deepens anteriorly. As discussed above, the quadratojugal contacted the posterior end of the maxilla to exclude the jugal from the ventral skull margin, but the nature and extent of that contact is unknown (see 'Maxilla', above).

Palatal complex

The palatal complex of *Nemegtosaurus* is represented by the paired vomers, pterygoids, quadrates and ectopterygoids. Of these elements, only the incomplete vomers and the quadrate have been adequately figured (Nowinski 1971: pls 11–12); other palatal elements have received less attention and the palate of *Nemegtosaurus* has never been reconstructed. In part, this is attributable to the incomplete preservation of the palatal elements, but also to their derived morphology. The supposed absence of an ectopterygoid has provided additional difficulty. Below the five palatal elements are redescribed and reinterpreted.

Vomer

Fragments of the right and left vomer are preserved, but the nature of their connection to other palatal elements posteriorly and to the dermal skull anteriorly was not preserved (Fig. 6). Nowinski (1971: 64) described the vomer as a single element comprising an elongate median process and a transversely orientated crossbar positioned just posterior to the premaxillae. McIntosh & Berman (1975: 195) questioned this interpretation and suggested that Nowinski's T-shaped element was actually two elements; the elongate portion representing part of one paired vomer (they did not specify right or left) and the crossbar representing part of some other element. Upchurch (1999: 113) agreed that the elongate process represented one of the vomers and that, the crossbar represented 'broken portions of the vomerine processes [of the maxilla]'. Re-examination of the palate indicates that the crossbar represents the left maxillary anteromedial process (Fig. 6; see 'Maxilla', above) and the elongate portion represents the paired right and left vomers. No posterior divergence can be recognised between the two vomers, which are incomplete. In other sauropods, these elements diverge posteriorly

to embrace the tips of the anterior processes of the pterygoids (e.g. *Camarasaurus*; Madsen *et al*. 1995: fig. 5B).

The anterior contact of the vomers cannot be observed in this specimen. Their preserved position, however, suggest that the vomer contacted the anteromedial process of the maxilla (Fig. 6). A posteriorly directed vomerine process is not present on the posterior aspect of the premaxilla, as it is in *Camarasaurus* (Madsen *et al.* 1995: fig. 7).

Ectopterygoid

In sauropod outgroups (Prosauropoda and Theropoda), the palatine and ectopterygoid flank the vomer and pterygoid in a fairly consistent fashion. The palatine of *Plateosaurus* contacts the maxilla laterally, the pterygoid medially and the vomer anteriorly (Galton 1984). In *Herrerasaurus*, the palatine additionally contacts the jugal laterally (Sereno & Novas 1993: fig. 8D). In both genera, the ectopterygoid contacts the jugal laterally and the pterygoid medially to form the transverse palatal hook. The palatine and ectopterygoid do not contact one another and the post-palatine fenestra is relatively large. These topological relationships are conserved in sauropods, but with one notable difference. Perhaps related to the overall infraorbital shortening of the eusauropod skull, the ectopterygoid's contact with the skull margin is shifted forward onto the maxilla (Wilson & Sereno 1998). By virtue of the approximation of the lateral processes of the ectopterygoid and palatine on the maxilla, the postpalatine foramen is much smaller in neosauropods than in their outgroups and there is a novel posteromedial contact between the ectopterygoid and palatine.

Only one paired marginal element is preserved in position on the anterior palate of *Nemegtosaurus* (Fig. 6). Because remnants of nearly all of the other cranial elements have been preserved, it has been assumed that one of the marginal palatal elements did not ossify. Nowinski (1971: 64–65) identified the preserved element as the palatine, a decision followed by McIntosh & Berman (1975), McIntosh (1990) and Madsen *et al*. (1995). Nowinski (1971: 58) further considered the ectopterygoid unossified and regarded this as diagnostic of the genus. However, neither the anterior pterygoids nor the posterior vomers have been preserved, indicating that the mid-palate has been damaged. For this reason, a preservational absence for either the palatine or ectopterygoid cannot be ruled out.

The shape and sutural connections of the preserved marginal element may allow discrimination between the three alternative explanations for why only one element was preserved: one element was not preserved, one element did not ossify, or two elements fused into one composite element. The preserved marginal palatal bone is elongate, straight and orientated sub-parallel to the skull midline. Its anterior and posterior articular extremes are flattened and orientated orthogonally to one another. The anterior end is dorsoventrally compressed and tongue-shaped in ventral view, contacting the maxilla on the underside of the palatal shelf (Fig. 6). The element has been forwardly displaced on both sides of the skull and extends beyond the anterior extreme of the palatal shelf. In contrast, the posterior end of the element is transversely compressed and has a vertically-orientated contact with the pterygoid. Between its extremes, the element is nearly cylindrical in cross-section. The shape of its anterior end most closely resembles that of a typical sauropod palatine, as does its elongate, uncurved shape. Unlike a typical palatine, however, this element has no medially directed process to abut the pterygoid medially or the vomer anteriorly. Moreover, the palatine typically does not contribute to the transverse palatal hook in reptiles. However, the participation of this element in the transverse palatal hook and its anterior connection to the palatal shelf matches the connections of the sauropod ectopterygoid. However, the ectopterygoid is typically hooked and orientated orthogonal to the skull axis, as its alternative name 'transversum' suggests.

The topological connections of the element best agree with those of an ectopterygoid, despite the morphological differences listed above. I identify it here as such, raising the question of the absence of the palatine on both sides of the skull, as well as the nature of its connection to the maxilla. The morphology of *Quaesitosaurus* is informative in this regard. As in *Nemegtosaurus*, there is but one marginal element, the ectopterygoid, preserved on both sides of the skull of *Quaesitosaurus*. Its morphology is identical – it is a strap-shaped element twisted 90° at midlength and connecting to the underside of the palate and the transverse palatal hook. The ectopterygoid of *Quaesitosaurus*, however, has not been forwardly displaced and a shallow facet for a second marginal element, which I suggest is the palatine, is present on the underside of the palatal shelf on the right side (see Fig. 17). This facet, if also present in *Nemegtosaurus*, would be obscured by the forwardly displaced ectopterygoid. Thus, it appears that a strap-shaped ectopterygoid is present in both *Nemegtosaurus* and *Quaesitosaurus* and that the absence of the palatine is preservational, rather than phylogenetic.

Palatine

A fragment attached to the ventral portion of the right pterygoid may represent the posterior tip of the palatine (Figs 4, 10 & 11). This piece is uninformative otherwise.

Pterygoid

The posterior (quadrate) and ventral (ectopterygoid) processes of the pterygoid are preserved on both sides of the skull (Fig. 11). The anterior (palatine) process is nearly completely preserved but is partially covered by matrix and obscured by adjacent elements. Transverse compression of the skull has altered the orientation of the pterygoids so that they are nearly vertically orientated and separated by only a narrow gap (Fig. 10). The apparent difference in pterygoid orientation between *Nemegtosaurus* and *Rapetosaurus* (Curry Rogers & Forster 2004: 139) is a preservational artifact.

The pterygoid is platelike and its three processes are coplanar and arranged symmetrically about a central point. *Nemegtosaurus* and *Rapetosaurus* share this feature in common (Curry Rogers & Forster 2004), in contrast to other sauropods in which the pterygoid processes are not coplanar (e.g. *Diplodocus*, McIntosh & Berman 1975: fig. 4). The pterygoid contacts the vomer anteriorly, the palatine and opposite pterygoid anteromedially, the ectopterygoid ventrally and it is sandwiched by the basipterygoid processes and quadrate posteriorly. The ventral (ectopterygoid) process and posterior (quadrate) processes are nearly collinear, as they are in *Rapetosaurus* (Curry Rogers & Forster 2004: fig. 26). The ventral process contacts the ectopterygoid at nearly a right angle to form the transverse palatal hook. The pterygoid wraps around the posterior portion of the ectopterygoid, extending further laterally than medially

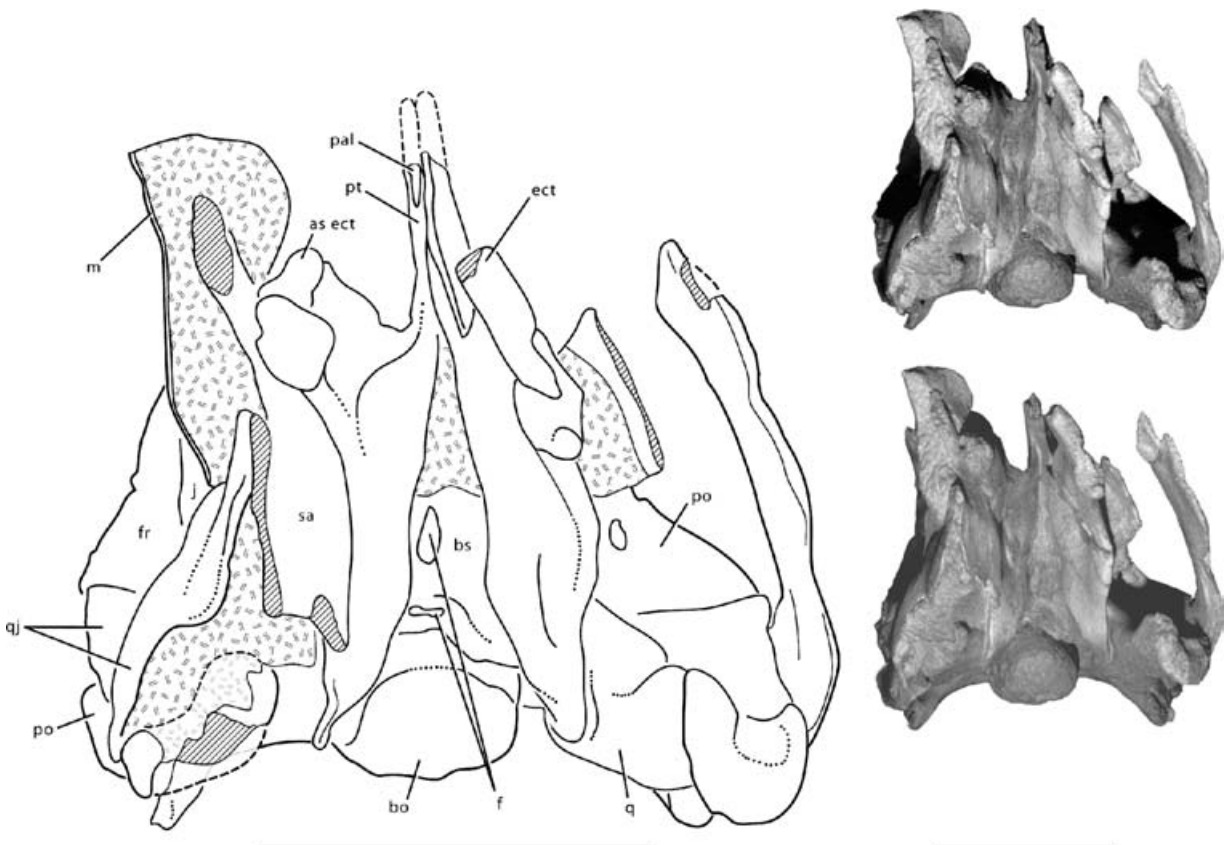

Figure 11 Stereopairs and interpretive line drawing of the posterior portion of the skull of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in ventral view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

(Figs 9 & 11). The transverse palatal hook is positioned near the middle of the preserved portion of the antorbital fenestra (Figs 3 & 4).

The posterior process, or quadrate flange, is intercalated between the quadrate and braincase, as visible in posterior and ventral views (Figs 9 & 11). Its contact with the quadrate is flat and vertically orientated. The articular surface of the basipterygoid bears a ventrally concave, 'rocker-like' shape (Fig. 9) that is shared by *Rapetosaurus* and *Quaesitosaurus*. The pterygoid lacks the hook-like process that encloses the basipterygoid process in some sauropods (e.g. *Dicraeosaurus*, *Camarasaurus*).

Quadrate

The quadrate is nearly completely preserved on both sides of the skull, but it is fairly damaged in the region of the quadrate fossa. The quadrate is visible in anterior and posterior views, but it is partially obscured by the quadratojugal and squamosal in lateral view (Figs 8–11). The right quadrate has been shifted anteriorly by the forward shearing of that side of the skull, as noted previously (Salgado & Calvo 1997; Upchurch 1999; compare Figs 3 & 4).

The quadrate forms the upper condyle of the jaw joint and contacts the temporal elements (quadratojugal, squamosal), occipital elements (paroccipital process, basal tuber) and the palate (pterygoid). In posterior view, the quadrate cants medially from its articulation with the socket of the squamosal on the posterodorsal corner of the skull to contact the basal tubera (Fig. 9). Ventral to this contact, the quadrate bends back laterally to its contact with the quadratojugal at the posteroventral corner of the skull. Consequently, the axis of the quadrate appears bent in posterior view, with the angle of that bend occupied by the quadrate fossa. The novel palate–braincase contact, via the quadrate and basal tuber, is restricted to *Nemegtosaurus* and related forms such as *Rapetosaurus* (Curry Rogers & Forster 2004: fig. 1A) and *Quaesitosaurus* (see Fig. 18). The quadrate–basal tuber contact, which is not a preservational artifact (*contra* Salgado & Calvo 1997: 42), can be recognised in isolated braincases by well-marked rugosities derived from this articulation (see 'Basisphenoid', below). The quadrate fossa is deep (*contra* Madsen *et al*. 1995: 15), broad and finished laterally by the squamosal and quadratojugal. When these latter elements are not preserved, the quadrate fossa appears to face laterally, as was the case in *Quaesitosaurus*, which was reconstructed with a laterally facing quadrate fossa termed a 'resonator depression' by Kurzanov & Bannikov (1983: 92; fig.1).

The pterygoid flange of the quadrate is only partially visible in the left lateral and ventral views (Figs 8 & 11) due to the close approximation of the quadrate and basal tubera and to matrix. The quadrate distal condyle is complete on the left side (Fig. 8). As seen in ventral view, the condyle is kidney-shaped, with a convex posterior margin and slightly concave anterior margin (Fig. 11). The condyle is undivided and its medial aspect is narrower anteroposteriorly than is the lateral. The long axis of the quadrate condyle is orientated

anteromedially, but this may be due to postmortem rotation of the quadrate from its original position. The quadrate condyle of *Quaesitosaurus* – which is similar in other respects but uncrushed – is transversely oriented (PIN 3906/2). As seen in posterior view, the quadrate condyle of *Nemegtosaurus* is bevelled such that the medial side hangs lower than the lateral side (Fig. 9).

Braincase

The braincase is firmly co-ossified and well preserved. Sclerotic plates are present on the right side of the skull, held in position by matrix (Figs 4 & 10). The left side of the skull is nearly free of matrix, as is the occiput and the ventral aspect of the braincase. The endocranial cavity is completely filled by matrix.

Basioccipital

The basioccipital is the median element that forms the occipital condyle. It contacts the paired exoccipital–opithotics on either side of the foramen magnum and abuts the median basisphenoid anteriorly near the basal tubera (Figs 9 & 11). The basioccipital contribution to the metotic foramen, which conveys cranial nerves IX–XI, cannot be determined because it is obscured by matrix. Cranial nerve XII is completely enclosed within the exoccipital–opisthotic and does not pass through the basioccipital (Fig. 9).

Both the basioccipital and the exoccipital–opisthotic contribute to the occipital condyle. The basioccipital forms the main body of the occipital condyle and the exocccipital–opisthotic its 'shoulders', based on the faint sutures preserved (Fig. 9). The occipital condyle is downwardly orientated when the supraoccipital is orientated vertically. The dorsal margin of the occipital condyle is concave where it forms the floor of the foramen magnum, but the remainder is strongly convex. The condyle is slightly broader transversely than deep dorsoventrally (60 × 50 mm) and more than twice as broad as the foramen magnum. The surface of the occipital condyle is rugose and was probably covered by a modest layer of articular cartilage. The suture between the basioccipital and basisphenoid cannot be identified, so the contribution of the former to the basipterygoid processes cannot be determined.

Basisphenoid

The basisphenoid is well preserved but only visible in posterior and ventral views because of matrix (Figs 9 & 11). This large, median element floors part of the braincase and forms part of the basal tubera, basipterygoid processes and the parasphenoid rostrum. It contacts the basioccipital and quadrate posteriorly, the pterygoid ventrally and the prootic and laterosphenoid dorsally.

The basisphenoid of *Nemegtosaurus* has two contacts with the palate: the plesiomorphic basipterygoid–pterygoid contact and a novel basisphenoid–quadrate contact that is evidenced by the bevelled, roughened surface of the basal tubera. This contact is not due to postmortem depression (see 'Quadrate' above). This contact does not appear to be present in *Saltasaurus*, in which the basal tubera are transversely narrow and smooth (Powell 1992: fig. 1).

The basipterygoid processes are ventrally directed and diverge from one another at an angle less than 45° (Fig. 9). A single, transversely elongate opening for the internal carotid artery emerges from between the basipterygoid processes, as in *Quaesitosaurus* (Figs 9 & 11). A second, median opening is present on the ventral surface of the basisphenoid further anteriorly. Distally, the basipterygoid processes are expanded anteroposteriorly and are narrow transversely (45 × ~10 mm). Their articular surface for the pterygoid is anteroposteriorly convex and fits into a similarly concave 'rocker' facet in the pterygoid (see 'Pterygoid', above). This facet is unlike the plesiomorphic socketed contact of most sauropods (e.g. *Brachiosaurus*, Janensch 1935–1936: figs 27–30) or the hooked contact present in *Camarasaurus* (Madsen *et al*. 1995: fig. 5E) and *Dicraeosaurus* (Janensch 1935–1936: fig. 105). The rocker-like basipterygoid process–pterygoid contact is shared by *Nemegtosaurus*, *Quaesitosaurus* (PIN 3906/2) and *Rapetosaurus* (Curry Rogers & Forster 2004: figs 23–27).

Supraoccipital

The supraoccipital is a median basicranial element that forms the dorsal margin of the foramen magnum. The supraoccipital contacts the exoccipital–opisthotic and the occipital process of the parietal laterally on the occiput; it contacts the skull roof via the parietal dorsally (Figs 7 & 9).

The supraoccipital is triradiate, with a relatively flat ventral surface and dorsal and lateral projections separated by a sharp notch. In posterior view, the supraoccipital contacts the parietal along the L-shaped notch formed by the lateral aspect of its dorsal process and the dorsal aspect of its lateral process (Fig. 9). The remainder of the lateral process of the supraoccipital is enclosed by the exoccipital–opisthotic, which extends medially to form the lateral margin of the foramen magnum. Whereas the course of its suture with the parietal is well marked, that with the exoccipital–opisthotic is difficult to trace in places. Consequently, the supraoccipital contribution to the dorsal margin of the foramen magnum is difficult to determine. The supraoccipital bears a vertically-orientated median ridge that begins near the middle of the element and extends dorsally to its summit. This supraoccipital ridge can be seen in dorsal view as a small, triangular process posterior to the parietals (Fig. 7).

Prootic

The prootic cannot be examined because it is obscured by matrix.

Exoccipital–Opisthotic

This paired composite element forms the breadth of the occiput, extending laterally as the paroccipital processes. The right exoccipital–opisthotic is nearly completely preserved, lacking only the distalmost portion of the paroccipital process. The left is less complete and lacks the distal extreme of the paroccipital process. In posterior view, the exoccipital–opisthotic fits between the supraoccipital, parietal, squamosal and basioccipital (Fig. 9). Anteriorly, the exoccipital–opisthotic is appressed against the prootic, which forms part of the lateral wall of the braincase.

The occiput is broadest across the paroccipital processes, which expand dorsoventrally and anteroposteriorly at their distal ends. Prior to this distal expansion is a smooth dorsal notch that forms the lower margin of the post-temporal foramen, which was bounded dorsally by the squamosal

(Fig. 9). The rugose bone at the distal paroccipital process is sharply demarcated. In lateral view, the distal end of the paroccipital process is fusiform, with its anteroposteriorly thickened dorsal half fitting in a well-marked facet in the posterior aspect of the squamosal and its concave ventral half accommodating the quadrate head (Fig. 8). The distoventral tip of the paroccipital process is not completely preserved on either side in *Nemegtosaurus*. In *Quaesitosaurus*, the completely preserved right paroccipital process is prolonged ventrally by a smooth, narrow prong (see Fig. 18). This distoventral prong is preserved in other titanosaur braincases, including *Rapetosaurus* (Curry Rogers & Forster 2004: fig. 19), *Antarctosaurus wichmannianus* (Huene 1929: fig. 1), *Saltasaurus* (Powell 1992: fig. 1) and cf. *Antarctosaurus septentrionalis* (Chatterjee & Rudra 1996: fig. 11).

The exoccipital–opisthotic forms the lateral margin of the foramen magnum and part of its ventral margin. Sutures with the basioccipital within and lateral to the occipital condyle, however, are difficult to discern. Cranial nerve XII exits through the exoccipital–opisthotic lateral to the occipital condyle. A conspicuous ridge crosses the exoccipital–opisthotic from the dorsolateral margin of the foramen magnum to midlength on the paroccipital process (Fig. 9). This ridge may have formed the lower boundary of the occipital fossa. A similar ridge is present in *Quaesitosaurus* (see Fig. 18), which preserves low proatlantal facets that are apparently reduced or absent in *Nemegtosaurus*.

Laterosphenoid

The lateral wall of the braincase is best seen on the left side of the skull (Fig. 8). The laterosphenoid forms the posterior portion of the braincase sidewall. The laterosphenoid is transversely orientated and partially separates the temporal region of the skull from the orbital region via its contact with the frontal and postorbital. Anteriorly, the laterosphenoid contacts the orbitosphenoid along the border of cranial nerves IV, V and a large opening dorsal to IV, as in *Quaesitosaurus* (PIN 3906/2) and other sauropods. Two deeply impressed grooves pass anteroventrally and posteroventrally from the opening of cranial nerve V. These grooves mark the exits of the inferior orbital (V_2) and mandibular (V_3) branches of the trigeminal nerve, respectively. The opening for cranial nerve IV is slit-shaped and transversely orientated; a larger opening of unknown identity is located dorsal to it. The exit for cranial nerve III is relatively small and positioned along the line connecting cranial nerves II and V. A small opening for cranial nerve VI is located anteroventral to that for cranial nerve V. A similar arrangement of cranial nerves II–V is present in *Quaesitosaurus*.

Orbitosphenoid

The paired orbitosphenoids meet anteriorly to close the braincase (Fig. 10). They contact the laterosphenoid posteriorly and the basisphenoid ventrally. Large, paired openings for cranial nerve I pass through a dorsal breach in the orbitosphenoid symphysis. Paired openings for cranial nerve II exit through the orbitosphenoid just anterior to that for cranial nerve III (Fig. 8). A smaller opening posterolateral to these may have carried cranial nerve VI. At its posterior margin, the orbitosphenoid forms the anterior border for cranial nerves IV, V and a large opening dorsal to IV; their posterior border is finished by the laterosphenoid. The ventral portion of the orbitosphenoid is obscured by matrix.

Lower jaw

Both right and left lower jaws are well preserved (Figs 12–14). Nearly all of the bones are complete on one or both mandibles (dentary, surangular, angular, coronoid) or can be reconstructed from preserved portions on both jaws (splenial), but neither the prearticular nor articular were preserved on either. The lower jaw is deepest in the coronoid region, which is expanded dorsally and somewhat ventrally. The jaw rami are shallow between the coronoid and tooth row, but then deepen anteriorly. No external mandibular fenestra is present. Thirteen teeth are preserved in each jaw ramus, these are discussed in a subsequent section (see 'Teeth', below). The articulated mandibles form an elongate, U-shaped structure, due to the inward curvature of the dentaries (Nowinski 1971: pl. 14, fig. 1A).

The right lower jaw, which is the source of most reconstructions (e.g. Nowinski 1971; McIntosh 1990) has experienced forward crushing, which has displaced the completely preserved angular out of its articulation with the dentary (Fig. 2). A portion of the right surangular remains adhered to the posterior skull block (Figs 4, 9 & 11).

Dentary

Both dentaries are well preserved, although preservational distortion has shifted them out of their symphyseal articulation (Fig. 2C). The complete disarticulation of the dentary symphysis may suggest a weak connection between the two elements; no other skull elements were as distorted.

The dentary forms the anterior half of the mandible, contacting its opposite at the symphysis, the surangular and angular posterolaterally and the splenial and coronoid medially. In lateral view, the dentary deepens both anteriorly and posteriorly (Fig. 13). The dorsal margin of the dentary is nearly horizontal, but the ventral margin is concave, accounting for the expansion at either end of the element. The anterior half of the dentary is dentigerous, but only the posterior teeth are visible laterally; the anterior half of the tooth row is orientated nearly transversely. Numerous vascular foramina open in the anterior region of the dentary, similar to the upper snout. The dentary extends posteriorly as two asymmetrical processes separated by an embayment (Fig. 13). The shorter, posterodorsal process reaches the base of the coronoid eminence and overlaps the surangular. The longer, posteroventral process extends to a position below the summit of the coronoid eminence and overlaps the angular and part of the surangular. The posterior portion of the splenial extends beyond the posterior dentary on the medial side of the lower jaw (Fig. 12; see 'Splenial', below).

A conspicuous Meckelian groove is visible medially (Figs 12 & 14). From its elevated position posteriorly, the groove descends to the ventral portion of the dentary. Near the symphysis, the groove rises slightly to form a prominent notch extending up the ventral third of the articular surface. The dentary symphysis is narrow transversely and lacks the roughened sutural surface present in other sauropods (e.g. *Camarasaurus*; Madsen *et al*. 1995: figs 41–42). The long axis of the dentary symphysis is perpendicular to the long axis of the lower jaw (Nowinski 1971: 70), as in *Quaesitosaurus* and *Antarctosaurus wichmannianus* but unlike other

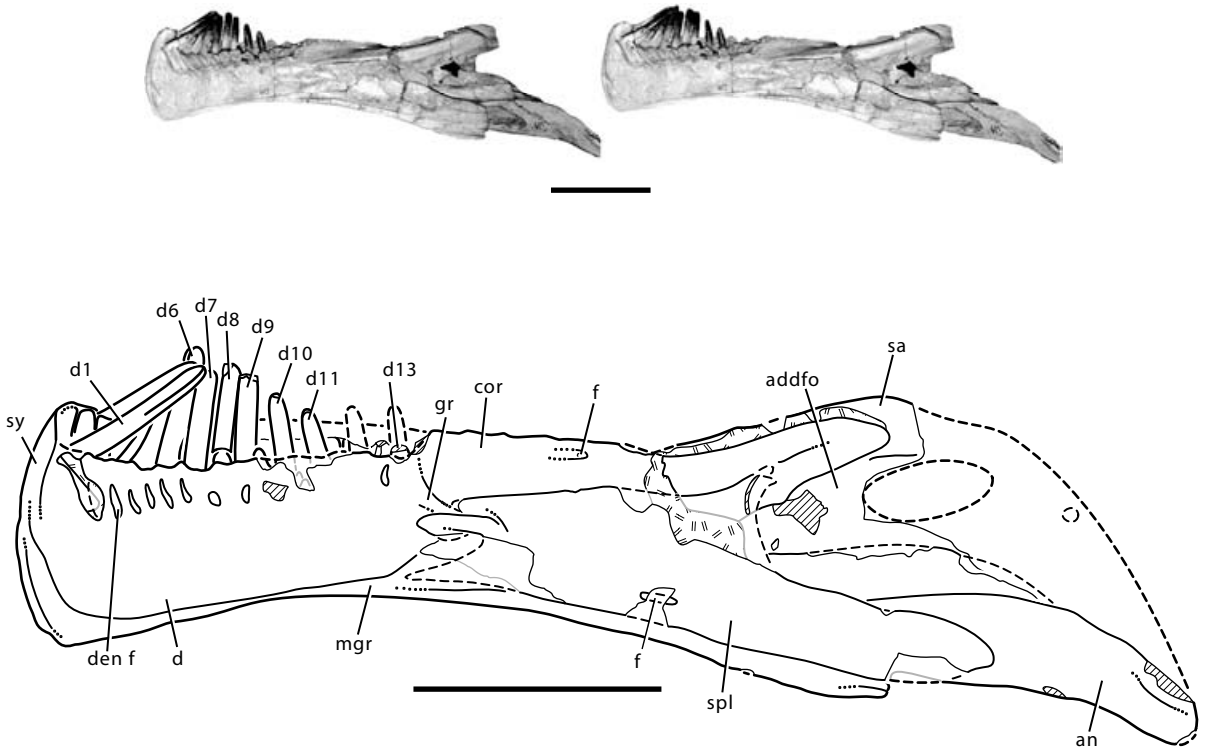

Figure 12 Stereopairs and interpretive line drawing of the right lower jaw of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in medial view. See Figure 3 for abbreviations. Scale bars = 10 cm.

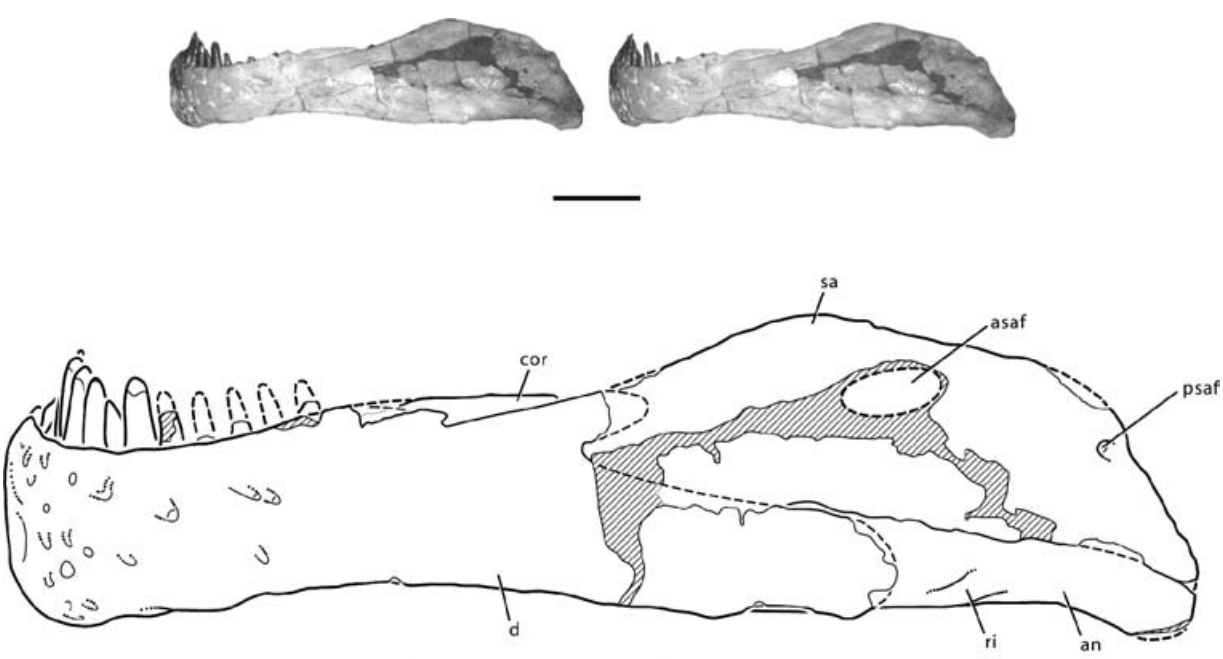

Figure 13 Stereopairs and interpretive line drawing of the left lower jaw of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in lateral view. See Figure 3 for abbreviations. Scale bars = 10 cm.

sauropods, in which the axis cants forward (Calvo 1994). The tooth row begins just posterior to the symphysis. Thirteen teeth are present in each dentary; replacement foramina are visible on the medial margin of the tooth row. Posterior to the tooth row, the dentary is overlapped medially by the coronoid, to which it is partially fused (see 'Coronoid', below).

The lower jaws are nearly U-shaped in dorsal view (Nowinski 1971: pl. 14, fig. 1A). All of the curvature is accommodated by the dentaries, which bend medially near

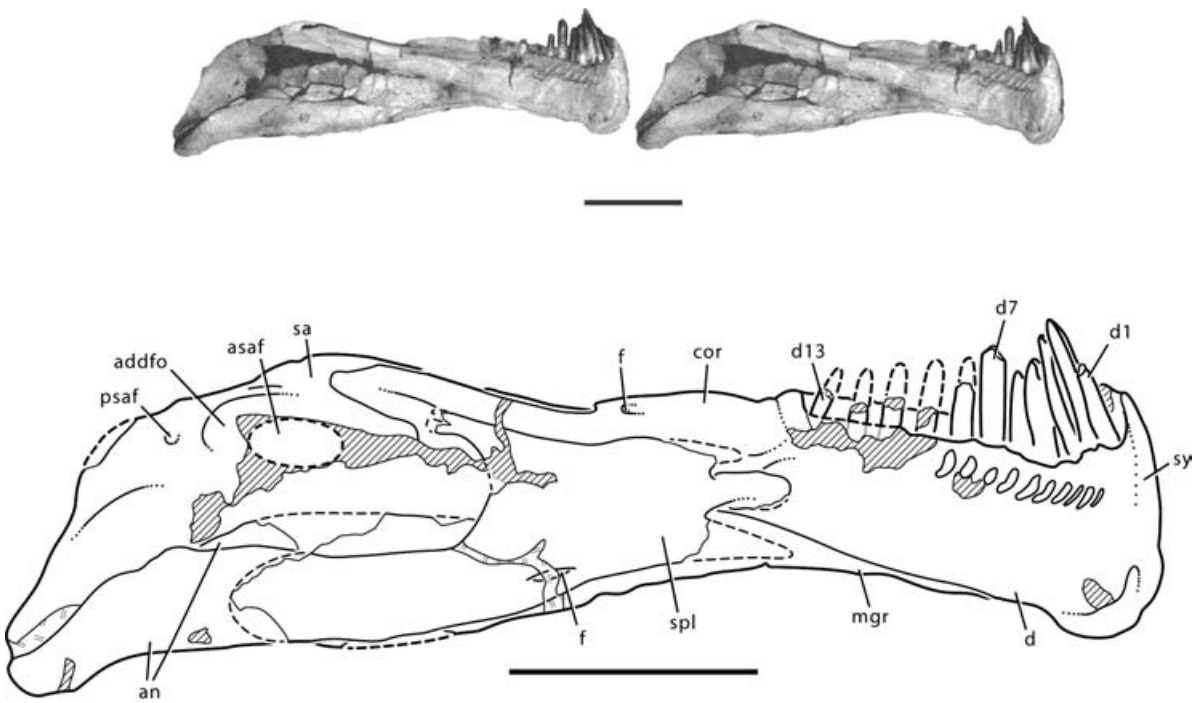

Figure 14 Stereopairs and interpretive line drawing of the left lower jaw of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in medial view. See Figure 3 for abbreviations. Scale bars = 10 cm.

the middle of the tooth row. This condition resembles that in *Rapetosaurus* (Curry Rogers & Forster 2004: 140) and *Quesitosaurus* (PIN 3906/2) and is distinct from the rectangular dentary present in diplodocoids such as *Diplodocus* (McIntosh & Berman 1975: fig. 5C).

Surangular

The surangular is nearly completely preserved on the left side (Figs 13–14), but the thin central portion of the element is damaged, as it is in *Quaesitosaurus*. Much less of the right surangular is preserved, owing to its impingement against the quadratojugal during fossilisation (Figs 2A & 12). The surangular forms the coronoid process and the outer wall of the adductor fossa.

The anterior portion of the surangular is clasped by the dentary laterally and the coronoid medially. The posterodorsal process of the dentary does not extend as far posteriorly as does the coronoid, which extends to near the summit of the coronoid process (Fig. 12). Following the shape of these two elements, the coronoid process rises sharply to reach its summit at approximately two-thirds jaw length. From this summit, the coronoid process descends flatly (nearly concave) before curving downwards towards the articular. The dorsal margin of the surangular is thickened medially and borders an elliptical coronoid fossa that stretches from the posterior surangular foramen to within the adductor fossa (Nowinski 1971: pl. 14, fig. 1A). The bone in this fossa is thin and incompletely preserved. The less complete right surangular preserves the margin of a large opening in this region, which Nowinski termed the 'mandibular vacuity' (1971: fig. 2). This opening was originally complete on the left surangular (Fig. 2A), but its margins have been since damaged (Fig. 13). This large, elliptical opening corresponds in position to the anterior surangular foramen. A smaller opening positioned near the arched portion of the posterior coronoid process (Figs 12–15) represents the posterior surangular foramen. Although the surangular is not completely preserved in *Quaesitosaurus*, the presence of a depression and extremely thin bone in this region suggests the presence of an enlarged anterior surangular foramen; the presence of a posterior surangular foramen cannot be determined. *Rapetosaurus* bears a large 'surangular foramen' on the anterior half of the surangular, as well as a smaller, posterior opening (Curry Rogers & Forster 2004: 142, fig. 30). These resemble in shape and position the anterior and posterior surangular foramina of *Nemegtosaurus*.

Angular

The angular is well preserved on both lower jaws. This strap-shaped postdentary element is exposed both medially and laterally and it forms the floor of adductor fossa (Figs 12–14). It is overlapped by both the surangular and dentary laterally and by the splenial medially. The prearticular and articular would have also contacted the splenial medially, but these elements were not preserved.

The angular is deepest near its midlength; it tapers posteriorly towards the jaw joint and anteriorly towards its articulation with the dentary. Its ventral surface is slightly concave posterior to the level of the coronoid process. Medially, a sharply defined shelf marks the articular surface for the prearticular, which is not preserved on either side (Figs 12 & 14). Although the articular is not preserved, it would have articulated in the medial expansion near the posterior extreme of the angular. The angular did not form an extended retroarticular process, as it does in *Diplodocus*. In lateral view, the ventral portion of the angular is developed into a low ridge that borders a shallow fossa (Fig. 13).

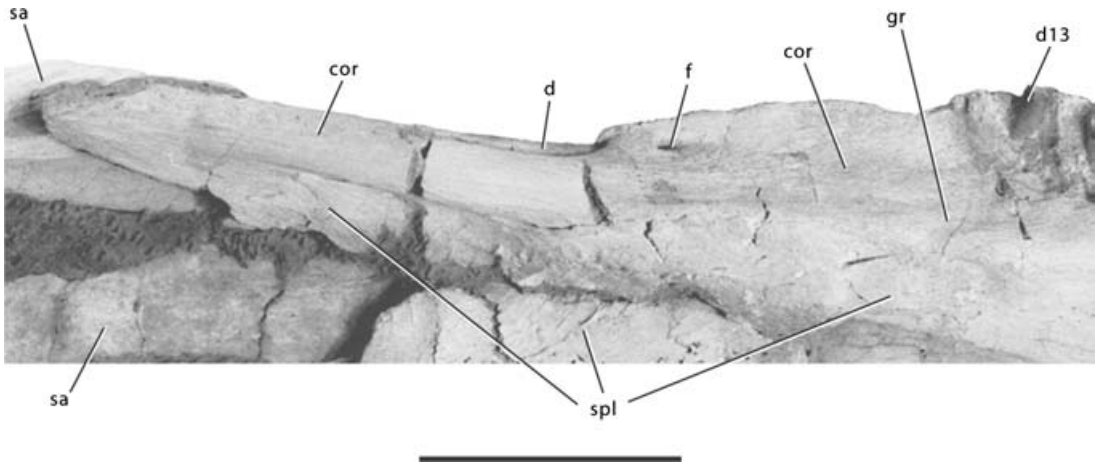

Figure 15 Detail of the left lower jaw of *Nemegtosaurus mongoliensis* (Z.PAL MgD-I/9) in medial view. See Figure 3 for abbreviations. Scale bar = 10 cm.

Splenial

Both splenials are nearly complete, but the left is better preserved than the right (Figs 12 & 14). The splenial is an anteromedial jaw element that forms part of the floor and inner wall of the adductor fossa and of the Meckelian canal. It contacts the coronoid and surangular dorsally and the angular and dentary ventrally. It would have also contacted the prearticular posteriorly, but this element is not preserved.

The splenial is tetraradiate, with two closely approximated anterior processes and two widely divergent posterior processes. The anteroventral process of the splenial is not completely preserved on either side, but it can be reconstructed based on the shape of the Meckelian groove of the dentary, which it overlies. The anteroventral process was probably elongate, triangular and would have extended anteriorly to the level of the penultimate dentary tooth position (Figs 12 & 14). The adjacent anterodorsal process is more completely preserved, especially on the right side. The anterodorsal process is rounded and elongate; it extends to the level of the posterior-most dentary tooth position. The anterodorsal process is itself divided into two smaller, tonguelike processes by a conspicuous notch that is preserved on both sides. A small groove extends from this notch towards the posterior margin of the tooth row (Figs 12, 14 & 15). Posteriorly, the dorsal margin of the splenial follows the upward curvature of the coronoid, terminating before the summit of the coronoid process. The shape of the posterior portion of the splenial roughly parallels that of the dentary. A narrow posterodorsal process is separated from the broad, elongate posteroventral process by a broad embayment. The posterodorsal process of the splenial is divided distally into two short, smaller processes. The posteroventral process of the splenial is relatively straight, tongue-shaped and overlaps the angular. A slit-shaped, anteroposteriorly elongate splenial foramen is preserved on both sides (Figs 12 & 14).

Coronoid (= 'Intercoronoid')

The presence of an elongate, flat element positioned flush against the posterior portion of the lower tooth row has been recognised in the sauropods *Brachiosaurus*, *Camarasaurus* and *Mamenchisaurus*. A similar element is also present (but was not identified) in the lower jaw of *Omeisaurus maoianus* (Tang *et al*. 2001*a*: fig. 13). In *Camarasaurus* and *Brachiosaurus*, this element covers all but dentary teeth 1–4, whereas in *Omeisaurus* and *Mamenchisaurus* it covers all but dentary teeth 1–8. So far, it has not been identified in any skull of *Shunosaurus* (Zhang 1988; Chatterjee & Zheng 2002) or *Diplodocus* (McIntosh & Berman 1975) and it has been regarded as absent in *Nemegtosaurus* (Madsen *et al*. 1995: 32). It is found behind the tenth tooth in *Plateosaurus* (Brown & Schlaikjer 1940: fig. 4), which suggests its presence and posterior position may be primitive for sauropodomorphs. In these basal forms, the posterior position of this element may be correlated with the greater number of teeth present in the lower jaw. This lower jaw element has been called the 'complementare' (Janensch 1935–1936), 'intercoronoid' (Madsen *et al*. 1995) and 'coronoid' (Russell & Zheng 1993; Ouyang & Ye 2002). Because 'complementare' is synonymous with 'coronoid' (Romer 1956), only 'coronoid' and 'intercoronoid' remain as alternative names for this element. Brown & Schlaikjer (1940: 4–5) applied the term 'intercoronoid' to describe in dinosaurs 'a jaw element which was present only in some of the early amphibians of the Carboniferous' that has 'exactly the same relationship with the other lower jaw elements in amphibians and early reptiles'. Brown & Schlaikjer (1940) did not specify which early amphibians or which lower jaw elements they were comparing, but it is probable that they were referring to the middle of the three coronoid elements present in basal tetrapods. The anterior and middle coronoids are positioned at the anterior and posterior ends of the tooth row, respectively, whereas the posterior coronoid was positioned near the coronoid eminence (Laurin 1998). The smaller coronoid element preserved in *Camarasaurus* near the coronoid eminence probably corresponds to the posterior coronoid, whereas the elongate element appressed against the posterior end of the tooth row in *Brachiosaurus*, *Mamenchisaurus* and *Omeisaurus* corresponds to the middle coronoid of amphibians. This element will be referred to as 'coronoid' here.

A modified coronoid is present in *Nemegtosaurus* (Figs 12–15). This elongate element is positioned just anterior to the coronoid eminence of the surangular and can be distinguished from adjacent elements. Here, the coronoid

Table 1 Principle measurements of the teeth of *Nemegtosaurus mongoliensis*.

						Upper teeth								
Crown measure		1	2	3	4	5	6	7	8	9	10	11	12	13
Length	R	46	44	50*	41	40*	26*	–	–	45	41	30*	34	–
	L	41	51	28*	–	44*	42	–	–	39	39	27*	–	30
Anteroposterior width	R	–	–	–	10	–	10	–	10	10	–	9	–	9
	L	10	10	10	10	10	10	10	–	10	10	–	–	–
Labiolingual width	R	9	9	9	9	–	9	–	9	8	8	8	7	–
	L	10	10	9	9	10	9	9	–	9	8	–	–	6
Wear pattern	R	0/1	2	0	3	0	–	–	–	0	0/1	3	1	0
	L	2/3	1	3	–	–	3	–	–	1	1	–	–	1
						Lower teeth								
Crown measure		1	2	3	4	5	6	7	8	9	10	11	12	13
Length	R	34	25*	–	–	–	30	31	–	29	27	–	–	–
	L	36*	32	38	25	29	34	31*	24	13	–	–	–	–
Anteroposterior width	R	8	8	–	–	8	8	8	–	6	7	–	–	–
	L	8	8	8	8	8	8	–	8	8	7	8	6	6
Labiolingual width	R	8	7	8	7	7.5	7	7	7	6	6	6	–	–
	L	–	7	8	7	7	7	–	7	6	7	–	–	–
Wear pattern	R	1	2	–	1	2/3	2/3	1	3	3	3	0	–	–
	L	0	2	0	2/3	2/3	1	0	2	–	–	–	–	–

Measurements are in millimetres for each tooth position (columns) in both right (R) and left (L) jaws. Asterisks (*) indicate measurements of incomplete crowns. Wear facet abbreviations: 0, no wear; 1, apical wear; 2, V-shaped wear (symmetrical); 3, V-shaped wear (asymmetrical).

is visible in lateral view, where it extends dorsally above the margin of the dentary (Fig. 13). It passes anteriorly and merges with the dentary near the posterior margin of the tooth row. In medial view, the anterior margin of the coronoid is difficult to identify, but it may be marked by a small groove that is preserved on both mandibles, just dorsal to the anterodorsal process of the splenial (Fig. 15). If this assessment is correct, then the coronoid extended to the posterior margin of the tooth row but did not overlap any alveoli. A foramen opens in the middle of the coronoid on both sides (Figs 12, 14 & 15). Nowinski (1971: 71, fig. 6) identified this element as a partially fused coronoid, an identification that is supported here. It is not clear whether the modified coronoid element of *Nemegtosaurus*, which reaches the summit of the coronoid process, has incorporated part of the posterior coronoid element. A structurally similar coronoid is present in *Bonitasaura* (Apestiguía 2004), *Quaesitosaurus* (PIN 3906/2) and possibly *Malawisaurus* (Jacobs *et al*. 1993: fig. 1B). Curry Rogers & Forster (2004:141) note a 'short, rugose ridge of bone' on the oral margin of the mandible that resembles in shape, position and texture that of *Nemegtosaurus* and *Quaesitosaurus*.

Teeth

Nearly complete crowns are preserved in both upper and lower tooth rows of both sides of the skull. The anterior lower teeth have been displaced somewhat posteriorly as a result of the postmortem deformation that shifted the lower jaws forward (Figs 2A & B). The premaxillary teeth have also been shifted by the transverse compression applied to the skull (Figs 2C & 5).

As discussed above, there were probably 13 teeth on each side of the upper and lower jaws. Despite identical tooth counts, there is a marked difference in upper and lower tooth breadth – lower crowns are about four-fifths the breadth of upper crowns (Table 1), a condition that is present in some diplodocoids (*Diplodocus*, Holland 1924; *Nigersaurus*, Sereno *et al*. 1999). There are other important differences between upper lower crowns. Upper crowns are D-shaped in cross-section and lingually curved, whereas lower crowns are elliptical in cross-section and slightly labially curved. As discussed below, tooth-to-tooth wear appears on the lingual side of upper teeth and on the labial side of lower teeth. Other aspects of the tooth crowns are identical. Both upper and lower crowns are narrow and neither expand from their root. They taper near their apex towards a somewhat blunt point. Conspicuous ridges are developed on both mesial and distal edges of upper and lower teeth (Nowinski 1971: 71). The ridges extend apically from the point at which the crown tapers to the tip. The enamel is finely wrinkled throughout the crown, but it is arranged into coarser, longitudinal ridges at the base of the crown. Tooth crowns do not overlap.

Replacement

Two types of tooth replacement are visible in *Nemegtosaurus*. At several tooth positions (LPM2, LPM4, LM2, RM6, RD10), replacing teeth appear on the lingual surface of the functional tooth. At other tooth positions, replacing crowns are pushed out by their roots. Fresh crowns in the pulp cavities of heavily worn teeth can be observed in both upper tooth positions (LPM3, LM4) and lower tooth positions (LD4, LD11; ?RD1, RD2, RD8) in *Nemegtosaurus*. In addition to these, Nowinski (1971: 72) reported replacing tooth tips in the pulp cavities of functional teeth RM 7, RM8 and RD 3, which have since been damaged. In the upper tooth row, the cycle of replacement appears to alternate between fresh and heavily worn teeth. The lower rows, in contrast have fresh teeth alternating with two heavily worn teeth (see Table 1).

Wear

All but the freshest teeth show signs of tooth-to-tooth contact. Fresh and more lightly worn teeth show fine enamel

wrinkling all over the crown. The enamel on moderately worn teeth, in contrast, smoothes towards the apex of the crown, although the coarse, longitudinal ridges at the base are never lost. Fresh and worn teeth also differ in the opacity of their enamel. Fresh teeth have thicker enamel and appear dark brown to black in colour, whereas heavily worn teeth have much thinner enamel and appear light brown. Upper crowns wear on their lingual surface, lower crowns wear on their labial surface.

Both V-shaped and apical wear facets are present in the jaws of *Nemegtosaurus* (Table 1). This is an uncommon condition, as sauropods typically bear one or the other but not both types of wear. It is not yet clear whether V-shaped and apical wear facets reflect ontogenetic variation, variation along the tooth row, or both. Most replacing teeth in *Nemegtosaurus* bear V-shaped wear facets, suggesting that they are produced later than the apical wear facet. However, two of these replacing teeth (LPM2, RM6) bear light apical wear. The difference in crown breadth between upper and lower teeth may also contribute to variation in wear facets, due to small differences in alignment along the tooth row. However, V-shaped and apical wear are not produced in other taxa with crown-breadth disparity (e.g. *Diplodocus*). Further investigation into the microwear will be required to distinguish between ontogenetic and tooth row variation, as well as to explain how wear was generated in *Nemegtosaurus*.

In his study of sauropod feeding mechanisms, Calvo (1994: 190) examined microwear on the surface of one tooth and reported long and thin scratches orientated parallel to the tooth axis. He concluded that the lower jaw of *Nemegtosaurus* moved in an up-and-down motion to produce an isognathous bite. Upchurch & Barrett (2000: 100, fig. 4.4) described similar microwear in *Rapetosaurus* (referred to as an 'unnamed titanosaur from Madagascar'), reporting coarse scratches extending parallel to the axis of the crown as well as randomly distributed pits. Upchurch & Barrett (2000: 103) also recognized V-shaped and apical wear facets in *Nemegtosaurus* (which they consider a diplodocoid) and suggested a 'shearing bite was employed' and that the 'presence of mesial and distal [i.e. V-shaped] wear could reflect some oral processing, or a less precise tooth-to-tooth contact than found in titanosauroids or diplodocoids'. Again, additional investigation into the distribution and orientation of wear facets is required to interpret chewing function in *Nemegtosaurus* and other titanosaurs.

Reconstruction

Although the original reconstruction of Nowinski included lateral, dorsal and posterior views (1971: figs 1, 2, 5A), a reconstructed ventral view of the skull was never presented. Salgado & Calvo (1997: fig. 8) presented the only other reconstruction of the *Nemegtosaurus* skull, but they provided only a lateral view. As discussed below, their reconstruction differs substantially from the original of Nowinski (1971), most notably in the narial and lateral temporal regions. Few other titanosaur skulls have been reconstructed. The first was a reconstruction of *Antarctosaurus wichmannianus* by Huene (1929: fig. 31), a species that many have considered to be an amalgam of both diplodocoid and titanosaur cranial elements (McIntosh 1990; Jacobs *et al.* 1993; Sereno *et al.* 1999; Upchurch 1999; but see Apestiguía 2004). Although the narial region of the skull was not preserved, Huene (1929) reconstructed *Antarctosaurus* to resemble *Diplodocus*, based on perceived phylogenetic affinities indicated by narrow tooth crowns. This reconstruction, in part, led to a long-held notion that diplodocoids and titanosaurs shared close phylogenetic history, despite few postcranial similarities (McIntosh 1990). Salgado & Calvo (1997: figs 5B, 7B) provided an alternative reconstruction of the *Antarctosaurus* skull, as well as that of *Quaesitosaurus*. Curry Rogers & Forster (2001: fig. 1A–C) reconstructed the nearly complete skull of *Rapetosaurus* in three views, but like Nowinski (1971) did not present a ventral view. The reconstructed *Rapetosaurus* is strikingly similar to *Nemegtosaurus*, as discussed below. Hunt *et al.* (1994: fig. 2) provided a 'hypothetical reconstruction' of the titanosaur skull based on titanosaur material from Malawi, India and Argentina, as well as *Camarasaurus*. Several reconstructed aspects of the skull, including nine premaxillary teeth, do not occur elsewhere in Sauropoda, while proposed derived characters such as a short, high snout and large antorbital fenestra may.

A new reconstruction of the skull of *Nemegtosaurus* is presented in Fig. 16. Compression and shearing during preservation have distorted the shape and configuration of the skull bones, especially on the right side. The reconstruction presented here relies on both sides of the skull but more heavily on the left, relatively undistorted, side. The portion of the skull between the posterior skull block and the snout piece was poorly preserved and some key regions such as the external naris and mid-palate were not preserved at all. I have reconstructed these regions based on interpretation of neighbouring bones and comparisons to skulls of other neosauropods, such as *Camarasaurus*, *Brachiosaurus* and *Diplodocus* (Wilson & Sereno 1998: figs 6–8). Photographs of the skull before preparation were used to estimate relative orientations of snout and posterior skull blocks, as well as the shape of the antorbital fenestra.

In lateral view (Fig. 16A), the skull is tipped posteriorly so that the jaw articulation is anterior of the occiput. The lateral temporal fenestra extends somewhat beneath the orbit, as in all sauropods, but is abbreviated antero-posteriorly. The nares are enlarged, but not so large as the orbit, which is teardrop-shaped. The nares are retracted to a position just anterior of the orbits, as in most sauropods, with their posterior margin between the prefrontals. The dorsal margin of the orbit is heavily ornamented. The snout is elongate, as in *Brachiosaurus*, *Rapetosaurus* and *Diplodocus*. As seen in dorsal view (Fig. 16B), the supratemporal fenestra is narrow antero-posteriorly and bounded only by the postorbital and parietal. The nares are relatively broad transversely, as indicated by preserved portions of the nasal bone (Fig. 6). The palate is reconstructed for the first time in a titanosaur in Fig. 16D. The palatine and anterior pterygoid were completely reconstructed, but the remainder of the palate was well preserved. The ectopterygoids are elongate elements that differ from the typically recurved and laterally orientated elements in other saurischians. The palate contacts the braincase via the quadrate–basal tubera and pterygoid–basipterygoid contacts. This novel double palatobasal contact is also visible in posterior view (Fig. 16C).

The reconstructed skull presented differs in several ways from the original *Nemegtosaurus* reconstruction of Nowinski (1971) and the *Rapetosaurus* reconstruction of Curry Rogers & Forster (2001). Although *Rapetosaurus* bears an exceptionally elongate antorbital fenestra, other

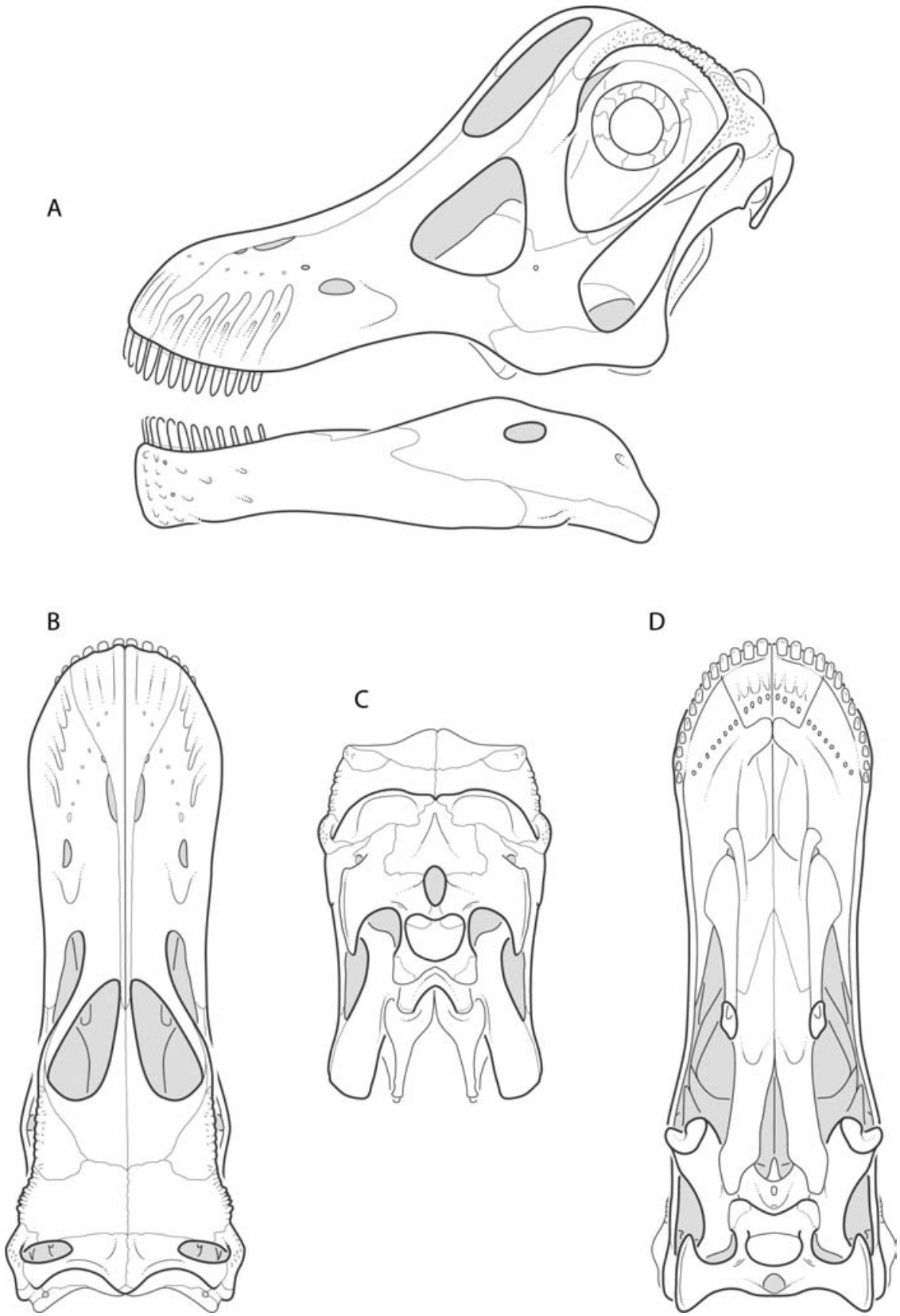

Figure 16 Reconstruction of the skull and lower jaw of *Nemegtosaurus mongoliensis* in left lateral (**A**), dorsal (**B**), posterior (**C**) and ventral (**D**) views.

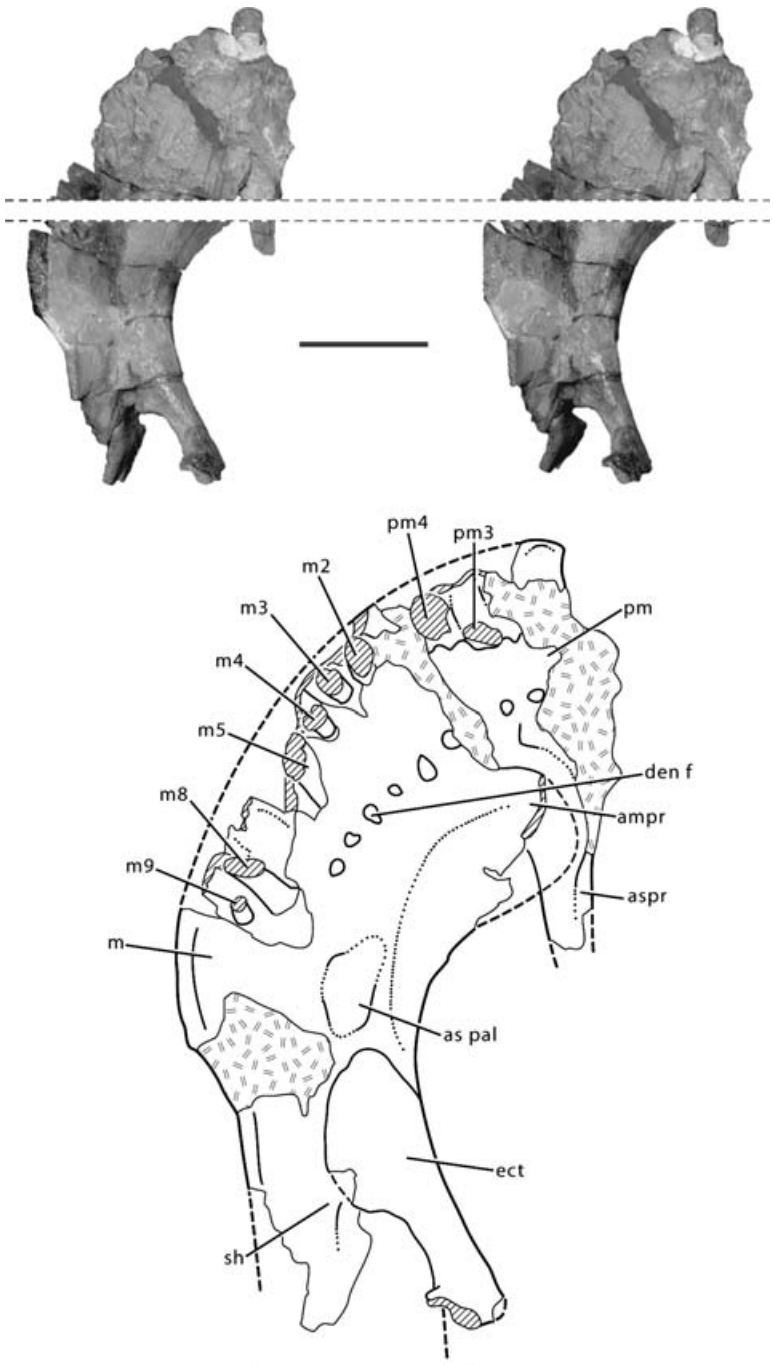

Figure 17 Composite stereopairs and interpretive line drawing of the right half of the upper snout of *Quaesitosaurus orientalis* (PIN 3906/2) in ventral view. Dashed lines separate individual stereopairs. See Figure 3 for abbreviations. Scale bars = 10 cm.

aspects of the skulls are quite similar. Both have elongate, gently sloping snouts, fully retracted and dorsally facing external nares and strongly anteriorly shifted quadrates. The reconstruction proposed here includes an arched internarial bar, as indicated by partially preserved nasals, which is primitive for Sauropoda. Likewise, the preservationally distorted lower lateral temporal fenestra has been restored, pushing the jaw articulation posterior slightly. In both these regards, the reconstruction presented here resembles that presented by Salgado & Calvo (1997). Nevertheless, it differs in not assuming *Brachiosaurus*-like external nares, triangular lateral temporal fenestra, rounded snout and sharply demarcated narial fossa.

Phylogenetic affinities of *Nemegtosaurus*

Traditional assessments of the phylogenetic affinities of *Nemegtosaurus* and *Quaesitosaurus* have suggested that they are close relatives with affinities to *Dicraeosaurus*. Although Nowinski (1971: 74) recognised a general resemblance to

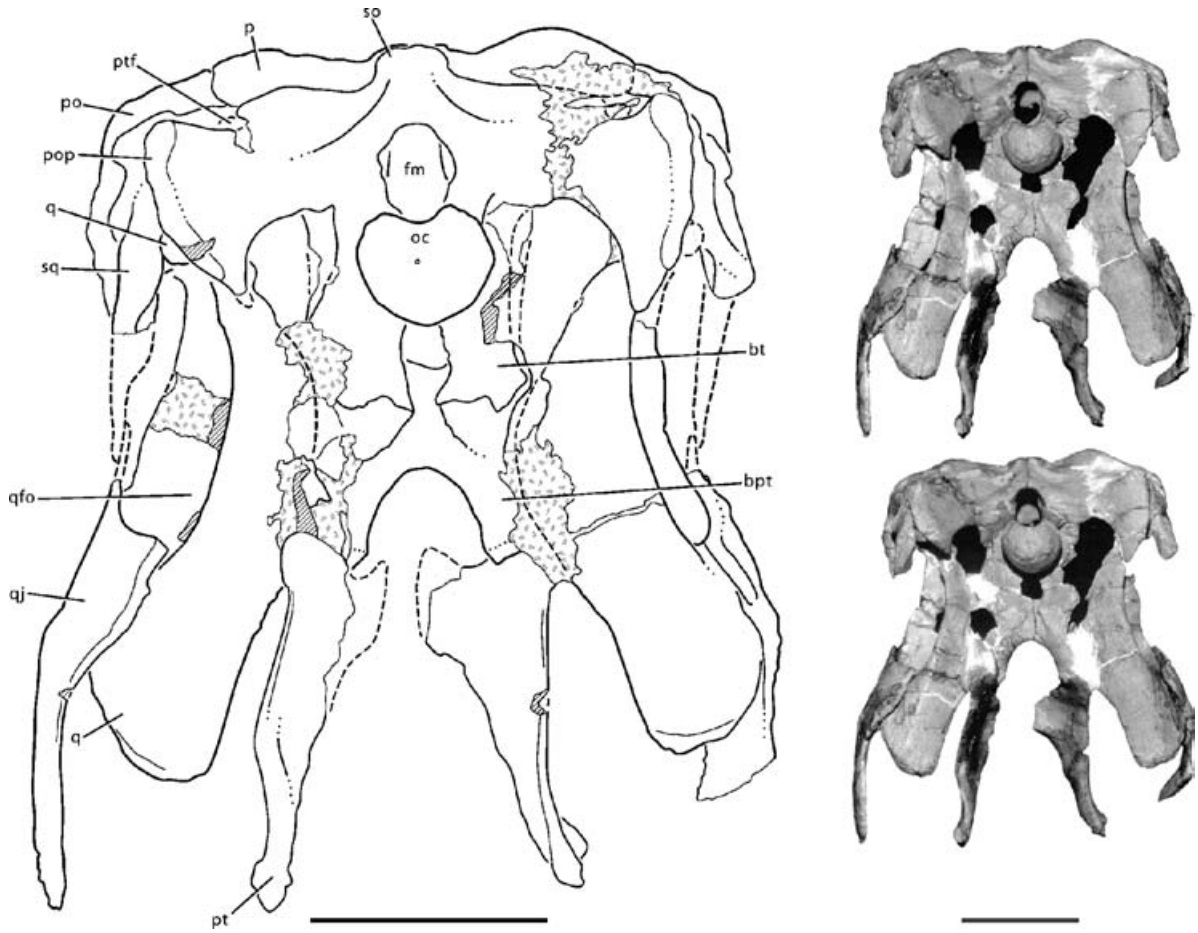

Figure 18 Stereopairs and interpretive line drawing of the posterior half of the skull of *Quaesitosaurus orientalis* (PIN 3906/2) in posterior view. Right stereo at top. See Figure 3 for abbreviations. Scale bars = 10 cm.

Diplodocus in the shape and proportions of the skull, he considered more important the specific resemblances to *Dicraeosaurus* in the 'structure of the occipital region, the size of the supratemporal fossa, the structure of the lacrimal, the lack of the accessory preorbital opening and the structure of the teeth.' Accordingly, he placed *Nemegtosaurus* in the Dicraeosaurinae. Kurzanov & Bannikov (1983) followed this assessment without further discussion. McIntosh (1990: table 16.1) also classified *Nemegtosaurus* within the Dicraeosaurinae, noting general resemblance to the skull of *Dicraeosaurus*. However, he observed differences in the length and positioning of the basipterygoid processes and cautioned that 'serious questions remain' regarding its affinities because no *Dicraeosaurus*-like vertebrae have been found in Upper Cretaceous rocks (McIntosh 1990: 393).

Previous cladistic hypotheses

Whereas the handful of cladistic analyses of Sauropoda agree on many aspects of the higher-level relationships of the group (see Wilson 2002), there has been no consensus on the phylogenetic affinities of *Nemegtosaurus* and *Quaesitosaurus*. Upchurch (1995, 1998, 1999), Curry Rogers & Forster (2001), Wilson (2002) and Upchurch *et al*. (2004) have coded one or both of these Mongolian sauropods as terminal taxa in a cladistic analysis. All but Upchurch agree that the Mongolian skulls *Nemegtosaurus* and *Quaesitosaurus* are members of Titanosauria.

Salgado & Calvo (1992, 1997)

Salgado & Calvo (1992) were the first to refute the traditional hypothesis that *Nemegtosaurus* and *Quaesitosaurus* were dicraeosaurids. They based this assessment on the absence of dicraeosaurid synapomorphies in *Nemegtosaurus*. Symplesiomorphies retained in *Nemegtosaurus* and *Quaesitosaurus* include short, downwardly projecting basipterygoid processes, a posteroventrally orientated occipital condyle, unfused frontals, dorsally facing supratemporal fenestrae and the absence of median skull roof openings (Salgado & Calvo 1992: 346). Although Salgado & Calvo (1992) formally excluded *Nemegtosaurus* and *Quaesitosaurus* from the Dicraeosauridae, they provided no synapomorphies supporting an alternative systematic assignment. Thus, they did not refute the hypothesis that *Nemegtosaurus* and *Quaesitosaurus* could be the immediate outgroup to diplodocids and dicraeosaurids, a position advocated by Upchurch (1995, 1998, 1999) and Upchurch *et al*. (2002).

In a subsequent paper, Salgado & Calvo (1997) provided synapomorphies linking *Nemegtosaurus* and *Quaesitosaurus* to *Antarctosaurus*, which they considered to be a titanosaur but did not include in their phylogenetic analysis (Salgado

et al. 1997: 5). These included the presence of peg-like dentition, sharp wear facets, a vertical dentary symphysis and narrow supratemporal fenestrae. Of these, only the presence of high-angled wear facets currently has a distribution supporting this claim. Peg-like dentition and narrow supratemporal fenestrae are homoplastic (shared by diplodocoids) and the vertical dentary symphysis is not present in the only other definitive titanosaur then known from a dentary (i.e. *Malawisaurus*). In addition, Salgado *et al*. (1997) suggested correlation amongst features supporting the traditional *Nemegtosaurus*–dicraeosaurid hypothesis. Hypothesised correlated characters included the posteriorly inclined quadrate, long and anteriorly orientated basipterygoid processes, ventrally orientated occipital condyle and anteriorly orientated olfactory tracts (hence the retracted position of the external nares). Some of these claims were answered by Upchurch (1999) and later by Chiappe *et al*. (2001), who observed the presence of some but not all of these putative correlated features in titanosaur embryos. Pachycephalosaurs represent another counter-example because they have anteriorly orientated basipterygoid processes, a ventrally deflected occipital condyle and a posteriorly inclined quadrate, but they retain terminal nares (pers. obs.).

Claims for *Nemegtosaurus*-titanosaur affinities are further complicated by controversy surrounding the affinities of, and associations amongst, skeletal remains attributed to *Antarctosaurus*. Although the postcranial skeleton attributed to *Antarctosaurus wichmannianus* is definitively titanosaurian (McIntosh 1990), the mandible described by Huene (1929: pl. 29) has been hypothesised to belong to a second, diplodocoid taxon (McIntosh 1990; Jacobs *et al*. 1993; Sereno *et al*. 1999; Upchurch 1999; but see Apestiguía 2004).

Upchurch (1995, 1998, 1999), Upchurch et al. (2002, 2004)

The only cladistic support for the traditional diplodocoid affinities of *Nemegtosaurus* has been provided by analyses by Upchurch (1995, 1998) and Upchurch *et al*. (2002, 2004) as well as his lengthier treatment of the then-assembled character information for and against the hypothesis (Upchurch 1999). As mentioned above, Upchurch (1999: 121–122) countered claims by Salgado & Calvo (1997) that several cranial characters are correlated with the rotation of the braincase in diplodocoids. This result is supported here and elsewhere (Chiappe *et al*. 2001).

Upchurch (1999: 118) identified seven characters supporting the diplodocoid affinities of *Nemegtosaurus*: (1) premaxilla narrow transversely and elongate anteroposteriorly; (2) subnarial foramen elongated along the premaxilla–maxilla suture; (3) posterior margin of the external naris posterior to anterior end of prefrontal; (4) vomerine (i.e. anteromedial) processes of the maxillae not visible laterally; (5) loss of the intercoronoid; (6) mandible subrectangular in dorsal view; and (7) teeth restricted to the anterior end of the jaws. Upchurch *et al*. (2004) did not include characters 4 and 5 but added two others: (8) premaxilla loses distinction between body and ascending process and (9) anteroposterior diameter of supratemporal fenestra is less than 10% occipital width. The redescription presented above confirms that characters 1, 3, 4, 7 and 9 are indeed present in *Nemegtosaurus*. The distribution of these features within sauropods requires additional comment. A narrow premaxilla (character 1) is probably correlated with the presence of narrow tooth crowns, since the number of premaxillary teeth does not vary in sauropods. Although a premaxilla is not preserved in *Rapetosaurus*: presence of narrow tooth crowns suggests a narrow premaxilla. Fully retracted external nares (character 3) are present in both diplodocoids (e.g. *Diplodocus*: Berman & McIntosh 1978) and titanosaurs (*Rapetosaurus*: Curry Rogers & Forster 2004) and do not link *Nemegtosaurus* with either clade. Likewise, exclusion of the anteromedial processes laterally (character 4), or at least greatly reduced lateral exposure as a narial fossa, is present in diplodocoids (e.g. *Diplodocus*) as well as titanosaurs (e.g. *Rapetosaurus*), so its presence in *Nemegtosaurus* does not support either hypothesis. Restriction of the tooth row anterior to the antorbital fenestra (character 7) is shared between diplodocoids and *Nemegtosaurus*. Character 9 is present in both diplodocoids and derived titanosaurs, as Upchurch *et al*. (2004: 303) acknowledge. In contrast, the present redescription concludes that characters 2, 5 and 6 are not present in *Nemegtosaurus*. The elongate opening on the anterior snout previously identified as an elongate subnarial foramen (character 2) by Upchurch (1999) opens into the maxilla and is here identified as the anterior maxillary foramen (see 'Maxilla' above). A specialised coronoid (= 'intercoronoid') is present in *Nemegtosaurus*, *Quaesitosaurus*, *Bonitasaura* and, possibly, *Rapetosaurus* and *Malawisaurus* (see 'Coronoid' above). Finally, the mandibles of *Nemegtosaurus* are not subrectangular in dorsal view (character 6). Although the anteriormost 3–4 teeth are obscured in lateral view, this is distinct from the condition in diplodocids such as *Diplodocus* and *Nigersaurus*, in which most or all teeth are positioned on the transverse portion of the ramus.

Curry Rogers & Forster (2001)

The discovery of *Rapetosaurus* provided the first association between a skull and titanosaur postcranial skeleton and, thus, the first opportunity to compare *Nemegtosaurus* and *Quaesitosaurus* to a well-preserved titanosaur skull (Curry Rogers & Forster 2001, 2004). The strong similarity between *Rapetosaurus*, *Nemegtosaurus* and *Quaesitosaurus* was reflected in a cladistic analysis, in which Curry Rogers & Forster (2001) listed several shared derived characters linking these three forms (posterodorsal process of splenial present, symphysis perpendicular to jaw axis), as well as features uniting them to *Malawisaurus* (frontals fused, parietal excluded from post-temporal fenestra, anteroposteriorly deep occipital region, basipterygoid processes four times basal diameter). Among these three, *Rapetosaurus* and *Nemegtosaurus* were found to have a sister-taxon relationship based on retraction of the nares between the eyes, frontal contribution to supratemporal fossa, anterodorsally facing nares, absence of a stepped snout profile, ectopterygoid process of pterygoid positioned caudoventral to the lacrimal and slender tooth crowns. As discussed in Wilson (2002: 246–247), none of these features is uniquely derived. Even the perpendicular orientation of the dentary symphysis relative to the jaw axis was used to support both the titanosaur (Salgado & Calvo 1997) and diplodocoid (Upchurch 1995, 1998; Upchurch *et al*. 2004) hypotheses.

Wilson (2002)

The phylogenetic position of *Nemegtosaurus* among titanosaurs suggested by Wilson (2002) and others is defended

here. This hypothesis nested *Nemegtosaurus* within a group of titanosaurs more derived than *Malawisaurus*. Relatively high decay indices (4) supported monophyly of the Titanosauria and of the group uniting *Rapetosaurus*, *Nemegtosaurus* and Saltasauridae (Wilson 2002: table 12). in addition, the monophyly of Nemegtosauridae (*Nemegtosaurus*, *Rapetosaurus*) was supported by 13 synapomorphies, five of which are unique (Wilson 2002: appendix 3).

Nemegtosauridae

The phylogenetic definition of Nemegtosauridae initially suggested by Upchurch *et al.* (2004) specified a stem-based group including all diplodocoids more closely related to *Nemegtosaurus* than to *Diplodocus*. The phylogenetic relationships proposed by Curry Rogers & Forster (2001) and Wilson (2002), which nest *Nemegtosaurus* within Titanosauria not Diplodocoidea, render this definition synonymous with Macronaria. Consequently, a new definition of Nemegtosauridae is required to accompany the phylogenetic hypothesis that *Nemegtosaurus* is a titanosaur. Nemegtosauridae is here phylogenetically defined as the stem-based clade including all titanosaurs more closely related to *Nemegtosaurus* than to *Saltasaurus*. Following the analyses of Curry Rogers & Forster (2001) and Wilson (2002), this definition includes at least *Nemegtosaurus*, *Quaesitosaurus* and *Rapetosaurus*. Proposed synapomorphies of Nemegtosauridae include (Wilson 2002: appendix 2):

Lacrimal with anterior process,
Parietal occipital process short, less than long diameter of foramen magnum,
Quadrate fossa orientated posterolaterally,
Palatobasal contact 'rocker'-like, pterygoid with convex articular surface,
Pterygoid with reduced quadrate flange, palatobasal and quadrate articulations approach,
Basisphenoid–quadrate contact,
Dentary symphysis perpendicular to jaw ramus (Salgado & Calvo 1997; Upchurch 1999),
Tooth crowns do not overlap (shared with *Brachiosaurus* and *Diplodocus*),
Tooth crowns with narrow cross-section (shared with diplodocoids).

Synapomorphies of *Nemegtosaurus* and *Quaesitosaurus* include (Wilson 2002: appendix 3):

Symphyseal eminence on external aspect of premaxillae,
Premaxilla and maxilla with sinuous contact,
Anterior process of the maxilla dorsoventrally deep,
Tooth bearing portion of snout highly vascularised, delimited by transverse groove (shared with *Diplodocus*),
Palatal shelf on maxilla enclosed to form 'maxillary canal',
Postorbital, prefrontal and frontal with orbital ornamentation,
Prefrontal diverges laterally,
Skull roof broadest across prefrontals,
Squamosal excluded from supratemporal fenestra,
Pterygoid with tongue-and-groove articulation with ectopterygoid–palatine,
Quadratojugal with sinuous ventral margin,
Intercoronoid partially fused to dentary,
Dentary with weak, anteroposteriorly narrow symphysis,
Meckel's groove extending onto symphyseal portion of dentary,
Dentary teeth smaller in diameter than premaxillary and maxillary teeth (shared with *Diplodocus*).

Comments on several nemegtosaurid taxa follow.

Quaesitosaurus

Most studies have considered *Quaesitosaurus* and *Nemegtosaurus* to be close relatives (e.g. Upchurch 1995), if not conspecific (Wilson 1997). However, several differences between the two taxa have been identified. Kurzanov & Bannikov (1983: 91–92) distinguished *Quaesitosaurus* from *Nemegtosaurus* on the basis of the former's (1) broader skull, (2) shorter squamosal that does not contact the quadratojugal, (3) absence of a parietal aperture, (4) rounded occipital condyle, (5) higher maxillary tooth count (9 versus 8), (6) longer mandibular tooth row, (7) 'resonator cavity' on the quadrate and (8) canal passing between the basal tubera. McIntosh (1990: 393) considered the first six to be minor differences that could be accounted for by preservation or individual variation. However, he considered the presence of a quadrate concavity and canal between tubera in *Quaesitosaurus* to be generic differences. Salgado & Calvo (1997: 41) further differentiated *Nemegtosaurus* and *Quaesitosaurus* by the (9) orientation of the basipterygoid processes, which they suggested are anteroventrally directed in the former and ventrally directed in the latter. These nine differences are discussed briefly below.

As suggested by McIntosh (1990), several of the differences listed by Kurzanov & Bannikov (1983) are preservational rather than taxonomic. The skulls of *Nemegtosaurus* and *Quaesitosaurus* have been deformed in different ways. *Nemegtosaurus* experienced transverse compression and forward shear, whereas deformation in *Quaesitosaurus* was due to dorsoventral compression (pers. obs.). These preservational differences account for the difference in snout breadth (1). The squamosal is damaged in *Quaesitosaurus* and neither its length nor its contact with the quadratojugal (2) can be determined. There is no parietal aperture (3) in *Quaesitosaurus*, but it is also absent in *Nemegtosaurus* (see 'Parietal', above). Differences in the shape of the occipital condyle (4) are minor and can be attributed to slight damage to that of *Nemegtosaurus*. The number of maxillary teeth (5) in *Nemegtosaurus* is uncertain because of damage to the last few alveoli on both sides of the skull, along with displacement of the teeth in their sockets. Although Nowinski (1971) originally recorded eight teeth in the maxilla of *Nemegtosaurus*, it is possible a ninth tooth was present, as in *Quaesitosaurus*. The apparent difference in the shape of the quadrate (7) results from the absence in *Quaesitosaurus* of the quadratojugal and the ventral process of the squamosal, which form the lateral margin of the quadrate fossa. The shape of the quadrate is otherwise similar (see Figs 9 & 16 and see 'Quadrate' above). Differences in the length of the mandibular tooth row (6) and in the orientation of the basipterygoid processes (9) are minor. However, the median canal passing between the basal tubera appears to differentiate *Quaesitosaurus* from *Nemegtosaurus*. This canal, which passes between the basal tubera

and basipterygoid processes, is open posteriorly in *Quaesitosaurus* but fully enclosed in *Nemegtosaurus*. Additional differences (not previously mentioned) include the presence in *Quaesitosaurus* of well marked grooves on the anterior quadrate, lack of a posterior process of the postorbital and the quadrate articular surface extending from the basal tubera to the basipterygoid processes. The differences between these two taxa and the autapomorphies that can be used to distinguish them are subtle. Ultimately, retention of both genera or sinking of *Quaesitosaurus* into *Nemegtosaurus* rests on the taxonomic value given to these differences, which is arbitrary. Perhaps the most conservative decision is to retain both genera, which does not require revision of existing taxonomy, anticipates additional differences that may come to light when postcranial remains are discovered and recognises that these taxa come from distinct stratigraphic horizons.

Opisthocoelicaudia

The presence of both the bodyless skull of *Nemegtosaurus* (Nowinski 1971) and the skull-less body of *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) in the Nemegt Formation has led to speculation that they represent the same taxon (e.g. Paul 1996). Interestingly, the early referral of these Mongolian forms to the Dicraeosaurinae and Camarasauridae, respectively, forbade this hypothesis. The more recent referral to Titanosauria of both *Opisthocoelicaudia* (e.g. Gimenez 1992; Salgado & Coria 1993; Upchurch 1995) and *Nemegtosaurus* (e.g. Calvo 1994; Wilson 1997; Calvo *et al.* 1998*a*) once again allows the possibility that these could actually pertain to the same genus. However, this hypothesis cannot be evaluated until associated cranial and postcranial material is discovered. The Nemegt region has thus far produced two distinct titanosaur skulls morphs (*Nemegtosaurus*, *Quaesitosaurus*), *Opisthocoelicaudia* and potentially a fourth taxon represented by a series of dorsal vertebrae (V. Alifanov, pers. commu.). Opisthocoelous caudal vertebrae from the early Late Cretaceous of China attributed to the new genus *Borealosaurus* (You *et al.* 2004) suggest *Opisthocoelicaudia*-like taxa were not restricted to the Nemegt Formation. Sues & Averianov (2004) have reported a slightly opisthocoelous anterior caudal vertebra from the Cretaceous of Kazakhstan, which may later be shown to have opisthocoelicaudiine affinities. The recent discovery of articulated titanosaur tails with an opisthocoelous, procoelous, amphicoelous and biconvex vertebrae (*Rinconsaurus*: Calvo & González Riga 2003), underscores the notion that phylogenetic inferences based on a single character are susceptible to homoplasy. Sauropod trackways recently recovered from the Nemegt Formation (Currie *et al.* 2003) cannot be attributed to a specific trackmaker subgroup.

Mongolosaurus

Gilmore (1933) described an associated partial braincase, fragmentary teeth and anteriormost three cervical vertebrae as *Mongolosaurus haplodon*. Despite the well preserved anatomy of this specimen, relatively little has been said of its affinities. McIntosh (1990: 398) suggested possible diplodocid affinities but classified it as Sauropoda *incertae sedis*. Upchurch (1995, 1998, 1999) did not suggest phylogenetic affinities for *Mongolosaurus* and Upchurch *et al.* (2004: table 13.1) considered it to be a *nomen dubium*. Both Barrett *et al.* (2002) and Wilson (2002) regarded it as Neosauropoda *incertae sedis*, but the former considered it to be a *nomen dubium*. Re-examination of the original material (AMNH 6710) reveals that the basal tubera are bordered laterally and ventrally by a raised lip, which may represent the contact surface for the quadrate. If so, then *Mongolosaurus* possesses at least one synapomorphy of Nemegtosauridae. *Mongolosaurus* is diagnosed by at least three autapomorphies pertaining to the anterior cervical vertebrae. These include an extremely reduced neural spine, well developed epipophyses and spinoprezygapophyseal (sprl) and spinopostzygapophyseal (spol) laminae aligned nearly horizontally and along the vertebral axis.

Antarctosaurus wichmannianus

Wichmann (1916) collected cranial and postcranial elements that he interpreted as representing one individual from Late Cretaceous rocks in General Roca (Río Negro Province), Argentina. Cranial remains include the posterior skull (a nearly complete braincase, both frontals and parietals and the upper portion of the left lateral temporal fenestra), a smaller piece pertaining to the right posterior corner of the same skull (squamosal, parietal, quadrate), an isolated quadrate, isolated mandibular fragments (a portion of the left dentary and a complete right dentary in articulation with a partial splenial, coronoid, angular and prearticular) and many postcranial bones. These postcranial remains included a cervical vertebra, caudal vertebrae, dorsal ribs, a left scapula, portions of the right forelimb (proximal and distal humerus, proximal ulna and radius, partial manus), pelvis (partial left ilium, right ischium, distal right pubis) and left hindlimb (femur, tibia, astragalus, calcaneum, metatarsals). Huene (1929: 1) studied these remains in Buenos Aires between 1923 and 1926 and described them as *Antarctosaurus wichmannianus*. No holotype was specified, so the elements he described may be considered the type series, or syntypes (Huene 1929: 66–75). As mentioned above, the attribution of all of these elements to a single individual remains problematic, owing to the lack of documented field associations and derived cranial features of two disparate sauropod groups (see Salgado & Calvo 1992, 1997; Upchurch 1999). Only the posterior portion of the skull will be discussed here.

The posterior portion of the skull of *Antarctosaurus wichmannianus* (Huene 1929: pls 28–29) displays shared derived similarities with *Nemegtosaurus* and other nemegtosaurids. These include the presence of a pendant non-articular process on the distal paroccipital process, which is based on the figures of Huene (1929); the distal paroccipital processes are apparently no longer present on the specimen (Powell 2003: 45). The presence of a postorbital with reduced posterior process further supports affinities with *Nemegtosaurus*. The basal tubera appear to be bevelled, as in *Nemegtosaurus*, but the presence of a contact with the quadrate must be confirmed. The braincase can be referred to Nemegtosauridae, but other cranial elements attributed to *A. wichmannianus* require further study.

cf. 'Antarctosaurus' septentrionalis

An isolated braincase referred to '*Antarctosaurus*' (ISI R162, Chatterjee & Rudra 1996: fig. 11) shares the presence of a quadrate–basal tubera contact with *Nemegtosaurus*. The holotypic braincase of '*Antarctosaurus*' *septentrionalis* (GSI K27/497) may have had a quadrate–basal tubera contact

(pers. obs.). These specimens are tentatively referred to the Nemegtosauridae.

Phuwiangosaurus

A newly described braincase referred to *Phuwiangosaurus* (Buffetaut *et al*. 2002: fig. 5) preserves several details that indicate its close relationship to *Nemegtosaurus*. These include the novel contact between the quadrate and basal tubera. A quadrate from the same locality (Buffetaut *et al*. 2002: fig. 6) resembles that of *Nemegtosaurus*, but no shared derived characters could be identified. Similarities between the teeth of *Nemegtosaurus* and *Phuwiangosaurus* cited by Buffetaut & Suteethorn (1999), do not necessarily indicate close phylogenetic relationship because narrow crowns are present in other sauropod taxa. *Phuwiangosaurus* has been interpreted as a basal titanosaur, retaining hyposphene–hypantrum articulations between dorsal vertebrae and amphicoelous anterior caudal vertebrae, among other features (Upchurch 1998). The derived cranial features noted here, however, have not been included in a phylogenetic analysis and their effect on tree topology is not yet known.

Bonitasaura

Apestiguía (2004) recently described a partial titanosaur skeleton from Santonian deposits of the Bajo de La Carpa Formation in Argentina. The associated skeleton includes both cranial and postcranial elements, the former of which include the anterior portion of the right mandibular ramus, parietal and frontal. The postcranial remains firmly establish the titanosaur affinities of *Bonitasaura* and the cranial remains facilitate comparisons to *Nemegtosaurus*. Although the parietal and frontal, which were not described, preserve no derived features linking them to *Nemegtosaurus*, the lower jaw does bear such resemblances. In particular, the lower jaw of *Bonitasaura* bears a partially fused coronoid bone that rises to a crest posterior to the tooth row (Apestiguía 2004: fig. 2C, E–F). Although not preserved posteriorly, the partially fused coronoid matches that of *Nemegtosaurus* (Fig. 15) and *Quaesitosaurus*, suggesting that *Bonitasaura* is a nemegtosaurid. Apestiguía (2004: fig. 2D) interpreted the coronoid as the bony support for a beak that functioned as a 'guillotine crest' that cut against a matching crest on the upper jaw, which was not preserved in *Bonitasaura*. In *Nemegtosaurus*, there is no sharp crest in the post-dentigerous portion of the upper jaw (Figs 3 & 4), so it is not clear what the purported beaked structure would have cut against. The function, if any, of the partially fused coronoids of nemegtosaurids remains unknown.

Effect of ambiguous features

The nemegtosaurids *Nemegtosaurus*, *Quaesitosaurus* and *Rapetosaurus* are the only titanosaurs for which nearly complete cranial remains have been described. Of these, only *Rapetosaurus* is known from associated postcranial remains. *Malawisaurus* is known from a nearly complete skull and skeleton that have not yet been fully described (Gomani 1998). Two nearly complete adult and several embryonic titanosaur skulls, each associated with postcranial remains, have been reported from the Upper Cretaceous of Patagonia (Calvo *et al*. 1997; Martinez 1998; Chiappe *et al*. 1998), but also await description. Braincases have been attributed to several other titanosaurs, but associations to postcranial remains are not well established (*Saltasaurus* Powell 1992; *Antarctosaurus wichmannianus* Huene 1929; *Phuwiangosaurus* Buffetaut *et al*. 2002). Isolated braincases are known from the Indian '*Antarctosaurus septentrionalis*' (Huene & Matley 1933; Chatterjee & Rudra 1996) and the Dongargaon braincase (Berman & Jain 1982).

The nearly complete skeleton of *Rapetosaurus* provides the only link between the isolated Mongolian skulls and titanosaurs, which are known predominantly from postcrania. Although numerous characters support the monophyly of *Rapetosaurus*, *Nemegtosaurus* and *Quaesitosaurus*, nearly all are ambiguous because few titanosaurs are known from cranial remains. Thus the close relationship among these three taxa must be treated with caution. As more well-preserved titanosaur skulls are discovered, the distribution of characters supporting nemegtosaurid monophyly will likely broaden to diagnose more inclusive groups. This tendency of character distributions to broaden so that they diagnose progressively more inclusive groups has been previously recognised (Grande & Bemis 1998: 19; Sues 1998: 241) and recently termed 'obsolescence' by Wilson & Upchurch (2003). Obsolescence is particularly dangerous when few characters support a given taxon, as was the case with '*Titanosaurus indicus*'. Fortunately, the large number of nemegtosaurid synapomorphies makes it likely that both higher- and lower-level characters have been identified. Thus, whereas some nemegtosaurid features will obsolesce to characterise all titanosaurs, others will probably remain diagnostic at lower levels.

Implications for Late Cretaceous sauropod diversity

The redescription of *Nemegtosaurus* and *Quaesitosaurus* presented here supports the titanosaur affinities of these taxa and identifies novel features supporting the monophyly of that group and of Nemegtosauridae. As such, *Nemegtosaurus* and *Quaesitosaurus* join the Asian titanosaurs *Phuwiangosaurus*, *Opisthocoelicaudia*, *Borealosaurus*, ?*Jiangshanosaurus*, ?*Mongolosaurus* and ?*Huabeisaurus*, along with the Asian titanosauriforms *Tangvayosaurus* (= '*Titanosaurus falloti*'), *Mongolosaurus*, *Gobititan* and *Euhelopus* (Table 2). Thus, all Cretaceous Asian sauropods are titanosauriforms, all Late Cretaceous Asian sauropods are titanosaurs and diplodocoids have not yet been recorded in Asia. These results imply a taxonomic composition for Cretaceous Asian sauropods that contrasts with those implied by traditional studies and some cladistic analyses of sauropods, which suggested a mixed Asian fauna consisting of either camarasaurids, dicraeosaurids and titanosaurs (McIntosh 1990) or basal diplodocoids, 'euhelopodids' and titanosaurs (Upchurch 1998; Upchurch *et al*. 2002; Barrett *et al*. 2002), respectively. This hypothesis has important implications for the sauropod faunal transition from the Jurassic to the Cretaceous, both in Asia and globally.

Origin of Asian Cretaceous sauropod fauna

Neosauropod lineages (e.g. Diplodocoidea, Macronaria) first enter the body fossil record in Upper Jurassic horizons in North America, Africa and Europe. Neosauropod sister-group relationships imply a Middle Jurassic origin (Upchurch

Table 2 Spatial and temporal distribution of Cretaceous Asian sauropod genera, listed in order of their stratigraphic appearance.

Taxon	Formation	Country	Age	Reference
'Asiatosaurus kwanshiensis' (*n.d.*)	Napan	China	Cretaceous	Hou *et al.* 1975
'Asiatosaurus mongoliensis' (*n.d.*)	Oshih	Mongolia	Early Cretaceous	Osborn 1924
Mongolosaurus haplodon (?T)	On Gong	Mongolia	Early Cretaceous	Gilmore 1933
Phuwiangosaurus sirindhornae (T)	Sao Khua	Thailand	Early Cretaceous	Martin *et al.* 1994
Unnamed (TSF)	Kuwajima	Japan	?Barriasian-?Hauterivian	Barrett *et al.* 2002
Euhelopus zdanskyi (TSF)	Mengyin	China	?Neocomian	Wiman 1929
Pukyongosaurus millenniumi (TSF)	Hasandong	South Korea	Barremian	Dong *et al.* 2001
'Chiayusaurus asianensis' (*n.d.*)	Hasandong	South Korea	Barremian	Lee *et al.* 1997, 2001
Chiayusaurus lacustris (?TSF)	Xinminbao Group	China	Barremian-Aptian	Bohlin 1953
Unnamed (TSF)	Xinminbao Group	China	Barremian-Aptian	Dong 1997
Unnamed (TSF)	Jinju	South Korea	Barremian-Aptian	Lim *et al.* 2001
'Ultrasaurus tabriensis' (n.d.)	Gugyedong	South Korea	Aptian	Kim 1983; Lee *et al.* 1997
Tangvayosaurus hoffeti (TSF)	Grès Supérieurs	Laos	Aptian-Albian	Allain *et al.* 1999
Jianshanosaurus lixianensis (?T)	Jinhua	China	Aptian-Albian	Tang *et al.* 2001*b*
Unnamed (TSF)	Ilek	Russia	Aptian-Albian	Averianov *et al.* 2002
Gobititan shenzhouensis (TSF)	Xinminbao Group	China	Albian	You *et al.* 2003
Unnamed	Jiufotang	China	Albian	Wang *et al.* 1998
Borealosaurus wimani (T)	Sunjiawan	China	early Late Cretaceous	You *et al.* 2004
Huabeisaurus allocotus (?T)	Huiquanpu	China	Late Cretaceous	Pang & Cheng 2000
Unnamed	Dzarakuduk	Uzbekistan	Turonian	Sues & Averianov 2004
'*Antarctosaurus*' *jaxarticus'* (*n.d.*)	Dabrazinskaya Svita	Kazakhstan	Turonian-Santonian	Ryabinin 1939
Quaesitosaurus orientalis (T)	Barungoyot	Mongolia	Santonian-Campanian	Kurzanov & Bannikov 1983
'Nemegtosaurus pachi' (*n.d.*)	Subashi	China	?Campanian-Maastrichtian	Dong 1977
Nemegtosaurus mongoliensis (T)	Nemegt	Mongolia	Maastrichtian	Nowinski 1971
Opisthocoelicaudia skarzynskii (T)	Nemegt	Mongolia	Maastrichtian	Borsuk-Bialynicka 1977

(Early and Late Cretaceous genera separated by solid line).
Abbreviations in parentheses after species name indicate phylogenetic affinities: n.d., nomen dubium; T, Titanosauria; TSF, Titanosauriformes.

1995, 1998; Wilson & Sereno 1998), which is supported by Middle Jurassic 'wide-gauge' sauropod trackways (Santos *et al.*1994; Day *et al.* 2002) attributed to the neosauropod lineage Titanosauria (Wilson & Carrano 1999). Definitive neosauropods have not yet been reported from the Jurassic of India, Australia, South America or Madagascar, all of which have comparatively poor or non-existent Upper Jurassic records. Asia, by contrast, has well sampled Middle and Upper Jurassic sediments but no definitive Jurassic neosauropods. This apparent anomaly has been interpreted as geographical isolation of Asia during Middle Jurassic until Cretaceous times (Russell 1993; Upchurch 1995; Buffetaut & Suteethorn 1999; Luo 1999; Barrett *et al.* 2002; Upchurch *et al.* 2002; Zhou *et al.* 2003). Although this hypothesis explains the absence of neosauropods from Asia, there are few examples of endemic Asian dinosaur clades. 'Euhelopodidae', for example, is often hailed as one such clade (Upchurch 1995, 1998; Barrett *et al.* 2002), but the monophyly of the group has been shown to be suspect (Wilson 2002).

Sauropods first appear in Asia in the Upper Triassic (*Isanosaurus*) and persist in greater numbers into the Lower Jurassic (Lufeng sauropod, *Kunmingosaurus*, *Gongxianosaurus*). The Middle Jurassic fauna of Asia includes both basal eusauropods (*Shunosaurus*, *Datousaurus*, ?*Abrosaurus*) and slightly more derived forms (*Bellusaurus*, *Klamelisaurus*). The Upper Jurassic fauna, in turn, includes a clade of long-necked omeisaurids (*Omeisaurus*, *Mamenchisaurus*) that are closely related to Neosauropoda. A purported *Camarasaurus* tooth crown from the Upper Jurassic of Siberia (Kurzanov *et al.* 2003) and a brachiosaurid manus from the Upper Jurassic of China (Dong *et al.* 2001) cannot yet be confidently referred to Neosauropoda. Furthermore, although Upchurch *et al.* (2004) consider *Abrosaurus* and *Bellusaurus* to be neosauropods, the character evidence supporting this assessment is not yet conclusive.

The abrupt transition from a predominantly or exclusively non-neosauropod Jurassic fauna to an exclusively titanosauriform Asian Cretaceous fauna (Table 2) has been interpreted as the end of Asia's geographical isolation (Barrett *et al.* 2002; Upchurch *et al.* 2002). This interesting pattern raises several questions about the origin of the Cretaceous Asian titanosauriform fauna. Upchurch *et al.* (2002) provided paleogeographical and paleobiogeographical evidence supporting convergence between Europe and Asia during the Aptian–Albian or perhaps earlier. Barrett *et al.* (2002) suggested that this exchange may have taken place as early as the Berriasian, based on the early appearance of titanosauriforms in Japan (Table 2), but did not specify an origin. Results from this analysis are consistent with *Nemegtosaurus* and *Quaesitosaurus* forming part of an endemic group because they are each other's closest relatives. The recent claim that *Opisthocoelicaudia* and *Borealosaurus* are sister-taxa may suggest a second endemic Asian titanosaur subclade. The recent discovery of an *Euhelopus*-like tooth in Lower Cretaceous (Neocomian) of Spain (Canudo *et al.* 2002) support the Upchurch *et al.* (2002) hypothesis of an Early Cretaceous communication between Europe and Asia. Further support is provided by the presence of gobiconodontid mammals in the Early Cretaceous of Spain (Cuenca-Bescós & Canudo 2003).

Titanosaur predominance in the Late Cretaceous

Zhou *et al*. (2003: 813) suggested that Asia may have served as a 'centre of diversification' for many taxa, including titanosauriforms. Although the absence of neosauropods from the Upper Jurassic of Asia is anomalous in the context of the records in other landmasses, the appearance of titanosaurs in the Lower Cretaceous seems to be a more general phenomenon. Titanosaur body fossils make their first appearance in Lower Cretaceous horizons of North America (Ostrom 1970; Britt *et al*. 1998), South America (Leanza *et al*. 2004), Australia (Coombs & Molnar 1981), Africa (Jacobs *et al*. 1993) and Europe (Seeley 1869, 1876). In Madagascar and India, which have poorly sampled Lower Cretaceous strata, titanosaurs appear with the first sampled Cretaceous rocks, which are Maastrichtian (Curry Rogers & Forster 2001) or Turonian (Khosla *et al*. 2003) in age. These distributions suggest that Titanosauria achieved a near-global distribution by the Early Cretaceous. The Middle Jurassic first appearance of 'wide-gauge' trackways suggest a much earlier origin, which places the spread of titanosaurs sometime in the Late Jurassic when substantial land connections remained. Given these data, it is surprising that only one Late Jurassic titanosaur body fossil is known (*Janenschia*: Janensch 1961).

Other neosauropod lineages survived into the Cretaceous, most notably rebbachisaurid diplodocoids, which occupied Europe (Dalla Vecchia 1998; Pereda-Suberbiola *et al*. 2003), Africa (Lavocat 1954; Sereno *et al*. 1999) and South America (Calvo & Salgado 1995; Bonaparte 1996) until at least the early Campanian, based on a rebbachisaurid interpretation of the lower jaw of *Antarctosaurus wichmannianus* (Leanza *et al*. 2004). Although many basal titanosauriforms, individual basal diplodocoids (*Amazonasaurus*: Carvalho *et al*. 2003), dicraeosaurids (*Amargasaurus*: Salgado & Bonaparte 1991) and brachiosaurids ('French' *Bothriospondylus*: Lapparent 1943) survived into the Early Cretaceous, they did not appear to diversify. Titanosaurs and rebbachisaurids – both predominantly narrow-crowned clades – appear to be the only two sauropod clades that flourished during the Cretaceous (Barrett & Upchurch 2005). Moreover, in several cases they are preserved in the same formation, such as the Candeleros and Lohan Cura Formations of Argentina (Leanza e*t al*. 2004), the Tiouráren Formation of Niger (Sereno *et al*. 1999) and the 'Bale' locality in Croatia (Dalla Vecchia 1998). By the latest Cretaceous, titanosaurs were the predominant (if not exclusive) sauropods worldwide, represented on all continental landmasses except Antarctica, which has not yet yielded sauropod fossils. If connections between landmasses were severed by the Cenomanian (e.g., Smith *et al*. 1994; Hay *et al*. 1999; Sereno *et al*. 2004), then the survival and predominance of titanosaurs on each landmass may have been independent. Confirmation of this pattern will require further sampling of Cretaceous horizons, as well as a detailed framework of titanosaur interrelationships to evaluate their Late Cretaceous endemicity.

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