

The small-bodied ornithischian dinosaurs *Micropachycephalosaurus hongtuyanensis* and *Wannanosaurus yansiensis* from the Late Cretaceous of China

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ABSTRACT

The type material of the small-bodied ornithischian dinosaurs *Micropachycephalosaurus hongtuyanensis* and *Wannanosaurus yansiensis* from the Late Cretaceous of China is reviewed. *Micropachycephalosaurus*, from the Wangshi Formation (Campanian) of Shandong Province, was originally referred to the clade Pachycephalosauria, but some later authors have considered it a nomen dubium. However, despite the extremely fragmentary nature of the holotype specimen, *Micropachycephalosaurus* can be diagnosed by the presence of prominent grooves on the ventral surface of the centra of the posterior dorsal vertebra. Unambiguous pachycephalosaur synapomorphies cannot be identified in the currently available material, and we consider this taxon *Cerapoda incertae sedis*. *Wannanosaurus*, from the Xiaoyan Formation (Campanian–?early Maastrichtian) of Anhui Province, can be diagnosed by the extreme flexure of the humerus, and is clearly referable to Pachycephalosauria on the basis of a large number of synapomorphies. Assessment of the phylogenetic placement of this *Wannanosaurus* within Pachycephalosauria is complicated by the probable juvenile nature of the holotype and paratype specimens.

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1. Introduction

Pachycephalosaurs form a rare and distinctive clade of derived ornithischian dinosaurs. They are characterised by a suite of cranial and postcranial synapomorphies (see, for example, Sereno, 2000; Maryańska et al., 2004; Sullivan, 2006), of which the most distinctive is the thickening (and in the majority of forms, doming) of the skull roof, the function of which remains unclear, although many authors favour roles in intraspecific combat and/or intraspecific display (see reviews in Maryańska et al., 2004; Goodwin and Horner, 2004; Bakker et al., 2006; Snively and Cox, 2008). Within Ornithischia, pachycephalosaurs form the sister group to Ceratopsia, together comprising the clade Marginocephalia (Norman, 1984; Sereno, 1984, 1986, 1999, 2000; Cooper, 1985; Maryańska and Osmólska, 1985; Butler, 2005; Xu et al., 2006; Butler et al., 2008; however, see Sullivan, 2006; Bakker et al., 2006). Marginocephalia and Ornithopoda together comprise the node-based clade Cerapoda (Barrett et al., 2005; Butler et al., 2008).

The vast majority of pachycephalosaur material is known from the Late Cretaceous of North America and Mongolia (e.g. Gilmore, 1924; Maryańska and Osmólska, 1974; Sues and Galton, 1987; Sereno, 2000). In addition, four fragmentary and poorly known Late Cretaceous taxa from China have also been assigned to the clade: *Heishanosaurus pachycephalus* Bohlin, 1953, *Troodon bexelli* Bohlin, 1953, *Wannanosaurus yansiensis* Hou, 1977, and *Micropachycephalosaurus hongtuyanensis* Dong, 1978.

The holotype specimens of *Wannanosaurus yansiensis* and *Micropachycephalosaurus hongtuyanensis* comprise partial skeletons with cranial and postcranial material. Both have been proposed as basal members of the pachycephalosaurian clade (e.g. Sereno, 2000; Maryańska et al., 2004). Specimens of pachycephalosaurs preserving postcranial remains are rare; as a result the postcranial anatomy of the clade is poorly understood. Additionally, although no published cladistic analysis has to date refuted it, some authors consider the evidence for the monophyly of Marginocephalia to be weak due to the relatively small number of supporting characters (e.g. Dodson, 1990; Sereno, 2000; Sullivan, 2006; Bakker et al., 2006; but see: Xu et al., 2006; Butler et al., 2008). The detailed description of basal pachycephalosaurian taxa, particularly those with postcranial material, is a necessary precursor to further work on marginocephalian monophyly and pachycephalosaurian evolution.

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Previous descriptions of *Wannanosaurus* (Hou, 1977; Sereno, 2000) are limited by their lack of anatomical detail. *Micropachycephalosaurus* is described briefly in the literature (Dong, 1978), and some of the anatomical information provided therein is incorrect or cannot be confirmed (see below). Its validity, and status as a pachycephalosaur, has since been questioned (Sereno, 2000; Sullivan, 2003, 2006). A detailed redescription, rediagnosis, and discussion of the phylogenetic position of these two taxa is required and provided here.

The putative pachycephalosaurs '*Troodon*' *bexelli* and *Heishanosaurus pachycephalus* are not considered in this study, because the whereabouts of the fragmentary holotype specimens of these taxa is currently unknown (we were unable to locate them in the collections of IVPP, Beijing in March 2006; see also Sullivan, 2006). Discussion of their affinities by recent authors has been based upon the description and figures provided by Bohlin (1953). '*Troodon*' *bexelli* was considered to represent a new, unnamed, genus of pachycephalosaur by Maryańska (1990) and Maryańska et al. (2004), but a nomen dubium by Sullivan (2006). Sullivan (2006) reviewed the available evidence on the anatomy of *Heishanosaurus pachycephalus*, and suggested that it probably represents an indeterminate ankylosaur, rather than a pachycephalosaur.

Institutional acronyms: BMNH, The Natural History Museum, London, United Kingdom; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; SAM-PK, Iziko South African Museum, Cape Town, South Africa; UALVP, University of Alberta, Laboratory of Vertebrate Paleontology, Edmonton, Canada.

2. Systematic palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Cerapoda Cooper, 1985 (Sensu Barrett et al., 2005)

Micropachycephalosaurus hongtuyanensis Dong, 1978

Figs. 1–4

Revised diagnosis. Small-bodied cerapodan ornithischian distinguished by the presence of prominent anteroposteriorly extending midline grooves on the ventral surface of the centra of the posterior dorsal vertebrae. See Appendix 1 for discussion of the validity of characters previously used to diagnose *Micropachycephalosaurus hongtuyanensis*.

Holotype. IVPP V 5542, partial skull and skeleton (Dong, 1978: figs. 1, 2, pl. 1) including: left quadrate, partial tooth row with seven teeth preserved in original positions, partial tooth row with five alveoli (no teeth preserved), one loose tooth, partial basioccipital, centra of three posterior dorsal and two sacral vertebrae, associated with impressions of the neural spines of the posteriormost dorsal and four sacrals, four partial caudal vertebrae preserved in near articulation with associated chevrons, isolated centra of seven caudal vertebrae, one with a partial neural arch, isolated partial caudal neural arch, partial left ilium, left femur, and the proximal portion of the left tibia. Dong (1978) briefly described, but did not figure, a parietal and squamosal; however, no bone of the skull roof can be identified in the holotype specimen.

Occurrence. Wangshi Formation (Late Cretaceous: Campanian, Dong, 1978; Buffetaut and Tong, 1995; late Campanian, Sullivan, 2006). Laiyang, Shandong Province, People's Republic of China.

Description. The holotype of *Micropachycephalosaurus hongtuyanensis* is extremely fragmentary and poorly preserved. Nevertheless, a review of the material demonstrates characters that

allow a diagnosis of the taxon, and a discussion of its phylogenetic position.

Cranial skeleton. The left quadrate (Fig. 1A, C, D) is complete and preserved adjacent to one of the partial tooth rows. The lateral surface of the lateral wing of the quadrate is relatively well exposed although its anterior margin is broken and partially obscured ventrally by plaster, but the pterygoid wing is obscured by sediment, plaster and the tooth row. The anterior surface of the quadrate is completely unexposed. The quadrate is a slender, elongate bone, the ventral half of the shaft of which is near vertical in lateral view; dorsally the shaft curves posteriorly to form the transversely compressed head. The shaft undergoes torsion along its length, such that the transverse axis through the quadrate condyles is at approximately 45 degrees to the anteroposterior axis of the head. The lateral wing is concave anteroposteriorly, thickened at its anterior margin, and has an articulation surface for the quadratojugal ventrally, adjacent to the quadrate condyles. In ventral view the quadrate condyles (Fig. 1C) are anteroposteriorly compressed with a kidney-shaped cross-section, the long axis of which is transversely oriented. The anterior surface of the condyles is convex, whereas the posterior is concave. The distal surface of the condyles is convex, and lateral and medial condyles are only subtly divided from one another. The lateral quadrate condyle extends further distally than the medial condyle, and, when the quadrate is held vertically in posterior view, the articular surface slopes ventrolaterally at approximately 20 degrees to the horizontal.

The isolated basioccipital is broken anteroventrally and anterolaterally where it would have contacted the basisphenoid, as well as dorsally where it would have contacted the exoccipitals and possibly formed part of the margin of the foramen magnum. The occipital condyle is preserved (although its left lateral margin is broken) and has an ovoid shape in posterior view, broader transversely than dorsoventrally deep. The articular surface is convex transversely and dorsoventrally.

A fragment of a tooth row contains five alveoli. Two of these are empty; broken roots are present in the remaining three. Another partial tooth row (Fig. 1A, B, D, E; preserved adjacent to the quadrate) has been embedded in plaster, presumably during preparation, and only a small area of bone is exposed adjacent to the row. As a result, it is not possible to ascertain if this is the dentary (as identified by Dong (1978) and Maryańska (1990)) or the maxilla, or if it is exposed in medial or lateral view. Seven teeth are preserved in place, plus three empty alveoli, indicating that the preserved tooth count is 10, rather than nine as suggested by Dong (1978). In the rest of this description, numbers refer to tooth positions in the preserved portion of tooth row, beginning from the end of the tooth row closest to the head of the quadrate. 'Well exposed surface' refers to the surfaces of the crowns that are fully exposed; 'poorly exposed surface' refers to the surfaces of the crowns that are obscured by the pterygoid wing of the quadrate.

Adjacent teeth overlap each other as in all ornithischians. Dong (1978) identified a series of nutrient foramina below the tooth row. We are unable to identify definite nutrient foramina although a small opening is present below crown 5 and part of a tooth is exposed; however, it cannot be determined if it is a replacement crown (and the opening is a replacement foramina) or if it is the root of crown 5 (and the opening is merely a break in the alveolar margin).

Some crowns (1, 2, 10) are rather low and fan-like (Fig. 1B); other crowns are taller apicobasally relative to their mesiodistal width and more triangular in form (e.g. 4, 6; Fig. 1E). They lack recurvature, and the crown is weakly expanded labiolingually above the root on the well-exposed side, forming a weak basal 'cingulum'. The crown–root junction is not visible on the poorly exposed surface, so the presence of a comparable expansion cannot be ascertained. The crowns are set at an angle to the vertical axis of the roots, and

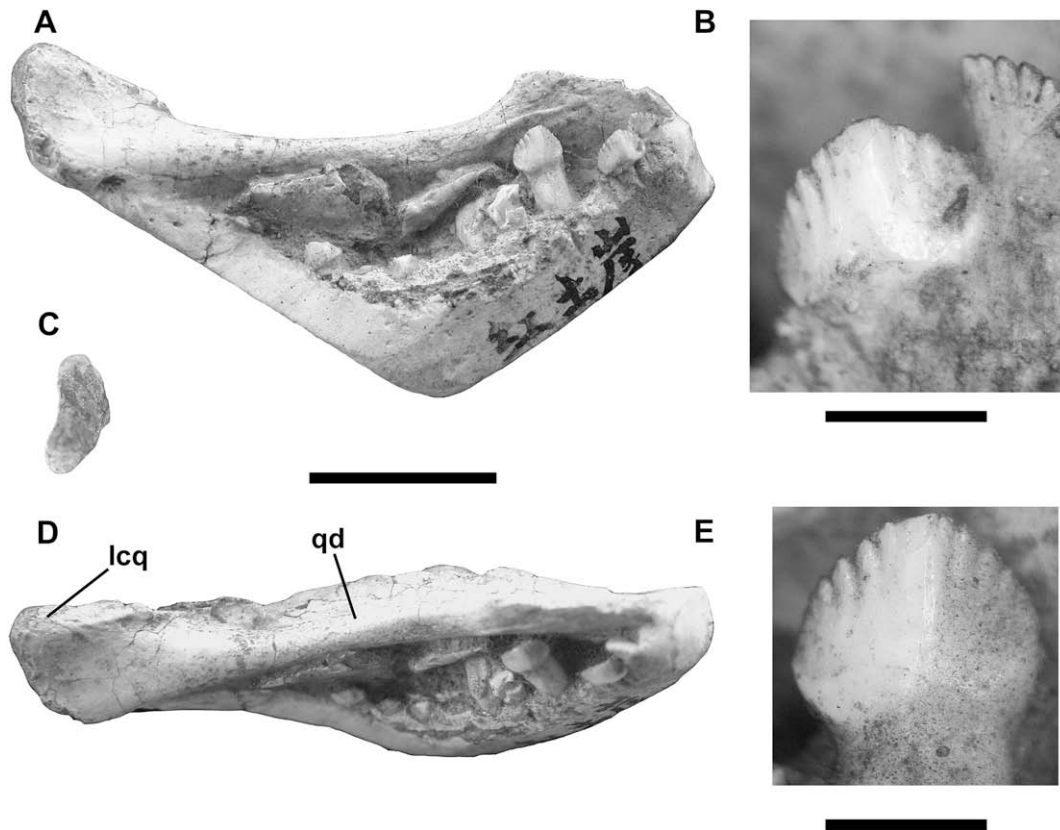


Fig. 1. *Micropachycephalosaurus hongtuyanensis*, left quadrate, fragment of dentary or maxillary tooth row, and dentary or maxillary teeth (IVPP V 5542, holotype). A, quadrate in posteromedial view; B, crowns 1 and 2, view of the well-exposed surface; C, quadrate condyles, distal view; D, quadrate in posterior view; E, crown 4, view of the well-exposed surface. Abbreviations: lcq, lateral condyle of quadrate; qd, quadrate. Scale bars equal 10 mm (A, C–D) and 2 mm (B, E).

enamel is present on both labial and lingual surfaces. The apices of the crowns are offset a short distance from the midline in lingual/labial view (although it is not possible to determine if this offset is in a mesial or distal direction). The well-exposed surface has a subtle apicobasally extending broad central eminence, ventral to the apex; mesial and distal to this a number of subtle secondary ridges extend onto the crown surface from the denticles. The well-exposed surface is flat to weakly concave on one side of the primary ridge and weakly convex on the other side. A series of denticles are developed along the mesial and distal margins of the crown; due to the offset of the apical denticle the number of denticles differs along mesial and distal surfaces. Around 4–5 denticles are present along the shorter surface, while 5–7 are present on the longer surface. The apical denticle is supported on the poorly exposed surface of the crowns by a broad apicobasally extending ridge, which basally expands mesiodistally. Mesial and distal to this ridge the crown surface is concave, and a number of apicobasally extending secondary ridges are present.

The teeth of *Micropachycephalosaurus* are similar to those of the pachycephalosaurs *Wannanosaurus yansiensis* (see below), *Goyocephale lattimorei* (Perle et al., 1982: pl. 42, figs. 8, 10, 11), and *Stegoceras valdium* (Lambe, 1902) (Sues and Galton, 1987: fig. 4D). In particular, at least some crowns in all of these taxa are low and fan-shaped, with mesiodistal lengths exceeding apicobasal heights. Basal cingula are weakly developed and a subtle primary ridge/central eminence is present, mesial and distal to which are weakly developed secondary ridges. However, with the possible exception of the low fan-shaped crown in labial view, all of these morphological features appear to represent plesiomorphies and are known in basal ceratopsians (psittacosaurids, e.g. Sereno, 1987) and basal ornithomorphs (e.g. *Orodromeus makelai* Horner and Weishampel, 1988; Scheetz, 1999).

Axial skeleton.—The centra of five vertebrae are preserved in close articulation in a block; impressions of neural spines, sacral ribs, and impressions and bone fragments of the left ilium are additionally present (Figs. 2A, B, 3). Dong (1978: fig. 1, pl. 1) identified these vertebrae as representing the fused sacrum, and suggested on the basis of additional neural spine impressions that six sacral vertebrae were present in *Micropachycephalosaurus*. The preservation of a prezygapophysis on the fourth vertebra (Fig. 2A: prz), and the posterodorsal slope of the neural spine impressions do not support the orientation of the vertebrae suggested by Dong (1978). The first three vertebrae (previously identified as sacra 3–5, Dong, 1978) are posterior dorsals. The succeeding two centra represent sacra 1–2, with the presence of at least two more sacra demonstrated by neural spine impressions. A large sacral rib is present between the first and second sacra on the left-hand side and distally contacts the pubic peduncle of the left ilium (Figs. 2B, 3: sr2). This indicates that the posterior dorsals, sacra and left ilium are preserved in articulation.

Dong (1978) suggested that the preserved centra were fused to each other. The centra of sacra one and two are completely fused, such that the suture between them cannot be readily distinguished. Sediment is present laterally between the centrum of the posteriormost dorsal and the first sacral; additionally the neural spines and zygapophyses of these vertebrae appear to be widely separated. Thus fusion cannot be confirmed between the most posterior dorsal and the first sacral. The centra of the three dorsals are fused to one another, but the boundaries between the centra remain visible.

The posterior dorsal centra are autapomorphic for *Micropachycephalosaurus*. The centra of the posterior dorsals are spool-shaped, with a smoothly rounded ventral margin, in basal ornithomorphs (e.g. *Lesothosaurus diagnosticus* Galton, 1978: BMNH RUB17; *Stormbergia dangershoeki* Butler, 2005: SAM-PK-K1105; *Hexinlusaurus*

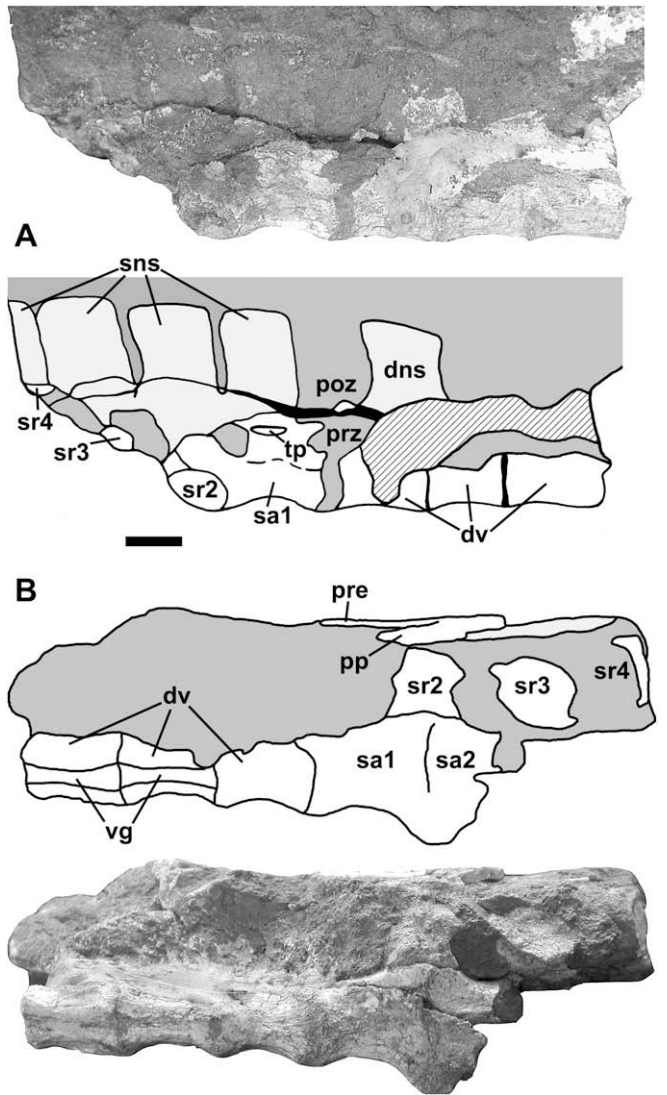


Fig. 2. *Micropachycephalosaurus hongtuyanensis*, posterior dorsals, anterior sacra, and ilium (IVPP V 5542, holotype). A, right lateral view; B, ventral view. Dark grey fill represents sediment, light grey fill represents bone impressions on sediment, cross-hatched fill represents area of artificial fill. Abbreviations: dns, neural spine of sacral vertebra; dv, dorsal vertebra; poz, postzygapophysis; pp, pubic peduncle of ilium; pre, preacetabular process of ilium; prz, prezygapophysis; sa1, sa2, sacral vertebrae; sns, neural spine of sacral vertebra; sr, sr2, sr3, sr4, sacral ribs; tp, transverse process; vg, ventral groove. Scale bar equals 10 mm.

multidens (He and Cai, 1983; He and Cai, 1984), ornithopods (e.g. *Hypsilophodon foxii* Huxley, 1869; Galton, 1974: fig. 22; *Orodromeus makelai*, Scheetz, 1999; *Zalmoxes robustus*, Weishampel et al., 2003: figs. 16–17), pachycephalosaurs (e.g. *Homalocephale calathocercos* Maryańska and Osmólska, 1974; Maryańska and Osmólska, 1974: fig. 5A2; *Stegoceras validum*, Sues and Galton, 1987: fig. 8) and ceratopsians (e.g. *Psittacosaurus* Osborn, 1923; Sereno, 1987; *Archaeoceratops oshimai* Dong and Azuma, 1997; You and Dodson, 2003: fig. 2). By contrast, in *Micropachycephalosaurus* a wide groove is present on the ventral margin of the two most anterior of the three preserved dorsal vertebrae (Dong, 1978: fig. 1; Fig. 2B: vg). This groove superficially resembles that present in the posterior sacral centra of some ceratopsian taxa (e.g. *Archaeoceratops oshimai*, IVPP V 11114) and may explain their misidentification in the original description (Dong, 1978), but, as noted above, numerous features indicate that these are indeed dorsals.

Sacral one is complete; however, only the anterior portion of the second sacral centrum is preserved. The sacral centra are expanded

such that their mediolateral width is greater than their dorsoventral height. A robust sacral rib is attached low on the junction between sacra one and two (Figs. 2A, B, 3: sr2). For comparison with the equivalent sacral rib in pachycephalosaurs (see below) this sacral rib is here referred to as sacral rib two. As noted above, laterally sacral rib two contacted the distal end of the pubic peduncle of the ilium. A complete neural arch, including pre- and postzygapophyses, is preserved on sacral one, but the transverse process is broken at its base and it is not known whether the rib of this sacral contacted the medial surface of the preacetabular process of the ilium. Impressions of the neural spines of four sacra are preserved.

Fragments of the third and fourth sacral ribs can be identified (Figs. 2A, B, 3: sr3, sr4). Sacral rib three arose from the boundary between sacra two and three, and appears to have contacted the ilium just medial to the acetabulum. The fourth sacral rib apparently contacted the ilium medial to the ischiadic peduncle.

The sacrum of pachycephalosaurs is best preserved in *Homalocephale* (Maryańska and Osmólska, 1974). In this taxon the sacrum consists of six fused vertebrae. The first sacral rib is fused to the diapophysis of the first sacral vertebra, and contacts the medial surface of the preacetabular process. The second sacral rib is fused intervertebrally between the centra of sacra one and two, and is directed posteriorly, contacting the distal end of the pubic peduncle of the ilium. Sacral rib three is placed on the anterior part of sacral three and is directed anteriorly, converging on sacral rib two and also contacting the pubic peduncle. Sacral rib four is slightly anteriorly directed and contacts the ilium medial to the ischiadic peduncle. In *Goyocephale* the sacrum is composed of only four vertebrae (Perle et al., 1982). The second sacral rib is incomplete, but originates between the first and second sacral vertebrae and appears to be posteriorly directed, presumably contacting the pubic peduncle of the ilium. The third sacral rib is also posteriorly directed. This suggests that, unlike the situation in *Homalocephale* the second and third sacral ribs did not converge upon one another distally, and the third sacral rib may not have contacted the pubic peduncle.

The sacrum of *Micropachycephalosaurus* is poorly preserved and difficult to interpret. However, unlike the situation in both *Goyocephale* and *Homalocephale* the second sacral rib appears to be directed laterally rather than posteriorly, and unlike the situation in *Homalocephale* (although probably not *Goyocephale*) only one sacral rib appears to have contacted the pubic peduncle of the ilium.

Dong (1978) briefly described a block containing semi-articulated caudal vertebrae. He noted the presence of three caudals in this block; a fourth is also present in the original figure (Dong, 1978: pl. 1, fig. 3). Neural spines and zygapophyses are not preserved in any of these vertebrae. The relatively elongate centra and low neural arches suggest these are probably mid-caudals, rather than anterior caudals as suggested by Dong (1978). The centra have gently excavated lateral faces that are concave anteroposteriorly and dorsoventrally, and weakly concave shield-shaped articular surfaces, with prominent facets for the chevrons. The preserved caudal ribs are nearly equal in length to the centra, and are directed upwards at an angle of about 20 degrees to the horizontal. In *Homalocephale* (Maryańska and Osmólska, 1974) the caudal ribs are notably elongate but are only present on the anterior eight caudals, and are absent from the mid caudal region. Caudal ribs are also absent from the mid caudal region of *Stegoceras validum* (Sues and Galton, 1987). Five chevrons preserved on the same block are unexpanded at their distal ends. Seven isolated centra also appear to be from the mid-caudal region, and their morphology is similar to those already described.

A 'basketwork' arrangement of fusiform ossified tendons surrounds the mid and posterior caudals of *Homalocephale* (Maryańska and Osmólska, 1974) and other pachycephalosaurs (Goodwin et al., 1998; Sereno, 2000). Similar fusiform tendons have been reported

for *Micropachycephalosaurus* (Maryańska et al., 2004: p. 471; ossified tendons were mentioned by Maryańska [1990: p. 575] but she did not state whether they were fusiform or not); however, these are not present on the preserved caudals, could not be located elsewhere amongst the holotype material, were not mentioned by Dong (1978), and have not been figured or described by Dong (1978) or Maryańska et al. (2004).

Appendicular skeleton. The partial left ilium is preserved in articulation with the sacrum (Figs. 2B, 3). Only a small amount of bone is preserved, representing the short pubic peduncle and the proximal 50% of the preacetabular process. However, impressions on the sediment surface allow the recognition of the morphology of the ilium anterior to the base of the ischiadic peduncle. No information is available on the morphology of the ischiadic peduncle or the postacetabular process. Dong (1978: fig. 2) reconstructed the ilium with an unusually small, posteriorly projecting ischiadic peduncle and an elongate postacetabular process; this reconstruction is not supported by the available material. The preacetabular process of the ilium is elongate and curves gently anteroventrally but only slightly laterally. In the pachycephalosaurs *Goyocephale* (Perle et al., 1982), *Homalocephale* (Maryańska and Osmólska, 1974) and *Stegoceras validum* (Sues and Galton, 1987), the dorsal margin of the preacetabular process is expanded transversely to form a horizontal shelf which anteriorly expands in transverse width. This transverse expansion extends along the entire preacetabular process, and continues posterior to the pubic peduncle. By contrast, the dorsal margin of the ilium of *Micropachycephalosaurus* is clearly unexpanded transversely along the proximal 50% of the preacetabular process. The preacetabular process is represented by a natural impression further anteriorly, obscuring any evidence for transverse expansion of the dorsal margin of the ilium. If such expansion was present it must have been limited to the anterior 50% of the preacetabular process. The acetabular margin is incomplete and there is no evidence for the well-developed supraacetabular flange of basal ornithischians (e.g. Thulborn, 1972).

The head of the left femur (Fig. 4A–F) is incomplete medially and the proximal portion of the anterior trochanter is missing. The edge of the fourth trochanter is incomplete, and its original shape cannot be determined. At the distal end of the bone, the medial condyle is badly damaged anteriorly and posteriorly. Sediment obscures the posterior portion of the lateral condyle (Fig. 4D). The shaft is bowed anteriorly in lateral view and is straight in posterior view. The

femoral head is well offset from the shaft and directed strongly dorsomedially above the level of the proximal trochanters. In proximal view (Fig. 4C) the anterior margin of the head is weakly concave, and the posterior margin is slightly convex but lacks a well-defined medial tuber or ligament sulcus (Novas, 1996). The inturned medial part of the femoral head is separated from the proximal trochanters by a prominent constriction, the fossa trochanteris (Langer, 2003), in anterior or posterior view.

In proximal and lateral views (Fig. 4A, C), the fan-shaped greater trochanter is expanded anteroposteriorly, so that it is much wider than the anterior trochanter. The anterior trochanter is set anterior and lateral to the greater trochanter and is separated from the greater trochanter by a low proximodistally extending ridge on the lateral surface. A second low proximodistally extending ridge is present on the posterolateral surface of the greater trochanter. A similar ridge in *Hypsilophodon foxii* was hypothesised as separating the attachment sites of *M. pubo-ischiofemoralis internus* from *M. ilio-trochantericus* (Galton, 1969, 1974). Distally this ridge continues down the posterolateral surface of the shaft to a point at approximately 60% of shaft length where the ridge bifurcates. One branch continues along the posterolateral surface and merges with the shaft at a point at approximately 80% of shaft length, and the other shifts onto the posterior surface of the shaft and connects to the fibular condyle. Langer (2003) identified an intermuscular ridge in an equivalent position on the femur of the basal sauropodomorph *Saturnalia tupiniquim* and referred to it as the ‘caudolateral line’. As in *Saturnalia* (Langer, 2003), two other longitudinal intermuscular ridges are present on the surface of the femoral shaft of *Micropachycephalosaurus*: the first extends along the anterior margin of the shaft, from the anterior trochanter to the anterior surface of the distal end (the ‘cranial line’ of Langer, 2003); the second is subtle and extends along the posterior surface from the base of the fourth trochanter towards the medial condyle (the ‘caudomedial line’ of Langer, 2003).

The fourth trochanter is situated entirely on the proximal half of the shaft, but is broken so its complete morphology cannot be ascertained. The surface of the shaft is depressed and concave anterior to the base of the fourth trochanter, forming a shallow fossa bounded anteriorly by a low ridge (Fig. 4F: cfl). This fossa represents the attachment of *M. caudofemoralis longus*. The posterior intercondylar groove of the distal end is broad and open. The presence or absence of an anterior intercondylar groove cannot be determined, due to the broken medial condyle.

The proximal half of the left tibia is expanded anteroposteriorly and compressed transversely. A prominent cnemial crest (Fig. 4G–I: cnc) projects strongly anterodorsally and weakly laterally. As a result of this anterodorsal projection the proximal articular surface slopes posteroventrally in lateral view. A ridge extends along the anterior margin of the shaft from the anterolateral corner of the cnemial crest. This ridge moves onto the anteromedial surface of the shaft and remains prominent along the preserved length of shaft distally. The cnemial crest is separated from the fibular condyle by a well-developed insisura tibialis (Fig. 4H: in). The fibular condyle is quadrangular in proximal view and supported distally by a subtle ridge which extends proximodistally along the lateral surface of the shaft. A small knob-like projection on the anterolateral surface of the fibular condyle (Fig. 4H: acc) may represent the accessory condyle present between the fibular condyle and the cnemial crest in other ornithischians (e.g. *Lesothosaurus diagnosticus*, Thulborn, 1972). A deep broad notch separates the fibular and inner condyles (Fig. 4H: int nt). The lateral surface of the tibia is concave below this notch. The inner condyle is supported by a narrow ridge, which extends distally along the posterior margin of the shaft. The medial surface of the proximal end is convex proximally, but flattened more distally. The shaft has a sub-triangular cross-section, with the rounded apices formed by the

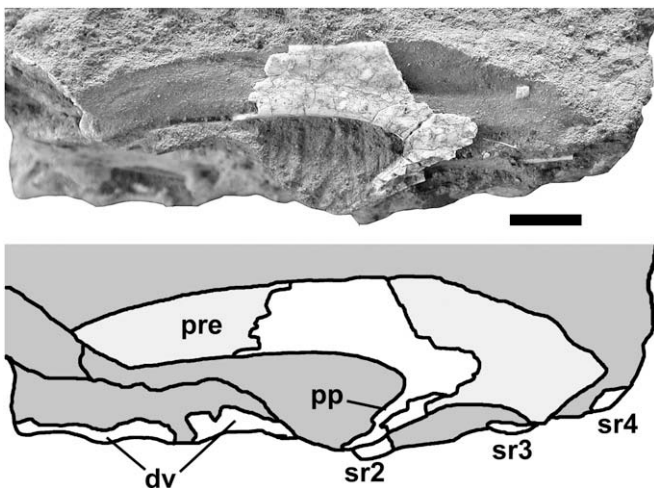


Fig. 3. *Micropachycephalosaurus hongtuyanensis*, left ilium, lateral view (IVPP V 5542, holotype). Dark grey fill represents sediment, light grey fill represents bone impressions on sediment. Abbreviations: dv, dorsal vertebrae; pp, pubic peduncle of ilium; pre, preacetabular process of ilium; sr1, sr2, sr3, sacral ribs. Scale bar equals 10 mm.

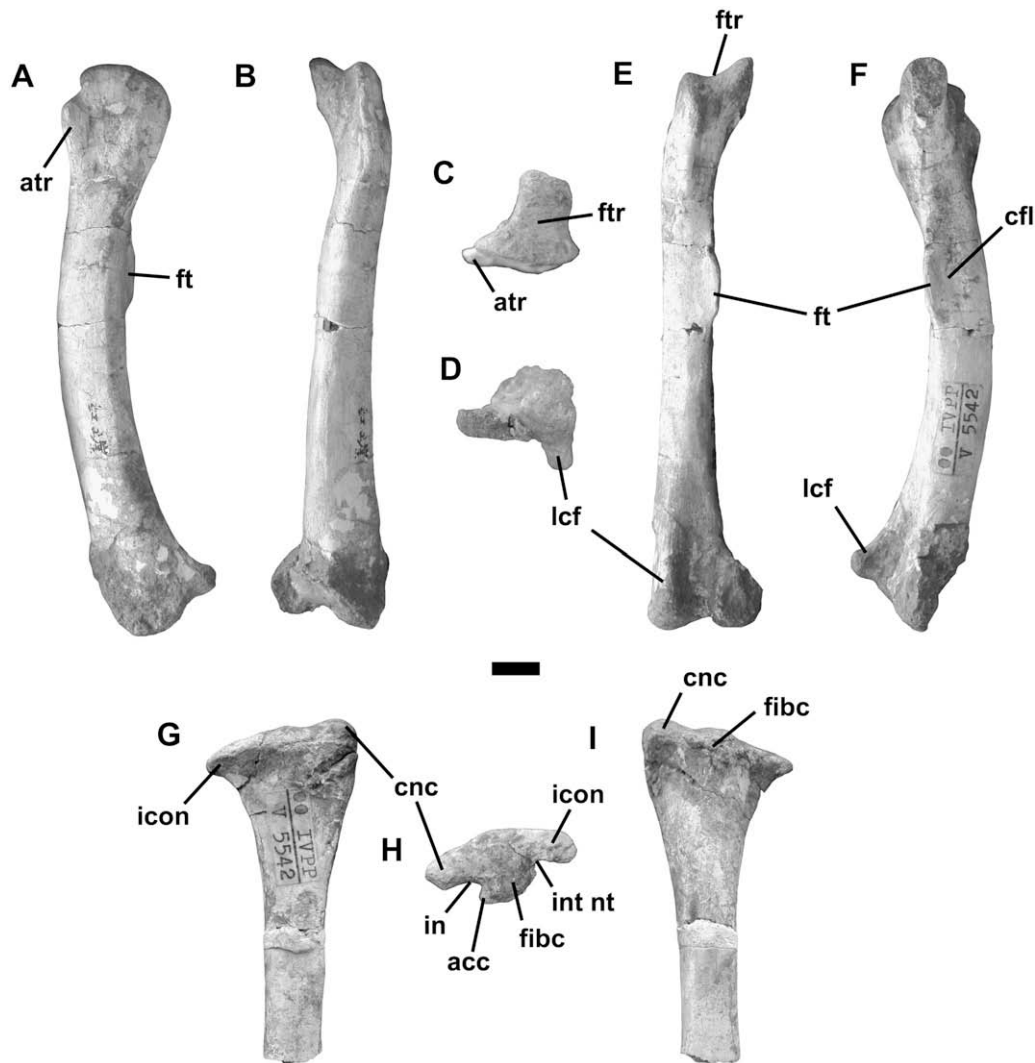


Fig. 4. *Micropachycephalosaurus hongtuyanensis*, hind limb elements (IVPP V 5542, holotype). A–F, left femur in: A, lateral; B, anterior; C, proximal; D, distal; and F, medial views; G–I, left tibia in: G, medial; H, proximal; and I, lateral views. Abbreviations: acc, accessory condyle of proximal tibia; atr, anterior trochanter; cfl, fossa for *M. caudofemoralis longus*; cnc, cnemial crest; fibc, fibular condyle; ft, fourth trochanter; ftr, fossa trochanteris on proximal surface between proximal trochanters and femoral head; icon, inner condyle of proximal tibia; in, insisura tibialis; int nt, intercondylar notch; lcf, lateral condyle of distal femur. Scale bar equals 10 mm.

ridges descending distally from the cnemial crest and fibular and inner condyles.

Size. Dong (1978) estimated *Micropachycephalosaurus* as 50–60 cm in length, making it one of the smallest non-avian dinosaurs, and probably the smallest known ornithischian. However, the femur of *Micropachycephalosaurus* is longer (121 mm) than that of the basal thyreophoran *Scutellosaurus lawleri* Colbert, 1981 (93.2–114 mm, Colbert, 1981), the basal ornithischian *Lesothosaurus diagnosticus* (104 mm, Thulborn, 1972) and the heterodontosaurid *Heterodontosaurus tucki* Crompton and Charig, 1962 (112 mm, Santa Luca, 1980). All of these taxa reached around a metre in length, and it seems reasonable to infer, from its longer femoral length, that *Micropachycephalosaurus* would have slightly exceeded these taxa in length.

Phylogenetic position. *Micropachycephalosaurus hongtuyanensis* was originally considered (Dong, 1978; Perle et al., 1982; Sues and Galton, 1987) to represent a member of Homalocephalidae, a family of ‘flat-headed’ pachycephalosaurs, also comprising *Homalocephale*, *Goyocephale* and *Wannanosaurus*. In recent studies Homalocephalidae is considered a paraphyletic grade of basal

pachycephalosaurian taxa (Sereno, 1986, 1999, 2000; Williamson and Carr, 2002; Sullivan, 2003; Maryańska et al., 2004; Butler et al., 2008; see below). Although *Micropachycephalosaurus* is regarded as a basal member of Pachycephalosauria by Maryańska (1990) and Maryańska et al. (2004), others (Sereno, 2000; Sullivan, 2006) consider this taxon a nomen dubium. Sereno (2000) excluded it from the pachycephalosaurian clade.

The phylogenetic position of *Micropachycephalosaurus* within Ornithischia remains questionable, due to the highly fragmentary and poorly preserved nature of the holotype. As noted by Sereno (2000), unequivocal pachycephalosaur synapomorphies cannot be identified from the available material. The thickened skull roof reported by Dong (1978) cannot be confirmed. Furthermore, the pattern of sacral ribs shows minor differences from that of known pachycephalosaurs (see above), elongate caudal ribs occur on mid caudal vertebrae (but are absent from mid caudal vertebrae of known pachycephalosaurs), the preserved fragments of the pre-acetabular process of the ilium lack the transverse expansion of the dorsal margin (present in pachycephalosaurs), and the fourth trochanter is set rather proximally on the femur compared to the condition in *Wannanosaurus* and *Homalocephale* (Maryańska et al., 2004: fig. 21.4j). Due to the paucity of postcranial material known

for most pachycephalosaurs, the phylogenetic significance of these differences remains difficult to determine. We have not been able to confirm the presence of fusiform ossified tendons reported by Maryńska et al. (2004) in the holotype; the presence of fusiform tendons would provide strong support for a pachycephalosaurian identity. The low fan-like shape of the cheek crowns (mesiodistal length exceeds apicobasal height in at least some crowns) is the only character that we are able to identify that might link *Micropachycephalosaurus* with pachycephalosaurs.

Butler et al. (2008) carried out a large-scale (46 taxa, 221 characters) phylogenetic analysis of Ornithischia, and included *Micropachycephalosaurus* as a terminal taxon. In the strict consensus of the 756 most parsimonious trees (MPTs) recovered by the analysis *Micropachycephalosaurus* grouped with basal ceratopsians rather than pachycephalosaurs; this phylogenetic position was supported by the presence in *Micropachycephalosaurus* and basal ceratopsians of a lateral quadrate condyle that is enlarged relative to the medial condyle. However, this character is subject to a high degree of homoplasy and statistical support for this phylogenetic position is exceedingly weak. In suboptimal trees *Micropachycephalosaurus* acted as a 'wildcard' taxon, destabilising relationships amongst basal members of the clade Cerapoda (pachycephalosaurs, ceratopsians, ornithopods) and resulting in reduced bootstrap support and decay indices for a number of ornithischian clades. Butler et al. (2008) concluded that a cerapodan identity is supported by femoral characters (anteroposterior expansion of the greater trochanter; fossa trochanteris forms a distinct constriction separating the head and trochanters; Sereno, 1986, 1999; Butler et al., 2008), but that the position of *Micropachycephalosaurus* within Cerapoda cannot be clarified with any certainty.

In summary, we currently consider the position of *Micropachycephalosaurus* within Cerapoda as unresolved, although we acknowledge the possibility that future discoveries of new specimens and/or rediscovery of missing portions (skull roof, ossified tendons) of the holotype specimen may support referral of this taxon to Pachycephalosauria.

Ornithischia Seeley, 1887

Cerapoda Cooper, 1985 (Sensu Barrett et al., 2005)

Pachycephalosauria Maryńska and Osmólska, 1974

Wannanosaurus yansiensis Hou, 1977

Figs. 5–8

Revised diagnosis. Pachycephalosaur distinguished by the extreme flexure of the humerus in anterior/posterior and lateral views. In anterior/posterior view, the humerus is flexed strongly laterally along its length, and the proximal and distal ends are set at approximately 30 degrees to one another (Sereno, 2000). In lateral view the proximal end of the humeral shaft is flexed strongly posteriorly, at an angle of around 50 degrees to the distal shaft. See Appendix 2 for discussion of characters previously used to diagnose *Wannanosaurus*.

Holotype. IVPP V 4447, fragmentary skeleton (Hou, 1977: fig. 1, pl. 1, pl. 2, figs. 1–2; Sereno, 2000: fig. 25.1). Cranial material includes the left postorbital, squamosal and jugal, an articulated portion of the right posterior skull roof including the right frontal, posterior supraorbital, postorbital, squamosal, and paroccipital process, with fragments of the parietal, supraoccipital and right ?laterosphenoid and quadrate, left dentary, coronoid, angular and surangular. Postcranial material includes an anterior cervical vertebra, right humerus, partial femora, and a right tibia. Hou (1977) additionally listed a portion of an ilium (Hou, 1977: pl. 2, fig. 2); the whereabouts of this material is currently unknown.

Paratype. IVPP V 4447.1, caudal vertebra, fragment of ilium, femora, left tibia and fibula (Hou, 1977: pl. 2, figs 3–6). Hou (1977) additionally listed six caudal vertebrae (Hou, 1977: pl. 2, fig. 5) and a partial right pes (Hou, 1977: pl. 2, fig. 6); the whereabouts of this material is currently unknown.

Occurrence. Red sandstones of the upper member of the Xiaoyan Formation (Late Cretaceous: Campanian, Chen and Chang, 1994; ?early Maastrichtian, Sullivan, 2006). Yansi, Shexian County, Anhui Province, People's Republic of China.

Description. As noted above, the location of some of the material comprising the holotype and paratype specimens of *Wannanosaurus*, as described by Hou (1977), was unknown at the time of writing. Anatomical discussion of this unavailable material is thus based on the description and figures of Hou (1977) and not on first-hand examination.

Cranial skeleton. The holotype specimen of *Wannanosaurus* (IVPP V 4447) includes a partial skull (Figs. 5–7). Hou (1977) described an articulated portion of the right posterior skull roof (Fig. 5A–D), which was also figured by Sereno (2000: fig. 25.1A, B). Hou (1977) additionally briefly mentioned the presence of three bones belonging to the left side of the skull: the left squamosal, postorbital (Hou, 1977: pl. 1, fig. 2) and jugal (Hou, 1977: pl. 1, fig. 3). Although not noted by Hou (1977) or Sereno (2000), these three bones are relatively complete and articulate with each other (Fig. 6A, G), allowing a more complete reconstruction of the lateral skull. At least some cranial sutures were open in IVPP V 4447, leading to the suggestion that the specimen represents a juvenile or subadult individual (Sereno, 2000). Although cranial sutures appear to be fused on the right side of the skull (Perle et al., 1982), it is possible for cranial sutural contacts in pachycephalosaurs to remain open internally although they may be difficult to trace on the external surface (Goodwin et al., 2004).

Many of the bones of the flat skull table are poorly preserved and sutures are unclear (Fig. 5A–D), except in the case of the squamosal–postorbital and parietal–frontal contacts. Much of the surface of the skull roof is covered with a series of low nodes, a possible juvenile character, the pattern of which is generally irregular, except for the low but distinct postorbital–squamosal row (most clearly preserved on the disarticulated left side). The partial right frontal is thickened relative to the condition in pachycephalosaurian outgroups and contacts a fragment of the parietal posteriorly. Laterally, the suture with the posterior supraorbital cannot be identified. Sereno (2000) identified anterolateral and anterior sutural surfaces for the anterior supraorbital and the prefrontal; however, we cannot confirm the position of these sutures. Although sutures defining its margins cannot be identified, the posterior supraorbital is probably present on the right side (Fig. 5A, C: pso): the extensive sutural surface present on the left postorbital (see below) suggests that this element was substantially overlapped laterally by the posterior supraorbital.

The isolated left postorbital is complete (Fig. 6C, D, G). The right postorbital is preserved in articulation with the posterior supraorbital and the squamosal (Fig. 5A–D: po) and lacks a descending process. The dorsal portion of the postorbital contributes to the skull roof, contacts the posterior supraorbital anteriorly, forms the anterolateral margin of the supratemporal fenestra, contacts the frontal medially, and overlaps the squamosal posteriorly. The suture for the frontal is a dorsoventrally deep and dorsomedially facing, with a complex surface of depressed and raised areas. It is visible in anterior and medial views of the postorbital (Fig. 6D: fr). Lateral to this surface, the anterolateral surface of the postorbital is broadly depressed where it is overlapped by the posterior supraorbital (Fig. 6C: so). This suture is relatively complex. The dorsal

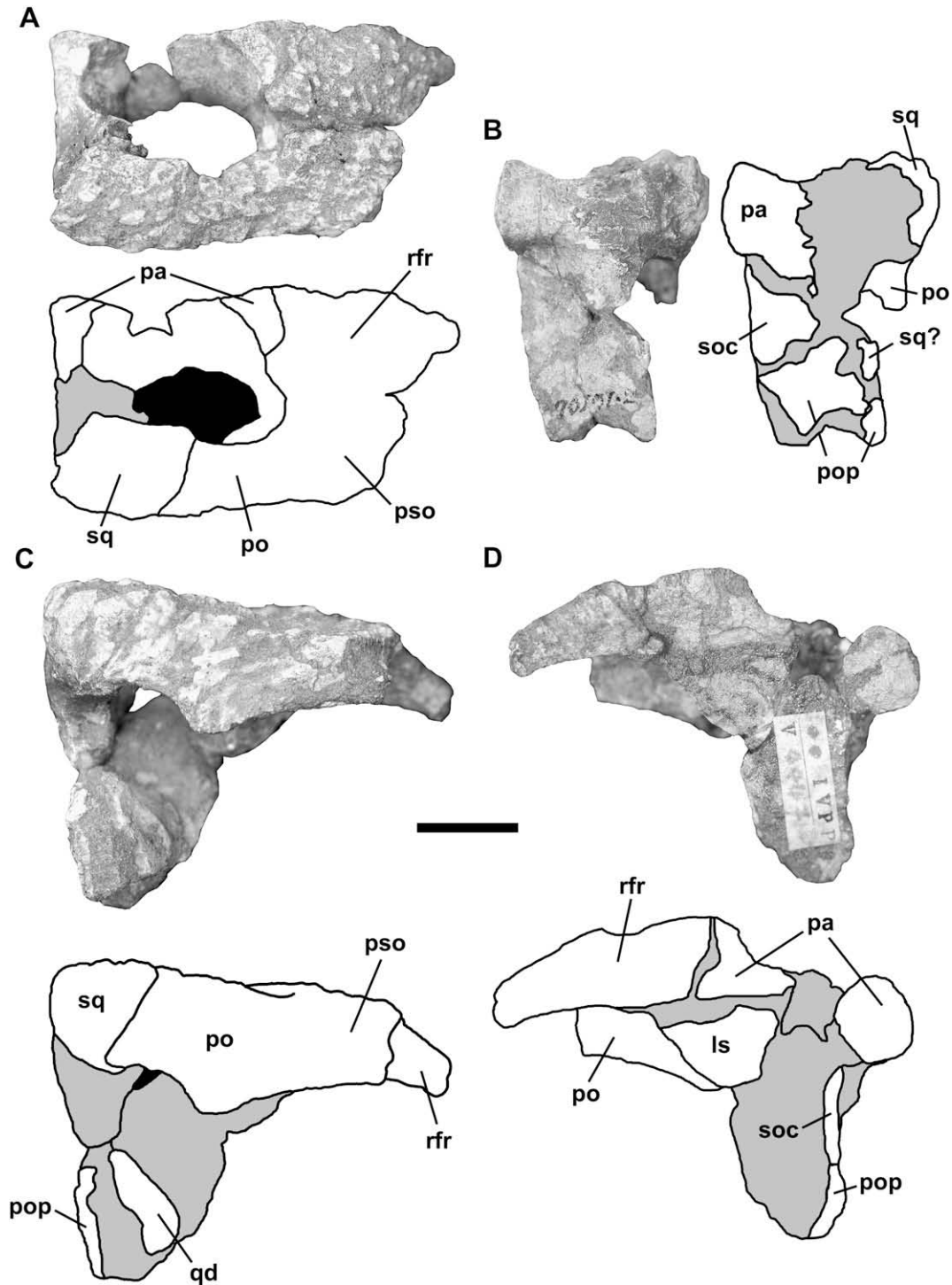


Fig. 5. *Wannanosaurus yansiensis*, articulated portion of right skull roof (IVPP V 4447, holotype) in: A, dorsal; B, posterior; C, lateral; and D, medial views. Abbreviations: ls, laterosphenoid; pa, parietal; po, postorbital; pop, paroccipital process; pso, posterior supraorbital; qd, quadrate; rfr, right frontal; soc, supraoccipital; sq, squamosal. Scale bar equals 10 mm.

part of this sutural surface is strongly depressed, concave, and presumably accommodates a ridge on the ventromedial surface of the supraorbital. A second concave depression is positioned ventral to the first. A broad, low convex ridge separates these surfaces, presumably corresponding to a groove on the ventromedial surface of the posterior supraorbital. The contact between the postorbital and squamosal is short, broad and robust (Fig. 6D, E, G). Dorsomedially the postorbital forms a butt joint with the squamosal, and ventrolaterally the posterior process of the postorbital overlaps the

anterior process of the squamosal (see below). The descending process of the postorbital is rather narrow anteroposteriorly compared to more derived pachycephalosaurs (cf. *Prenocephale prenes* Maryńska and Osmólska, 1974; Sereno, 2000: fig. 25.2) and is nearly square in cross-section. This descending postorbital process undergoes torsion along its length, causing the external surface to face slightly anterolaterally, rather than strictly laterally. The block-like distal end forms a short, broad, robust joint with the jugal, and overlaps the dorsal process of that bone anteriorly. The postorbital

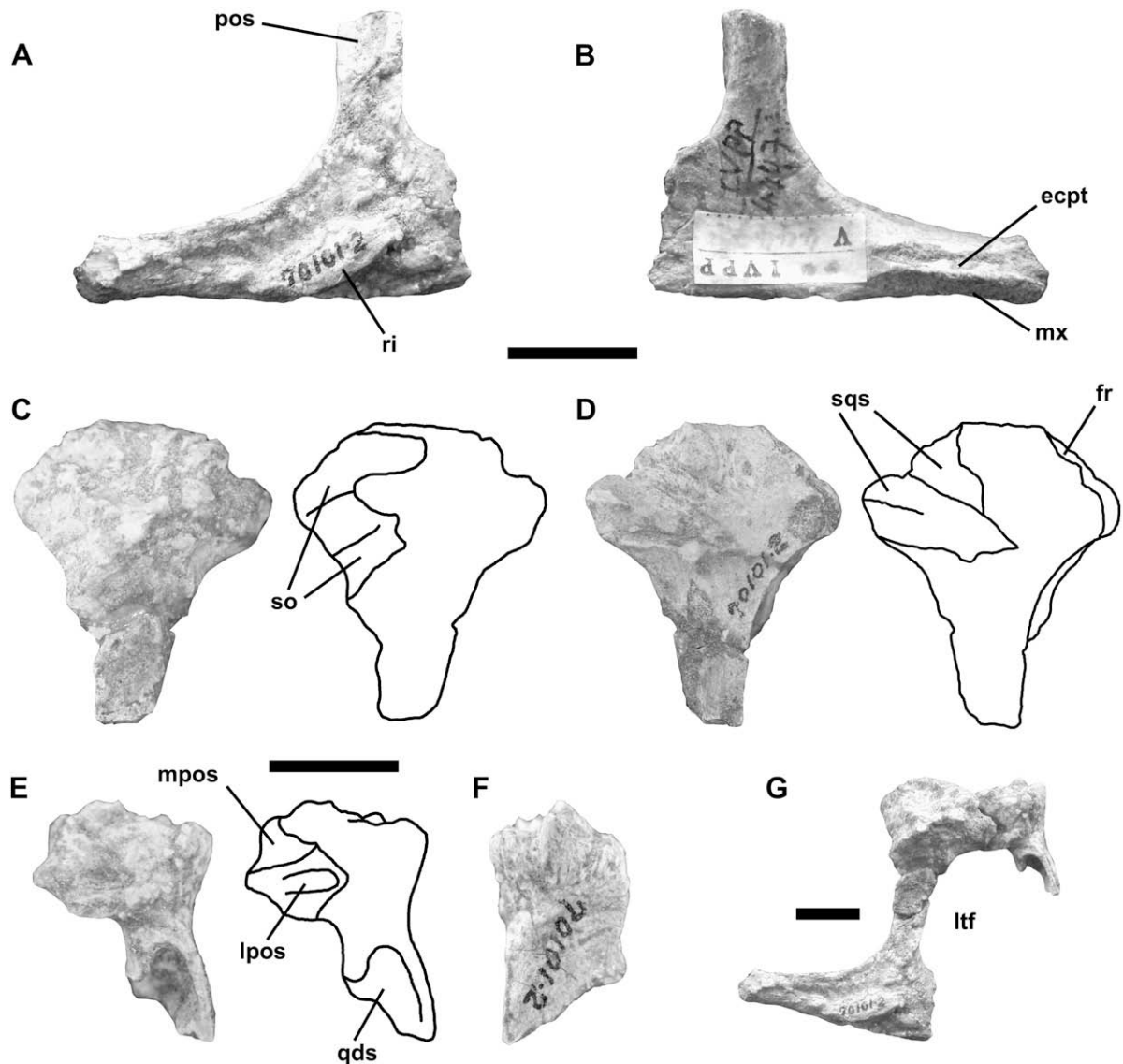


Fig. 6. *Wannanosaurus yansiensis*, left cranial elements (IVPP V 4447, holotype). A–B, jugal in: A, lateral; and B, medial views. C–D, postorbital in: C, lateral; and D, medial views. E–F, squamosal in: E, lateral; and F, posterior views. G, jugal, postorbital and squamosal in articulation, lateral view. Abbreviations: ecpt, surface on jugal for ectopterygoid; fr, surface on postorbital for frontal; lpos, lateral surface on the squamosal for the postorbital; ltf, laterotemporal fenestra; mpos, medial surface on squamosal for the postorbital; mx, surface on jugal for maxilla; pos, surface on jugal for postorbital; qds, socket for head of quadrate; ri, ridge on lateral surface of jugal; so, surface on postorbital for supraorbital; sqs, surfaces on postorbital for squamosal. Scale bars equal 10 mm.

formed a short portion of the smoothly curved posterodorsal margin of the orbit.

The isolated left squamosal is relatively complete (Fig. 6E–G), although the anteroventral part of the anterior process is broken. Fragments of the right squamosal articulate with the right postorbital. Two surfaces on the broad anterior process of the squamosal articulate with the postorbital. The medial surface is concave and faces anteriorly forming a butt joint with the postorbital (Fig. 6E: mpos). The lateral surface faces laterally and bears an anteroposteriorly extending concave groove into which a ridge on the medial surface of the postorbital fits (Fig. 6E: lpos). The ventral process of the squamosal forms a narrow socket for the head of the quadrate laterally (Fig. 6E: qds). On the occiput the squamosal is broadly exposed, contacts the paroccipital process ventrally and forms a dorsoventrally extensive butt joint with the parietal medially. Two small tubercles on the postorbital, above the postorbital–jugal bar, and five low nodes on the squamosal form the postorbital–squamosal tubercle row. This row of ornaments extends posteriorly along the postorbital–squamosal bar. Two larger

posterodorsally directed nodes are present on the posterolateral corner of the right squamosal. The squamosal and parietal, only fragments of which are preserved, form a shelf overhanging the occipital region (Fig. 5D), as in nearly all marginocephalians, with the exception of *Yinlong downsii* (Sereno, 2000; Xu et al., 2006).

The triradiate left jugal (Fig. 6A, B) is relatively complete, except for a broken posterior process. Its lateral surface is irregular and roughened, with low nodes, similar to those seen in other pachycephalosaurs such as *Prenocephale prenes* and *Stegoceras validus* (e.g. Sereno, 2000: figs. 25.2, 25.3) and in some outgroups (e.g. *Yinlong downsii*, Xu et al., 2006; *Archaeoceratops oshimai*, You and Dodson, 2003: fig. 1). A low, elongate, anteroventrally inclined ridge is present beneath the dorsal process (Fig. 6A: ri). This ridge does not closely resemble the distinct jugal boss located in a similar position in the heterodontosaurid *Heterodontosaurus tucki* and the ornithomids *Orodromeus makelai* and *Zephyrosaurus schaffi* Sues, 1980 (Norman et al., 2004), or the lateral extension of the jugal seen in ceratopsians (You and Dodson, 2004). The anterior process of the jugal is slender and its lateral surface is dorsoventrally concave. In

dorsal view, the anterior process of the jugal transversely expands below the orbit. This expansion is formed by two medially directed flanges of bone: the relatively narrower dorsal flange is separated from the wider ventral flange by an elongate shallow groove. This groove likely represents a surface for the attachment of the ectopterygoid (Fig. 6B: ecpt). A second sutural surface ventral to both flanges is probably the surface for receiving the maxilla (Fig. 6B: mx). The broken posterior process of the jugal is dorsoventrally deep and forms the anteroventral corner of the infra-temporal fenestra.

A small fragment of the pterygoid wing of the right quadrate is preserved ventral to the right squamosal. Sereno (2000: fig. 25.1A) identified this element with a question mark. The pterygoid wing approaches an unidentified portion of the right lateral wall of the braincase (Fig. 5C: qd).

Few bones of the occiput and braincase are preserved. The right paroccipital process is partially preserved, but few details of its morphology can be ascertained (Fig. 5B: pop). Dorsomedial to the paroccipital process, a concave area of bone probably represents a portion of the supraoccipital (Fig. 5B: soc). Anterior to the quadrate fragment, a bone fragment was identified as the right laterosphenoid by Sereno (2000: fig. 25.1A), although we consider this identification tentative.

The mandible was figured by Hou (1977), but has since been damaged at its anterior end. The area identified as a prementary by Hou (1977) is lost. The anteriormost crown identified and figured by Hou (1977) as possibly caniniform is now missing, but does not appear to have been apicobasally enlarged relative to more posterior teeth. The mandible as currently preserved is figured in medial view by Sereno (2000: fig. 25.1C; Fig. 7A–C). The lateral surface of the bone is obscured at the dentary–surangular–angular junction by a specimen label. However, an external mandibular fenestra and surangular foramina are clearly absent, and Hou (1977: fig. 1B) and Sereno (2000) suggest that a surangular tubercle row is also absent. Comparison with the well-preserved mandibles of *Stegoceras validum* (Sues and Galton, 1987; BMNH R10055, cast of UALVP 2) demonstrates that in IVPP V 4447 the splenial, prearticular and articular are not preserved medially. A prominent anteroposteriorly extending groove on the ventromedial surfaces of the dentary and angular represents an articulation surface for the splenial (Fig. 7B: sp). A large sutural surface for the prearticular/articular (assuming that the prearticular and articular were fused to one another, as occurs in *Stegoceras validum*, Sues and Galton, 1987) is present on the medial surface of the posterior portions of the angular and surangular (Fig. 7B: pr).

The dorsal and ventral margins of the dentary converge anteriorly, and the dentary tooth row is straight in lateral and dorsal views. The dentary tooth row is weakly inset medially, and the ventral surface of the anterior end is not strongly inturned to form a spout-shaped symphysis. The anterior margin of the coronoid process appears to be formed by a discrete element that is separate from the dentary and surangular (Fig. 7A, B: cnd), which we identify as a coronoid ossification following Sues and Galton (1987). This also appears to be the case in *Stegoceras validum*: the anterodorsal margin of the coronoid process in this taxon is formed by a discrete coronoid ossification (Sues and Galton, 1987: fig. 3; BMNH R10055, cast of UALVP 2), rather than a posterodorsal process of the dentary as occurs in all non-pachycephalosaurian ornithischians (Sereno, 1999).

The ventral margin of the dentary is inturned at 90 degrees to the lateral surface to form a horizontal, shelf-like transverse expansion. This transverse expansion continues onto the ventral margin of the angular. Posteriorly this expansion reaches a maximum expansion immediately anterior to the glenoid. The lateral surface of the angular and surangular is weakly convex dorsoventrally and anteroposteriorly. As in *Stegoceras validum* (Sues and Galton, 1987; BMNH R10055, cast of UALVP 2) the surangular

forms a small lateral portion of the adductor fossa (which is predominantly formed in *Stegoceras validum* by the fused prearticular and articular, Sues and Galton, 1987) and the lateral half of the incompletely preserved, posteromedially directed retroarticular process. A prominent ventrolaterally directed boss is present on the lateral surface of the surangular (Fig. 7A: bs), immediately lateral to the glenoid (also seen in *Stegoceras validum*, Sues and Galton, 1987). An anteroventrally descending buttress is present on the medial surface of the surangular and extends into the adductor fossa (Fig. 7B: bt). Comparison with *Stegoceras* indicates that his buttress abutted the anterodorsal margin of the prearticular. The jaw articulation is set a short distance beneath the dentary tooth row.

Seven tooth crowns are preserved. There is an elongate gap anterior to the first preserved crown, in which Hou (1977: fig. 1) identified a caniniform tooth. Sereno (2000: fig. 25.1C) considered this gap to represent the alveoli for a single tooth. In fact there is evidence for the roots of as many as three teeth in this gap, the most anterior of which probably represents the broken base of the caniniform tooth figured by Hou (1977). A gap is present between preserved crowns three and four that was probably occupied by a tooth. This indicates that the tooth count for the row is probably 11, rather than nine as suggested by Sereno (2000).

Teeth are unworn and replacement foramina are not preserved medially. The mesial margin of each tooth overlaps the distal margin of the preceding one lingually. The first, second and third preserved tooth crowns are the largest in the row, and some recurvature is retained in the second crown. This crown is apicobasally higher relative to mesiodistal length than those crowns situated more distally. The best-preserved teeth for description are the two distal-most crowns (Fig. 7C). The crowns are rather low and fan-shaped and are weakly expanded transversely above the root both medially and laterally. A vertical, broad, central eminence on the lingual surface is offset slightly distally such that the mesial margin of the crown is longer than the distal. The lingual crown surface mesial and distal to this ridge is depressed and weakly concave. Mesial and distal margins bear 4–5 denticles, each of which is supported by weak secondary ridges that extend onto the lingual surface. The labial crown surface is concave apicobasally and mesiodistally and lacks a central eminence (contra Sereno, 2000) or well-developed secondary ridges.

Postcranial skeleton.—A single anterior cervical vertebra with an incomplete neural arch is preserved (Fig. 8A, B). The neural arch and centrum are articulated, although the suture between the two remains clearly visible externally. The weakly concave articular faces are transversely broader than dorsoventrally deep. The neural canal is also transversely broad: its transverse width is nearly 50% of the transverse width of the anterior face of the centrum. The lateral flanks of the centrum are deeply excavated and a prominent anteroposteriorly extending ventral keel is present. The parapophysis is represented by a thickened area on the anterior neurocentral boundary; the diapophysis is located on the end of a short transverse process. Hou (1977: pl. 2, fig. 5) described an articulated series of caudal vertebrae. From his description these vertebrae appear to represent mid–posterior caudals with elongate, low centra and short neural spines. This cannot be confirmed as they are currently missing. There is a single, poorly preserved, distal caudal vertebra in the paratype specimen: the maximum length of the centrum (8 mm) slightly exceeds the maximum width (7 mm), the neural arch is fused indistinguishably to the centrum, and caudal ribs and a neural spine are absent. The anterior and posterior faces of the centrum and the zygapophyses are poorly preserved.

The humerus (Fig. 8C, D) is the right, rather than the left as identified by Hou (1977). It is less than 50% of the femoral length (humeral length: 43 mm; length of incomplete right femur:

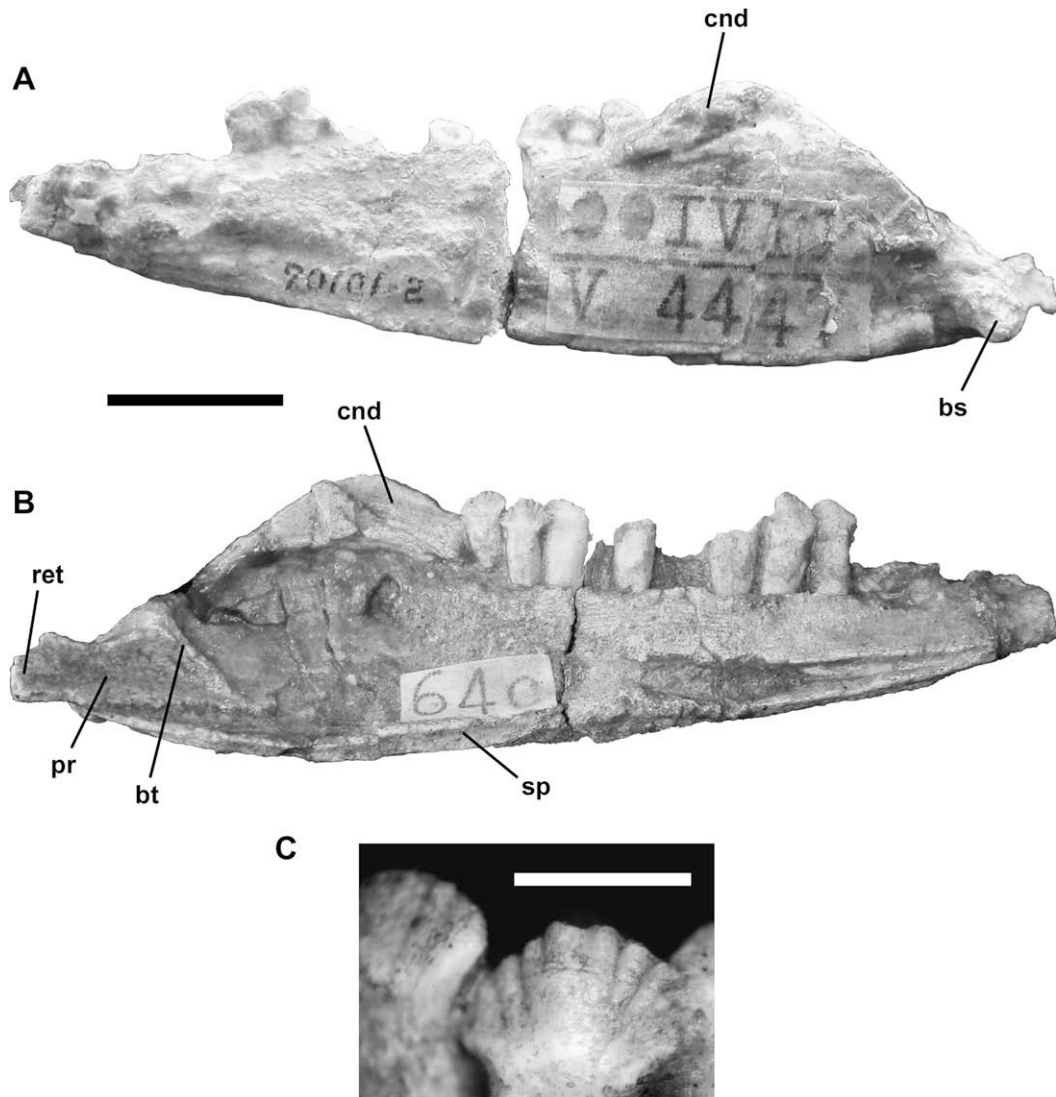


Fig. 7. *Wannanosaurus yansiensis*, left mandible (IVPP V 4447, holotype). A–B, mandible in: A, lateral; and B, medial views. C, dentary crown 10, medial view. Abbreviations: bs, boss on lateral surface of surangular; bt, buttress on medial surface of surangular; cnd, coronoid ossification; pr, surface for prearticular and articular; ret, retroarticular process; sp, surface for splenial. Scale bars equal 10 mm (A–B) and 2 mm (C).

92.5 mm). The strong flexure of the humerus along its length is an autapomorphy of *Wannanosaurus* (Sereno, 2000). In anterior or posterior view the humerus is flexed strongly laterally along its length (Fig. 8D), such that the proximal and distal articular surfaces are at around 30 degrees to each other. This differs from other pachycephalosaurs (e.g. *Goyocephale*, Perle et al, 1982: pl. 43, fig. 4a, c; *Stegoceras validum*, Sues and Galton, 1987: fig. 11) in which lateral flexure of the humerus is less, and proximal and distal articular surfaces are in the same mediolateral plane. It also differs from the condition in other cerapodans (e.g. Brown and Schlaikjer, 1940: fig. 27; Galton, 1974: fig. 38), in which the humeral shaft tends to be straight. In lateral or medial view the proximal end of the humerus is strongly flexed posteriorly (Fig. 8C), and is directed at an angle of nearly 50 degrees to the distal portion of the shaft. This strong posterior flexure does not occur in other pachycephalosaurs (e.g. *Goyocephale*, Perle et al, 1982: pl. 43, fig. 4b, d; *Stegoceras validum*, Sues and Galton, 1987) or other cerapodans (e.g. Brown and Schlaikjer, 1940: fig. 27; Galton, 1974: fig. 38).

The head of the humerus is a low and relatively wide thickening positioned on the posterior surface and offset slightly laterally. The anterior surface of the proximal end is depressed and weakly concave. The posterior surface is weakly convex. The deltopectoral

crest of the humerus is low and represented by a thickening of the anterior surface of the lateral shaft margin. The reduction in length of the humerus, the bowed shaft and reduced deltopectoral crest were identified as synapomorphies shared with other pachycephalosaurs by Sereno (2000). Distally, the medial condyle is nearly square in cross-section, whereas the lateral condyle is sub-rectangular, with the long axis oriented transversely. The medial condyle extends further distally than the lateral, and the two are separated by shallow fossae anteriorly and posteriorly.

A partial left ilium is preserved, although badly damaged. This fragment is labelled 'V4447.1', although an ilium was not reported for the paratype by Hou (1977). A fragment of a left ilium was reported by Hou (1977) for the holotype (IVPP V4447); however, the corresponding figure (Hou, 1977: pl. 1, fig. 2) and measurements do not match the element considered here, so we consider it part of the paratype specimen. Only the preacetabular process and a fragment of the main body of the ilium are preserved; the preacetabular process is poorly preserved and damaged at its base while the pubic and ischiadic peduncles, acetabular border and postacetabular process are all missing. The dorsal margin of the preacetabular process is expanded transversely to form a medially extending, narrow horizontal shelf (the transverse width of the

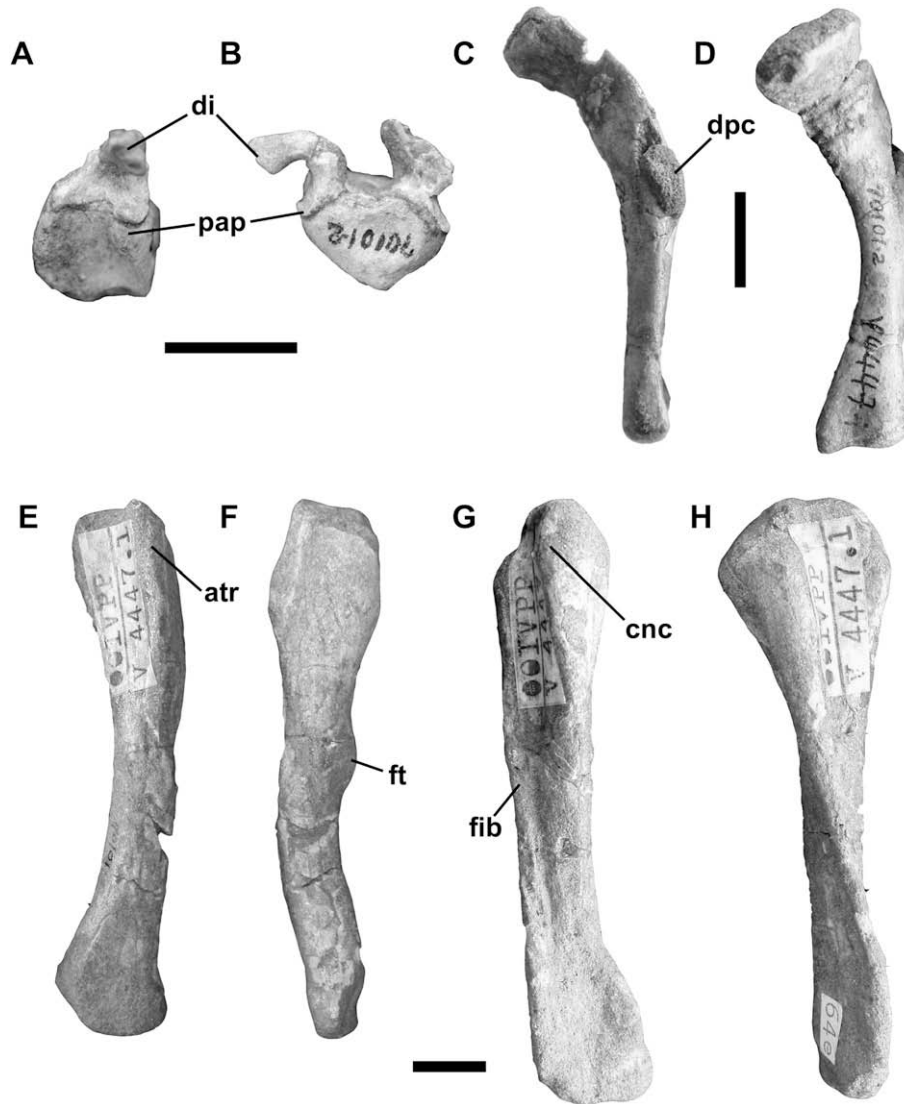


Fig. 8. *Wannanosaurus yansiensis*, postcranial elements (A–D, IVPP V 4447, holotype; E–H, IVPP V 4447.1, paratype). A–B, cervical vertebra in: A, right lateral; and B, anterior views. C–D, right humerus in: C, lateral; and D, posterior views. E–F, left femur in: E, anterior; and F, lateral views. G–H, right tibia and fibula in: G, anterior; and H, lateral views. Abbreviations: atr, anterior trochanter; cnc, cnemial crest; di, diapophysis; dpc, deltopectoral crest; fib, fibula; ft, fourth trochanter; pap, parapophysis. Scale bars equal 10 mm.

shelf at the midpoint of the process is less than the dorsoventral height of the process at the same point). Towards its distal end the process curves strongly laterally; furthermore, the expanded dorsal shelf undergoes torsion to face dorsolaterally rather than strictly dorsally while the lateral surface also twists to face dorsolaterally. As a result, the distinction between the dorsal and lateral surfaces decreases towards the distal end of the process, although they can still be distinguished from one another by a break in slope, and in dorsal view the process appears to expand towards its distal end.

Both femora are present in the holotype and the paratype (Fig. 8E, F), but in both cases they are poorly preserved, with damaged articular ends. The few femoral characteristics that can be discerned are consistent in both specimens. Hou (1977) suggested that the femora of the holotype were of different lengths and that this indicated the presence of two individuals in the specimen; however, it seems that the left femur is simply more incomplete than the right. There is thus no evidence to suggest that the holotype specimen (IVPP V 4441) contains bones of more than one individual.

Although the femora are poorly preserved and incomplete, they are sufficiently complete to indicate that the femur of the holotype

(right femur at least 92.5 mm in length) is longer than the tibia (right tibia 86 mm in length). The anterior and greater trochanters are expanded anteroposteriorly, although few morphological details can be ascertained. A proximodistally extending ridge is not present on the posterolateral surface of the greater trochanter, unlike the femur of *Micropachycephalosaurus* (see above). No information is available on the morphology of the head. The fourth trochanter is incompletely preserved in both holotype and paratype specimens, so its morphology cannot be adequately determined. It does appear to be located at approximately mid femoral length, as noted by Hou (1977), and reduced in size relative to the condition in other ornithischians. The distal condyles are not preserved. An anterior intercondylar depression may have been present, as indicated by a weak depression on the anterior distal surface of the right femur of the paratype, IVPP V 4447.1.

The right tibia and fibula of the paratype are preserved in articulation (Fig. 8G, H), but are badly abraded at their proximal and distal ends and few details of their anatomy can be determined. The astragalus and calcaneum may also be present distally, but are highly eroded and their presence or absence cannot be determined with certainty. The tibia is strongly anteroposteriorly expanded

proximally and mediolaterally expanded distally, with the shaft undergoing torsion along its length so that the articular ends are at 70 degrees to each other. The fibula is directed anteroventrally and narrows strongly in both anteroposterior and mediolateral width distally. Sereno (2000) noted that the narrow distal fibula shaft is a synapomorphy shared with more derived pachycephalosaurs.

Hou (1977: pl. 2, fig. 6) noted that an articulated, nearly complete, left pes is preserved in IVPP V 4447. Unfortunately, the location of this material is currently unknown, and few details can be determined from the original photograph. Hou (1977) suggested that the phalangeal formula was 1-2-3-?0-?0, and that metatarsal five was the longest metatarsal. If accurate, this would be autapomorphic. In most basal ornithischians the pedal formula is 2-3-4-5-0 (e.g. He and Cai, 1984) and the reduction of metatarsal five to a short splint has been considered an ornithischian synapomorphy (Sereno, 1986). In the absence of the original material, these unusual features of the pes cannot be confirmed.

Phylogenetic position. *Wannanosaurus* is clearly referable to the Pachycephalosauria, as previously demonstrated on the basis of ten synapomorphic characters by Sereno (2000). It should be noted, however, that character number 5 (presence of arched premaxilla-maxilla diastema with dentary caniniform) of Sereno (2000) cannot be confirmed in *Wannanosaurus*. The premaxilla and maxilla are absent in the holotype and paratype specimens and so the presence of an arched premaxillary-maxillary diastema cannot be confirmed. The putative caniniform mesial dentary tooth noted by Hou (1977) is missing. Additionally, the 'caniniform' figured by Hou (1977: fig. 1) is shorter apicobasally than the remaining dentary teeth, and does not resemble the enlarged caniniform seen in *Goyocephale lattimorei* (Perle et al., 1982). Maryańska et al. (2004: see data matrix and character list available online at <http://dinosaurs.ucpress.edu>) identified five characters linking *Wannanosaurus* with other pachycephalosaurs: thickening of the skull roof; flattened and broad postorbital-squamosal bar; caudolateral wings of the parietal absent; tubercles present on the caudolateral margin of the squamosal; tubercles present on postorbital.

A pachycephalosaurian identity is also supported by the presence of a short and robust jugal-postorbital suture, which differs from the elongate tongue-in-groove suture seen in outgroups (e.g. *Hypsilophodon foxii*, Galton, 1974; *Psittacosaurus*, Sereno, 1987), and by the presence of a preacetabular process that curves strongly laterally and expands towards its distal end in dorsal view, both of which features have been identified in more derived pachycephalosaurs (Sereno, 2000). Furthermore, characters of the mandible shared by *Wannanosaurus* and *Stegoceras*, but absent in outgroups (e.g. *Hypsilophodon foxii*, Galton, 1974; *Psittacosaurus*, Sereno, 1987), may prove to be synapomorphic for Pachycephalosauria. These include the presence of an additional coronoid ossification forming the anterodorsal margin of the coronoid process and the presence of a lateroventrally directed boss on the lateral surface of the surangular.

Hou (1977) suggested that *Wannanosaurus* represented a primitive pachycephalosaur, and noted similarities to the basal ceratopsian *Psittacosaurus*. Dong (1978) included *Wannanosaurus* within Homalocephalidae, which included those pachycephalosaurian taxa with an undomed skull roof, open supratemporal fenestrae and a quadrate that is not strongly anteriorly inflected. *Wannanosaurus* was retained within Homalocephalidae by some subsequent authors (Perle et al., 1982; Galton and Sues, 1987; Maryańska, 1990) and Galton and Sues (1987) and Maryańska (1990) considered *Wannanosaurus* the most basal member of this group. Sereno (1986) suggested that Homalocephalidae represents a paraphyletic grade of basal pachycephalosaurs, and that *Wannanosaurus* might represent the most primitive known pachycephalosaur. Subsequent phylogenetic analyses (Sereno, 1999, 2000;

(Williamson and Carr, 2002; Sullivan, 2003; Maryańska et al., 2004; Butler et al., 2008) supported homalocephalid paraphyly and the basal position of *Wannanosaurus*. However, Sereno (2000) noted that the probable juvenile nature of the holotype and paratype specimens means that assessments of the phylogenetic position of *Wannanosaurus* are problematic. Specifically, many relevant characters such as the size of the supratemporal fenestra, presence or absence of doming of the skull roof, and degree of development of cranial and mandibular ornamentation (nodes), are known to be ontogenetically variable within Pachycephalosauria (Goodwin et al., 1998: 374; Sereno, 2000; Goodwin and Horner, 2004; Horner et al., 2007). We recognise the problems inherent in assessing the phylogenetic position of a taxon based upon fragmentary remains of probable juvenile ontogenetic stage. Therefore, although all published numerical phylogenetic analyses (Sereno, 1999, 2000; Williamson and Carr, 2002; Sullivan, 2003; Maryańska et al., 2004; Butler et al., 2008) have considered *Wannanosaurus* a basal member of Pachycephalosauria, we follow Sullivan (2006) in considering the phylogenetic position of *Wannanosaurus* within Pachycephalosauria as uncertain.

3. Conclusions

Pachycephalosaurian dinosaurs are best known from the Late Cretaceous of North America and Asia. Proposed pachycephalosaur records from earlier temporal intervals and other geographical areas are either based on non-pachycephalosaurian material (e.g. *Majungatholus atopus* Sues and Taquet, 1979 from the Late Cretaceous of Madagascar; possibly also *Yaverlandia bitholus* Galton, 1971 from the Early Cretaceous of England; see Sullivan, 2006) or are highly contentious (e.g. *Stenopelix valdensis* Meyer, 1857 from the Early Cretaceous of Germany; see Sereno, 2000; Sullivan, 2003, 2006). The vast majority of confirmed Late Cretaceous pachycephalosaurian specimens are from North America, and only a handful are known from Asia. Of the Asian pachycephalosaurs, the well-preserved Mongolian specimens (*Goyocephale*, *Homalocephale* and *Prenocephale*) have commanded the greatest attention (Maryańska and Osmólska, 1974; Perle et al., 1982; Sereno, 2000). By contrast, the Chinese pachycephalosaur specimens have been largely neglected since their initial descriptions (Bohlin, 1953; Hou, 1977; Dong, 1978).

Micropachycephalosaurius hongtuyanensis is a valid taxon, based upon highly fragmentary but diagnosable remains. The pachycephalosaurian identity of this taxon cannot be confirmed based upon the currently available holotype material, and at present this taxon cannot be assigned beyond the level of Cerapoda incertae sedis. Previous estimates of body size for the holotype specimen appear to be too low, and *Micropachycephalosaurius* does not appear to have been smaller than other basal cerapodan and basal ornithischian taxa.

Wannanosaurus yansiensis can be diagnosed on the basis of its unique humeral morphology. Assessment of the ontogenetic stage of the holotype and paratype specimens (via approaches such as histological sectioning or CT-scanning) has not yet been carried out, but it seems likely that they represent juvenile individuals. The probable juvenile status of the holotype and paratype specimens complicates attempts to assess the phylogenetic placement of *Wannanosaurus* within Pachycephalosauria.

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Appendix 1

Current status of diagnostic features proposed for *Micropachycephalosaurus* by Dong (1978) and Maryańska (1990).

Dong (1978) originally diagnosed *Micropachycephalosaurus* on the basis of the following characters: 1) small body size (length approximately 50–60 cm); 2) thickened parietal and squamosal; 3) parietal and squamosal flat and undomed; 4) retention of supratemporal fenestrae; 5) absence of cranial ornamentation; 6) relatively 'high' mandible; 7) gracile, uniserial dentition, with median ridge laterally and denticles developed symmetrically mesially and distally; 8) six fused sacral vertebrae, the second of which is inflated, with robust sacral ribs. None of these characters can be demonstrated as autapomorphic for *Micropachycephalosaurus*. For example, the body size estimate provided by Dong (1978) is probably inaccurate (see above), and size is an insufficient criterion for taxon diagnosis. The absence of identifiable material of the skull roof in the holotype specimen means it is impossible to confirm other characters (characters 2–5). Even if material of the skull roof was originally present, and has been lost since its original description, most characters relating to skull roof anatomy (characters 2–4) represent pachycephalosaurian plesiomorphies (or juvenile characteristics), present in *Wannanosaurus* (see below; Hou, 1977) and *Goyocephale* (Perle et al., 1982), amongst others, and one (character 5) represents an ornithischian plesiomorphy. Other characters are poorly defined (character 6) and thus difficult to operationalise, or also appear to represent pachycephalosaurian plesiomorphies (e.g. characters 7–8, see above for details).

Maryańska (1990) suggested that *Micropachycephalosaurus* could be distinguished from other Asian pachycephalosaurs by the proximal position of the fourth trochanter on the femoral shaft and the caudally tapering postacetabular process of the ilium (based upon the reconstruction of Dong, 1978:fig. 2). The fourth

trochanter of pachycephalosaurs is usually positioned slightly more distally than in most other ornithischians; however, the proximally positioned fourth trochanter of *Micropachycephalosaurus* is a plesiomorphy shared with a wide range of ornithischians (e.g. *Lesothosaurus*, Sereno, 1991; *Hypsilophodon*, Galton, 1974; *Psittacosaurus*, Sereno, 1987; *Protoceratops* Granger and Gregory, 1923; Brown and Schlaikjer, 1940). The proximal position of the fourth trochanter in *Micropachycephalosaurus* might represent an autapomorphic reversal if other anatomical evidence implied a derived position within Pachycephalosauria. However, such evidence cannot be ascertained from the available material. As discussed above, there is no evidence to support the reconstructed morphology of the postacetabular process suggested by Dong (1978:fig. 2) and, thus, no diagnosis can be made based upon it.

Appendix 2

Current status of diagnostic features proposed for *Wannanosaurus* by Hou (1977) and Sereno (2000).

The original diagnosis of *Wannanosaurus* by Hou (1977) was based upon the following characters: 1) small size; 2) supratemporal fenestrae large; 3) parietal–squamosal flat and undomed, 4) thickened parietal–squamosal; 5) ornamentation present on skull roof, and on postorbital–squamosal bar; 6) parietal–squamosal not extended posteriorly; 7) occipital region and quadrate slope anteroventrally; 8) tooth row long, more than half the length of the lower jaw; 9) dentary crowns serrated; 10) posterior portion of lower jaw thin; 11) prominent retroarticular process.

However, none of these characters are autapomorphic for *Wannanosaurus*. The majority (1–9, 11) represent plesiomorphies for Pachycephalosauria. Character 10 is poorly defined, and it is impossible to estimate the true width of the posterior portion of the lower jaw, because the articular and prearticular are absent.

Sereno (2000) suggested that *Wannanosaurus* could be diagnosed on the basis of two autapomorphic features: the presence of low, fan-shaped dentary crowns with a marked median eminence on the lateral crown surface, and the extreme flexure of the humerus. The median eminence of the dentary teeth is actually located medially, rather than laterally; in addition, at least some of the crowns of *Micropachycephalosaurus* and *Goyocephale* are low and fan-shaped, and resemble those of *Wannanosaurus*, and this feature may represent a pachycephalosaurian plesiomorphy. However, as discussed above, the morphology of the humerus does appear to represent an autapomorphy of *Wannanosaurus*.

Sullivan (2006) speculated that *Wannanosaurus* might be synonymous with *Homalocephale calathocercos*, based largely upon stratigraphic position and general similarity. The humerus is unknown for *Homalocephale*, so cannot be compared with the apparently autapomorphic morphology seen in *Wannanosaurus*. Although Sullivan's suggestion is not untenable, it is unsupported due to the absence of identifiable discrete characters linking the two taxa. We currently retain *Wannanosaurus* as a distinct and valid taxon.