

A basal ceratopsian with transitional features from the Late Jurassic of northwestern China

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Although the Ceratopsia and Pachycephalosauria, two major ornithischian groups, are united as the Marginocephalia, few synapomorphies have been identified due to their highly specialized body-plans. Several studies have linked the Heterodontosauridae with either the Ceratopsia or Marginocephalia, but evidence for these relationships is weak, leading most recent studies to consider the Heterodontosauridae as the basal member of another major ornithischian radiation, the Ornithopoda. Here, we report on a new basal ceratopsian dinosaur, *Yinlong downsi* gen. et. sp. nov., from the Late Jurassic upper part of the Shishugou Formation of Xinjiang, China. This new ceratopsian displays a series of features transitional between more derived ceratopsians and other ornithischians, shares numerous derived similarities with both the heterodontosaurids and pachycephalosaurians and provides strong evidence supporting a monophyletic Marginocephalia and its close relationship to the Heterodontosauridae. Character distributions along the marginocephalian lineage reveal that, compared to the bipedal Pachycephalosauria, which retained a primitive post-cranial body-plan, the dominantly quadrupedal ceratopsians lost many marginocephalian features and evolved their own characters early in their evolution.

Keywords: Ceratopsia; Marginocephalia; Ornithischia; Late Jurassic; Shishugou Formation

1. INTRODUCTION

The Shishugou Formation of the Junggar Basin, Xinjiang, China was deposited during the Middle–Late Jurassic (Chen 1996; Eberth *et al.* 2001), a period that is critical to the origins and early evolution of the major dinosaurian lineages, including birds (Serenó 1999). Since 2001, we have prospected in this formation and collected numerous vertebrate specimens (Clark *et al.* 2004), among them a nearly complete ornithischian skeleton we here identify as a basal ceratopsian dinosaur. The two other possible Jurassic ceratopsians (Zhao *et al.* 1999, *in press*) are from the Tuchengzi and Houcheng Formations of China. However, a recent radiometric sample from the Tuchengzi Formation places its upper part in the Early Cretaceous (Swisher *et al.* 2002). Consequently, the Shishugou ceratopsian represents the first unquestionable Jurassic ceratopsian species.

2. SYSTEMATIC PALAEOLOGY

Ornithischia Seeley, 1887.

Heterodontosauriformes new taxon.

Marginocephalia, Sereno (1986).

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Ceratopsia Marsh, 1890.

Yinlong downsi gen et sp nov.

(a) Etymology

‘Yin’ and ‘long’ mean ‘hiding’ and ‘dragon’ in Chinese, respectively, derived from the movie ‘Crouching Tiger, Hidden Dragon’ which was filmed in the locality where the holotype was found; the specific name is in memory of Mr Will Downs, who joined many palaeontological expeditions in China including the one with us in 2003, shortly before his death.

(b) Holotype

IVPP V14530, a nearly complete skeleton missing only the distal tail (figure 1 and figures 1 and 2 of electronic supplementary material).

(c) Locality and horizon

Wucaiwan, Junggar Basin, Xinjiang, China; upper part of Shishugou Formation, correlated with the Oxfordian stage of the early Late Jurassic (Chen 1996; Eberth *et al.* 2001).

(d) Diagnosis

A small ceratopsian with the following unique features: a distinct fossa along the midline of the frontals, trapezoidal quadratojugal longer than deep, sharp ridges and grooves on the anterior surface of the proximal half of the paroccipital process, a long basiptyergoid process oriented posteroventrally, slit-like carotid canal laterally bordered

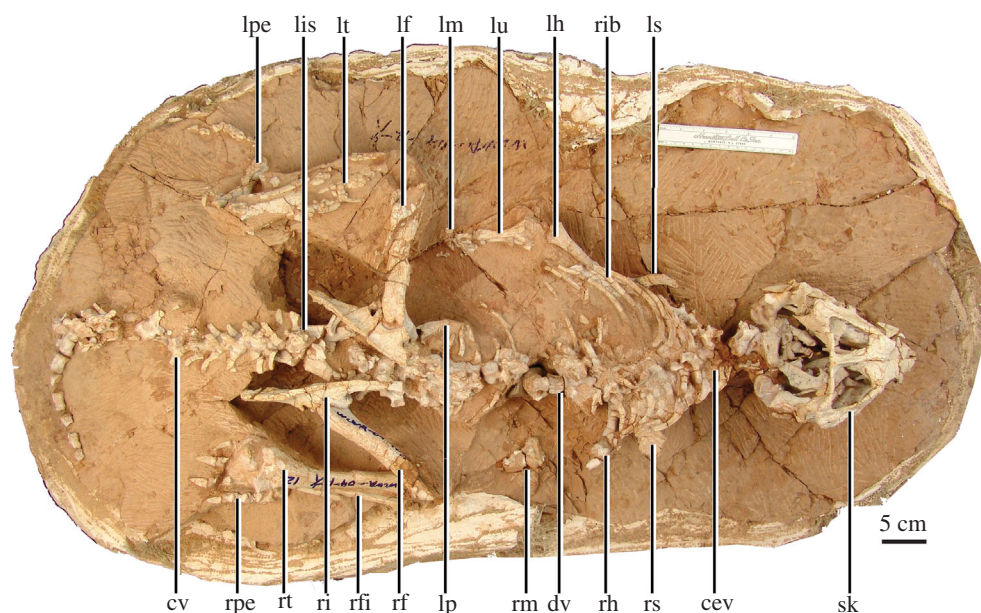
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Figure 1. *Yinlong downsii* (IVPP V14530, holotype). Abbreviations: cev, cervical vertebrae; cv, caudal vertebrae; dv, dorsal vertebrae; lf, left femur; lh, left humerus; lis, left ischium; lm, left manus; lp, left pubis; lpe, left pes; ls, left scapula; lt, left tibia; lu, left ulna; rf, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rpe, right pes; rs, right scapula; rt, right tibia; sk, skull. Scale bar, 5 cm.

by a lamina, a prominent tubercle on the posteroventral surangular and a vertical wear facet with a basal shelf on the premaxillary teeth (figures 1 and 2; figures 1 and 2 of electronic supplementary material).

(e) Description

The holotype is probably a sub-adult as indicated by the open neurocentral sutures on the presacral vertebrae (closed on the caudal vertebrae). The holotype is estimated to be 120 cm in total body length. Relatively short and slender forelimbs and very robust and long hindlimbs (forelimb less than 40% the hindlimb length) suggest that *Yinlong* was a bipedal animal.

The posterior part of the skull is proportionally deep in lateral view and extremely broad in the postorbital region in dorsal view (figures 1 and 2). The pre-orbital region is shallow and, as in some other basal ceratopsians, is relatively short. The orbit lies entirely above the posterior maxillary tooth row. The supratemporal and infratemporal fenestrae are proportionally large in size. The latter exceeds the orbit in diameter and is nearly circular in shape. The small antorbital fossa has distinct margins, is bordered ventrally by a prominent ridge, and is positioned under the anterior orbit.

As in all ceratopsians, a small rostral bone caps the anterior premaxillae. The palpebral has a distinct anterior process and a long posterior process reaching to the middle of the orbit. The skull roof bears two distinct midline fossae indenting the nasals and the frontals. The former is seen in *Heterodontosaurus* (Barrett, personal communication) and some basal ornithomorphs (He & Cai 1984; Peng 1992; Xu *et al.* 2000), and to a less degree, in some basal ceratopsians (Xu *et al.* 2002). As in *Heterodontosaurus* (Norman *et al.* 2004) and some basal ceratopsians, the jugal, with a blunt anterior end, contributes significantly to the posterior margin of the antorbital fossa. Posteriorly the jugal flares laterally and is significantly thickened transversely but lacks a jugal flange. The lateral surface of the jugal bears distinct sculpturing

that continues across the surface of the postorbital and temporal bar. The large quadratojugal is trapezoidal and longer anteroposteriorly than dorsoventrally. As in *Chaoyangsaurus* (Zhao *et al.* 1999), the quadrate slopes slightly anterodorsally. As in *Liaoceratops*, the quadrate has a longitudinal groove along its anterolateral margin and a paraquadratic foramen at mid-height on the posterior margin. A paraquadratic foramen is also seen in *Heterodontosaurus* (Norman *et al.* 2004). As in *Chaoyangsaurus* and an unnamed basal ceratopsian (Zhao *et al.* 1999), the distal quadrate condyles are separated by a deep groove, which is shallow or absent in *Psittacosaurus* and more derived ceratopsians (You & Dodson 2003). *Yinlong* shares with *Heterodontosaurus* (Norman *et al.* 2004) a post-orbital with a prominent ridge running along the jugal process and onto the postorbital process of the jugal. The squamosal process of the postorbital is long, forming nearly the whole length of the dorsal margin of the infratemporal fenestra. As in pachycephalosaurians (Maryńska *et al.* 2004), the temporal bar has a broader dorsal margin relative to the lateral margin. Similar to most ornithischians, but differing from other ceratopsians (Serenó 2000; Makovicky 2001; You & Dodson 2004; Dodson *et al.* 2004), the posterior margin of the parietal is positioned distinctly anterior to that of the squamosal and its posterolateral wing has a deep distal ramus facing caudally rather than ventrally. These features suggest a lack of parietal contribution to the frill, though the parietal near the midline slightly overhangs over the occiput. The squamosal overhangs the quadrate-squamosal articulation laterally and posteriorly, forming a small squamosal frill. Similar to pachycephalosaurians (Maryńska *et al.* 2004), a row of distinct tubercles runs along the posterior margin of the squamosal and the lateral margin of the squamosal process of the post-orbital. Similar to basal pachycephalosaurians (Maryńska *et al.* 2004), the articular fossa for the quadrate is separated from the main body of the squamosal by a robust ventral process, such that the quadrate-squamosal articulation is relatively ventrally

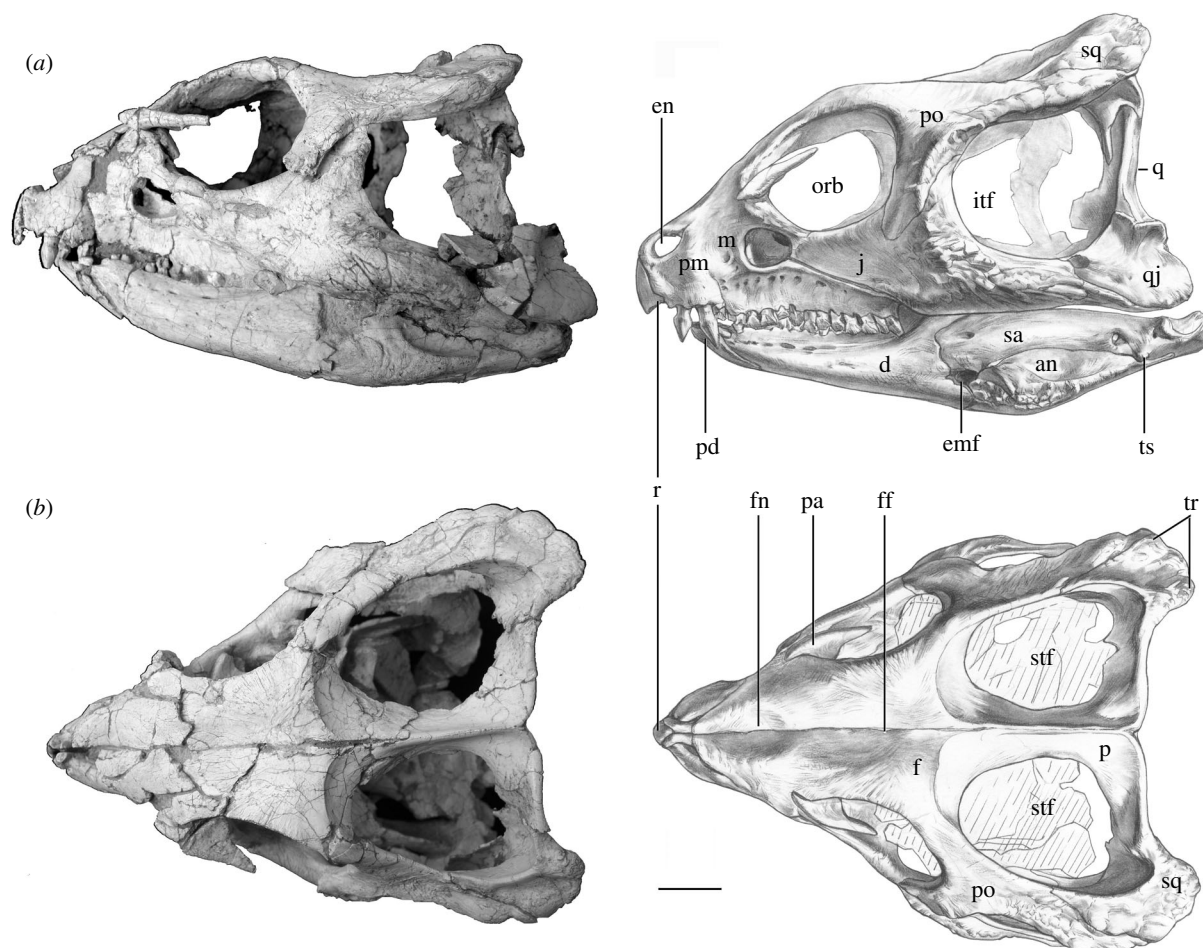


Figure 2. IVPP V14530. (a) Skull and mandible in lateral view. (b) Skull in dorsal view. Abbreviations: an, angular; d, dentary; emf, external mandibular fenestra; en, external naris; f, frontal; ff, fossa on frontals; fn, fossa on nasals; itf, infratemporal fenestra; j, jugal; m, maxilla; p, parietal; pa, palpebral; pd, prementary; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; r, rostral bone; sa, surangular; sq, squamosal; stf, supratemporal fenestra; tr, tubercle row; ts, tubercle on surangular. Scale bar, 2 cm.

located. The braincase displays many pachycephalosaurian features (figure 1 of electronic supplementary material). The three exits for cranial nerves XI–XII open further ventrally than caudally on the posterior surface of the proximal exoccipital, which is sharply deflected ventrally. The paroccipital process tapers distally, a feature seen in many basal ornithischians and ornithomorphs. The distal paroccipital process is ventral to the occipital condyle whereas in most ceratopsians it is positioned dorsal to the occipital condyle. As in the ornithomorph *Jeholosaurus* and some basal ceratopsians, a longitudinal ridge is present under the occipital condyle. As in pachycephalosaurians (Maryańska *et al.* 2004), the plate-like basal tuber is compressed anteroposteriorly, with a significant exposure of the basiosphenoid in posterior view. The posteroventrally oriented basiptyergoid process is long, with a large, flat, elongated elliptical articular facet facing more laterally than anteriorly. This basiptyergoid process indicates a medial and posterior extension of the pterygoid, covering much of the basicranium in ventral view. The pterygoid has an anteriorly directed, elongate, vertical plate for contacting the vomer, a plate-like ventral process and an extremely small posterior process. In psittacosaurids and neoceratopsians (You & Dodson 2004), the vomer process is dorsally directed.

The mandible has a small external mandibular fenestra, a large fossa on the external surface of the posterior

mandible and lacks a long retroarticular process. The prementary bears two small lateral processes and a long ventral process that is bifurcated distally. The oral margin of the prementary is somewhat bevelled. Similar to most ornithischians but differing from other ceratopsians (You & Dodson 2004), the dentary is straight and shallow. As in pachycephalosaurians (Maryańska *et al.* 2004), the posterior dentary and to an even greater degree the anterior angular, is sculptured, a feature also seen in *Liaoceratops* and *Archaeoceratops* (You & Dodson 2003), though less developed. The splenial is restricted to the medial margin of the mandible with little ventral exposure. As in other basal ceratopsians (You & Dodson 2004), the posterior end of the mandible is medially expanded and the glenoid fossa is elevated dorsally.

Three premaxillary teeth and 13 maxillary teeth are present per side. The premaxillary tooth crowns are notably larger than the maxillary ones and are symmetrical in lateral view with a mesiodistally convex labial surface and a flat lingual surface. The premaxillary teeth have a vertical wear facet and a horizontal shelf on the lingual surface (figure 1 of electronic supplementary material), indicating occlusion with the prementary, a feature also reported in the heterodontosaurid *Abrictosaurus* (Thulborn 1970). The second premaxillary tooth bears fine serrations along its distal margin. There is a very short diastema. As in heterodontosaurids and most basal

ceratopsians, the maxillary teeth are closely packed, chisel-shaped and bear prominent mesial and distal ridges (figure 1 of electronic supplementary material). Relatively low-angled wear facets are present on both mesial and distal margins of the maxillary tooth crowns. Most dentary teeth cannot be seen due to the closely occluded jaw, but the anteriormost ones are much smaller than the more posterior ones.

The cervical centra are short axially and tall dorsoventrally. The neural spines of the anterior and middle caudal vertebrae are tall, approximating the corresponding chevrons in length. The posterior sacral ribs are probably long as inferred from the lateral deflection of the posterior end of the ilium.

Three carpals are visible on the left manus. The manus is much smaller than the pes, with robust phalanges and both hoof-like unguals (flat and rounded distally) and claw-like unguals (transversely narrower and distally pointed). The ilium displays several features shared with pachycephalosaurians (Sereno 2000; Maryańska *et al.* 2004) including being longer than the femur and slightly S-shaped in dorsal view, having the distal half of the preacetabular process twisted such that its lateral surface faces more dorsally than laterally and having a blunt anterior end. The dorsal margin of the posterior ilium flares laterally and the iliac blade expands ventrally to form a flat, narrow brevis shelf. The ischial peduncle is broad axially with little lateral expansion, and appears to bear a ventral notch. The pubis bears a short and blunt prepubic process and a distally flattened postpubic rod, which is much shorter than the robust, plate-like ischium. As in typical bipedal ornithischians, the femur is distinctly bowed anteriorly. A longitudinal ridge is present along the posterolateral edge of the proximal half of the femoral shaft and a robust, pendant fourth trochanter is located along the posteromedial shaft. In most ceratopsians including *Psittacosaurus*, the femur is less bowed, a similar ridge is absent, and the fourth trochanter is thinner transversely and positioned mainly on the posterior margin of the femoral shaft. *Yinlong* has very flat, pointed pedal unguals.

Seven gastroliths, each 1–1.5 cm. in diameter, are exposed within the ribcage at the midlength of the trunk. As in psittacosaurids (Xu 1997), they are proportionally large relative to the body size of the animal.

3. DISCUSSION

The discovery of *Yinlong* has significant implications for ornithischian phylogeny. Although the Ceratopsia and Pachycephalosauria, two major ornithischian groups, are united as the Marginocephalia, only three synapomorphies have been previously identified due to their highly specialized body-plans (Sereno 2000; see electronic supplementary material for further comments). Another problem concerning ornithischian phylogeny is the systematic position of the Heterodontosauridae. Several studies have linked the Heterodontosauridae with either the Ceratopsia or Marginocephalia (Norman 1984; Cooper 1985; Maryańska & Osmólska 1985; Zhao *et al.* 1999; You *et al.* 2003), but evidence for these relationships has been weak, leading most recent studies to consider the Heterodontosauridae as the basal member of another major ornithischian radiation, the Ornithopoda (Sereno

1999; Norman *et al.* 2004), which is the sistergroup to the Marginocephalia (see electronic supplementary material for further comments). A recent analysis suggests a different ornithischian phylogeny: the Ceratopsia and Pachycephalosauria are nested within the Ornithopoda, which conforms to the pre-cladistic ornithischian phylogeny (Butler 2005). As *Yinlong* has a combination of derived character states found in the Ceratopsia, Pachycephalosauria and Heterodontosauridae, it provides substantial evidence for a close relationship of these three groups. A phylogenetic analysis places *Y. downsi* as the most basal ceratopsian, strongly supports a monophyletic Marginocephalia and suggests a sistergroup relationship between the Heterodontosauridae and Marginocephalia (figure 3; see electronic supplementary material).

Yinlong downsi has a skull proportionally larger relative to the body than most ornithischians but smaller than other ceratopsians (Sereno 2000), a thickened jugal but no jugal flange, an elevated posterior margin of the skull roof but no parietal contribution to the frill and has a posteriorly elevated but anteriorly shallow and straight mandible. These features are intermediate in conditions between basal ornithischians and more derived ceratopsians, documenting the incremental appearance of ceratopsian diagnostic characters, a pattern also suggested by other basal ceratopsians (Xu *et al.* 2002). The Psittacosauridae represents a lineage of the Ceratopsia that has diverged from this incremental line. For example, Psittacosauridae has a relatively lower posterior margin of the skull roof and slender postorbital and temporal bars, reversals to the more primitive conditions.

A calibrated phylogeny of the Ceratopsia suggests that the group evolved the unique rostral bone and enlarged, triangular head as early as the Oxfordian, but did not evolve the typical ceratopsian body-plan, characterized by quadrupedal posture and with a parietosquamosal frill, until the Early Cretaceous. Our character distribution suggests that ceratopsians first shortened their snout, broadened their occipital region and elevated the posterior margin of the skull roof, then deepened their snout and mandible, and finally extended their frill posteriorly (figure 3).

The Heterodontosauridae–Marginocephalia clade is characterized by many features related to the antorbital and temporal regions and dentition. Some dental features (e.g. enlarged premaxillary teeth) were previously used to diagnose the Heterodontosauridae (Norman *et al.* 2004) but now characterize the Heterodontosauridae–Marginocephalia clade, so we hereby name this clade Heterodontosauriformes (defined as a node-based group that includes the most recent common ancestor of *Heterodontosaurus* and *Triceratops* and all their descendents). Some heterodontosauriform features, such as very large infratemporal fenestra, are absent in known pachycephalosaurian species due to their highly modified postorbital region of the skull, but are expected in their basal members, which are currently poorly known. Noteworthy is that our analysis posits *Agilisaurus*, a Middle Jurassic ornithischian taxon suggested to be either a basal ornithopod or a basal ornithischian by previous phylogenetic analyses (Barrett *et al.* 2005), as the sister group to the Heterodontosauriformes, though the evidence is not strong (a bootstrap value for this relationship is 21%;

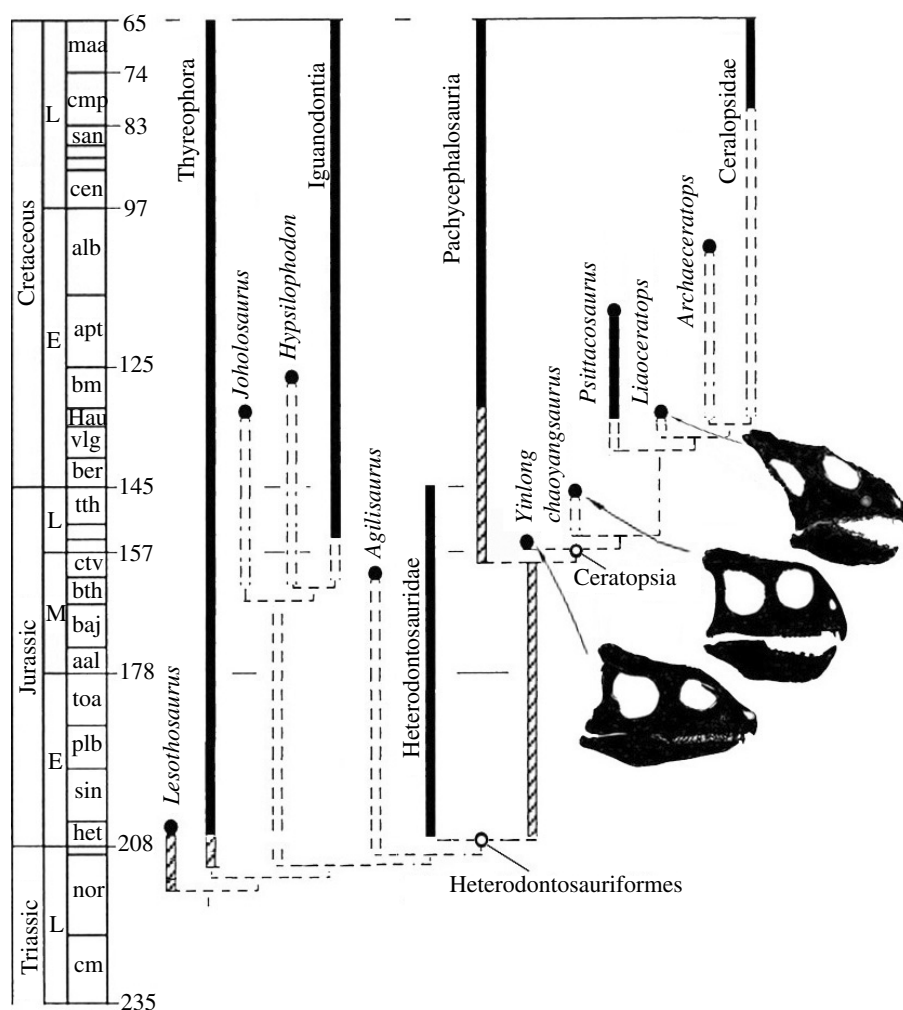
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Figure 3. A single most parsimonious tree recovered showing the phylogenetic position of *Yinlong downsi* and the interrelationships of the Ceratopsia. The proposed tree plotted against geological time indicates the timing of the major cranial changes among the Ceratopsia. The Marginocephalia node is supported by 22 synapomorphies and the Heterodontosauriformes by nine synapomorphies (see electronic supplementary material).

see electronic supplementary material). Although the discovery of *Y. downsi* provides strong support for the monophyly of the Marginocephalia (Serenó 1986, 2000), the overhanging parietosquamosal frill, the most obvious feature of the three previously recognized for the group, might have been independently developed in pachycephalosaurians and derived ceratopsians. *Yinlong* shares with pachycephalosaurians a squamosal frill but lacks a parietal contribution to the frill. The parietosquamosal frill evolved in more derived ceratopsians with the posterior extension of the parietal and the reorientation of the posterolateral wing of the parietal.

Meanwhile, several salient pachycephalosaurian features, such as the sculptured angular and jugal, broad and flat dorsal margin of the temporal bar, the squamosal-postorbital tubercles and the anteroposteriorly compressed basal tuber (Maryńska *et al.* 2004), are now synapomorphies of the Marginocephalia. These features are shared by pachycephalosaurians and basal ceratopsians, but are gradually reduced and lost in derived ceratopsians (Dodson *et al.* 2004). Two distinctly different evolutionary patterns are present after the splitting of the Marginocephalia into a pachycephalosaurian and a ceratopsian lineage. The pachycephalosaurians retain a bipedal body-plan and further develop several marginocephalian features, such as the cranial sculptures

and tubercles. Conversely, the ceratopsians adopted quadrupedalism, gradually lost a number of plesiomorphic marginocephalian characters, and evolved typical ceratopsian features, notably the jugal horn and an extensive parietosquamosal frill. Consequently, a classical taxonomical dichotomy is documented by the divergence leading to a more plesiomorphic pachycephalosaurian and a more specialized ceratopsian lineage within the Marginocephalia. The evolution of ceratopsians is particularly interesting in terms of the presence of a remarkable number of both reversals and specializations: while the derived ceratopsians reversed to the primitive conditions in many characters, they evolved highly specialized features related to a large frilled skull and a quadrupedal post-cranial skeleton, which make the group unique among the ornithischians.

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