A New Genus of Psittacosauridae (Dinosauria: Ornithopoda) and the Origin and Early Evolution of Marginocephalian Dinosaurs

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Abstract An almost complete juvenile dinosaur skull with lower jaw was discovered from the Early Cretaceous Yixian Formation in Beipiao, Liaoning Province, China. Here, the specimen is described and a cladistic analysis is performed in order to find its phylogenetic relationships. The result shows that this specimen represents a new genus of Psittacosauridae, *Hongshanosaurus houi*, gen. et sp. nov., and confirms the monophyletic status for Ceratopsia and Marginocephalia. However, *Heterodontosaurus* is found to be the sister taxon to Marginocephalia, rather than a basal Ornithopoda.

Key words: Dinosauria; Marginocephalia; *Hongshanosaurus houi*, gen. et sp. nov.; Yixian Formation; Liaoning Province

1 Introduction

Marginocephalian dinosaurs (Sereno, 1986; Dodson, 1990), which include the parrot-beaked psittacosaurs (Sereno, 1990), thick-headed pachycephalosaurs (Sues and Galton, 1987; Maryańska, 1990) and long-frilled neoceratopsians (Dodson and Currie, 1990; Dodson, 1996), are best known from the Late Mesozoic of the Northern Hemisphere. However, their origin and early evolution are not well understood, and are supported only by a few characters (Sereno, 1999, 2000). Here we describe a new genus of Psittacosauridae based on an almost complete juvenile skull with lower jaw from the Early Cretaceous of northeastern China. Phylogenetic analysis including this new taxon supports the non-conventional view that the Early Jurassic *Heterodontosaurus* is the sister group to Marginocephalia (Cooper, 1985). Both of them share many features, such as a short preorbital portion about half of the skull length, lateral expansion of the jugals, and less than five premaxillary teeth.

2 Systematic Paleontology

Dinosauria Owen, 1841
Ornithischia Seeley, 1887
Neornithopoda Cooper, 1985
Marginocephalia Sereno, 1986
Psittacosauridae Osborn, 1923
Hongshanosaurus houi, gen. et sp. nov.

Etymology: "*Hong Shan*" (Chinese), "red hill", for the "Red Hill Culture" which existed about 6,000 years ago in western Liaoning, northeastern China, where this specimen was found; "*saurus*" (Greek), "lizard". Specific name for Prof. Hou Lianhai, who allowed us to study this specimen.

Holotype: IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 12704, an almost complete juvenile skull with articulated lower jaw.

Type locality and horizon: Beipiao, Liaoning Province, China. Yixian Formation, Early Cretaceous (Wang et al., 1998; Swisher et al., 1999; Smith et al., 2001).

Diagnosis: Psittacosauridae distinguishable from *Psittacosaurus* in having prominent jugal-quadratojugal caudoventral process below the maxillary tooth row and elliptical and caudodorsally orientated orbit.

Description: The skull and lower jaw are almost complete, and slightly compressed dorsoventrally, missing only the rostral tip and right caudolateral corner (Fig. 1). The small size and relatively large orbit indicate that this specimen is probably a juvenile. In lateral view, the skull deepens caudally, reaching its greatest measure across the lower temporal fenestra. In dorsal view, the skull is widest across the centers of the orbits due to the lateral flaring of the jugals. The external naris is not visible. No antorbital fossa or fenestra are evident. Both the orbit and the lower temporal fenestra are relatively large, and direct caudodorsally.

Only the caudodorsal process of the premaxilla is

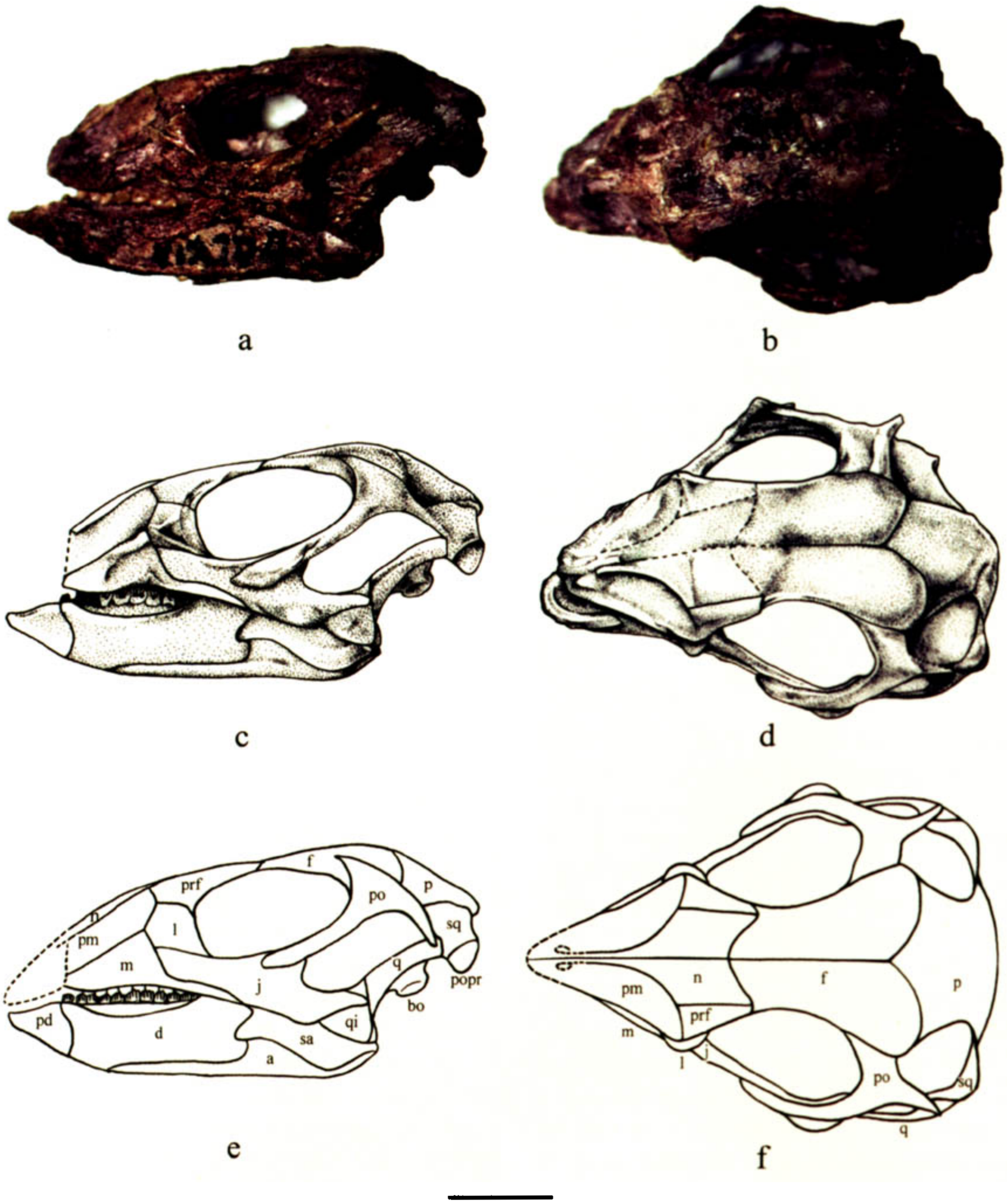

Fig. 1. Skull and lower jaw of *Hongshanosaurus houi* gen. et sp. nov. in left lateral (a, c, e) and dorsal (b, d, f) views.
a and b: photographs; c and d: schematics; e and f: reconstructions.
Abbreviations: a – angular; bo – basioccipital; d – dentary; f – frontal; j – jugal; l – lacrimal; m – maxilla; n – nasal; p – parietal; pd – predentary; pm – premaxilla; po – postorbital; popr – paroccipital process; prf – prefrontal; q – quadrate; qj – quadratojugal; sa – surangular; sq – squamosal.
Scale bar equals 1 cm.

preserved. It is relatively enlarged between the nasal dorsally and the maxilla ventrally, and contacts the prefrontal and lacrimal caudally. The rostral portion of the maxilla is situated below the caudodorsal process of the premaxilla. The caudal portion of the maxilla is largely overlapped by the rostral process of the jugal, and contacts the lacrimal caudodorsally. The dentigerous margin of the maxilla is well inset medially. The lacrimal is encircled by the prefrontal, the premaxilla, the maxilla, and the jugal, and forms the rostral border of the orbit. Two ridges on the

Table 1 Character-state listing

No.	Characters	0	1	2
1	Rostral bone	absent	present	
2	Ventral border of premaxilla	level with ventral border of maxilla	downward placed	
3	Diastema between premaxilla and maxilla	absent	present	
4	Caudodorsal process of premaxilla	narrow	enlarged	
5	Premaxilla-lacrimal contact	absent	present	
6	Maxillary buccal emargination	absent	present	
7	Rostral process of maxilla	absent	present	
8	Narial fossa position	adjacent to the ventral margin of the premaxilla	separated by a flat margin from, the ventral margin of the premaxilla	
9	External naris position	low	high and caudally positioned	
10	External naris size	small	enlarged	
11	Antorbital fenestra	present	absent	
12	Nasal: long rostral process beyond the external naris	absent	present	
13	Lacrimal: an open canal on the lateral surface	absent	present	
14	Lacrimal: rostrally enlarged	absent	present	
15	Preorbital length	more than 50% basal skull length	50-40% basal skull length	less than 40% basal skull length
16	Palpebral	present	absent	
17	Jugal infraorbital ramus: dorsoventral width	less than width of the infratemporal ramus.	equal or more than width of the infratemporal ramus.	
18	Jugal lateral expansion	absent	present	
19	Jugal lateral expansion position	from the midsection of the infrotemporal bar	from the caudal end of the jugal	
20	Jugal: caudoventral extension	absent	present	
21	Jugal-quadratojugal caudoventral projection below the maxillary tooth row	absent	present	
22	Quadratojugal reduction	absent	caudally	rostrally
23	Quadrate direction	vertical	slopes caudodorsally	
24	Quadrate foramen	absent	present	
25	Jugal-postorbital joint	long jugal process of the postorbital	solid joint	scarf joint
26	Tubercle on postorbital-squamosal bar	absent	present	
27	Frontal-parietal bulge	absent	present	
28	Domed skull roof	absent	present	
29	Supratemporal fenestra reduction	absent	present	
30	Parietal-squamosal shelf	absent	present	
31	Squamosal contribution to parietal-squamosal shelf	half	more than half	less than half
32	Paroccipital process	laterally extended	ventrally extended	
33	Paroccipital-squamosal contact	slender	stout	
34	Occipital condyle facing	caudally	caudoventrally	
35	Basicranial region	long	short	
36	Predentary size	small	enlarged	
37	Predentary rostral end in dorsal view	round	pointed	
38	Predentary bilobate and enlarged	absent	present	
39	Dentary coronoid depth	low	high	
40	Jaw articulation	level with maxillary tooth row	ventral to maxillary tooth row	
41	Predentary tooth number	more than 4	less than 5	
42	Premaxillary teeth	present	absent	
43	Premaxillary tooth row	level with	ventral to the maxillary tooth row	
44	Maxillary tooth number	more than 10	less than 10	

lateral surface of the lacrimal run caudodorsally and caudoventrally, respectively, surrounding a canal in between. The rostral process of the jugal covers the caudal end of the maxilla, and underlies the lacrimal. The jugal borders the orbit; its postorbital process is almost entirely covered laterally by the jugal process of the postorbital. Caudally, the jugal forms the ventral border of the lower temporal fenestra. A boss projects laterally from its ventral portion, below the lower temporal fenestra. The jugal tapers caudally, covering the quadratojugal laterally. The quadratojugal forms the ventral and caudolateral corner of the skull. The dorsal process of the quadratojugal wedges between the jugal laterally and the quadrate medially.

The nasal possesses a relatively long rostral process, and overlaps the premaxilla and the prefrontal ventrally. The prefrontal forms the rostrodorsal border of the orbit. It contacts the lacrimal ventrally, the premaxilla rostrally, the nasal dorsally, and the frontal caudally. The frontal forms

Table 2 Taxon character-state matrix

Taxon	5 10 15 20 25 30 35 40
Lesothosaurus	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Heterodontosaurus	0 0 1 0 1 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 0 0 0
Hypsilophodon	0 1 1 0 0 1 1 1 0 1 0 0 0 1 0 0 0 0 - 0 0 2 0 1 2 0 0 0 0 0 0 1 0 0 0 1 0 1 1 1 0 0 1 0
Hongshanosaurus	? 0 1 1 1 1 0 ? ? 0 1 ? 1 0 1 ? 1 1 1 0 1 1 1 0 0 0 1 0 0 1 1 0 1 1 1 1 0 0 1 1 ? ? 0 1
Stegoceras	0 0 1 0 0 1 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 1 0 0 1 1 1 1 1 0 0 1 1 1 1 0 ? 1 1 1 0 0 0
Psittacosaurus	1 0 1 1 1 1 0 1 1 0 1 1 1 0 2 0 1 1 1 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 1 1 - 1 0 1
Archaeoceratops	1 0 1 0 0 1 0 1 0 0 1 0 0 0 2 0 1 1 0 1 0 1 1 0 1 0 0 0 0 1 2 0 0 0 0 1 1 1 1 0 1 0 0 0

the caudodorsal border of the orbit, and sutures with the nasal and prefrontal rostrally, the parietal caudally, and the postorbital caudolaterally. The two frontals are not fused to each other, and bear a slightly longitudinal bulge on its dorsal surface. The parietals are fused together. They suture with the frontal rostrally and the squamosal caudolaterally, and form the medial walls of the upper temporal fenestrae. The long jugal process of the postorbital borders the orbit caudally. On the right side, the caudal end of the squamosal process of the postorbital is acute, and points to the squamosal. The squamosal is situated at the caudolateral corner of the skull roof, and borders more than half of the caudal margin of the upper temporal fenestra. The quadrate is thin and slopes caudodorsally in lateral view, with its ventral portion covered by the quadratojugal. It is wide in caudal view, with a groove running dorsoventrally along its midline.

The foramen magnum is surrounded by the supraoccipital dorsally, the exoccipitals laterally, and the basioccipital ventrally. The supraoccipital has a median ridge separating its two concave lateral parts. The exoccipitals form the lateral surface of the foramen magnum and possess stout, laterally projecting paroccipital processes. The basioccipital contributes a small portion to the ventral border of the foramen magnum, and constitutes most of the occipital condyle. The occipital condyle faces more ventrally than caudally, probably due to the dorsoventral compression. Rostrally, the basioccipital possesses a relatively short neck, then abuts the basisphenoid, together forming the relatively flat basal tubera with two widely separated processes. The basisphenoid is indistinguishable from the parasphenoid. Only the right pterygoid is clearly visible among the palatal bones. It has a medial process to meet its counterpart just rostral to the parasphenoid, and possesses a long quadrate process.

The predentary is short, and caps the dentary without a long ventral process. Its tip is round in dorsal view. The dentary is long and robust, contacting the surangular and the angular caudally. The angular is visible along the caudal two-thirds of the ventral margin of the lower jaw in lateral view, and extends beyond the articular joint in right lateral view.

It is unknown whether the premaxillary teeth exist or not. Six dentary teeth are preserved on each side. The width of their exposed crowns is larger than the height, and tightly arranged but do not overlap each other. There are about five distinct vertical ridges on the upper labial surface of each dentary crown.

3 Discussion

Hongshanosaurus shares a suite of features with *Psittacosaurus* (Coombs, 1982; Sereno et al., 1988; Russell and Zhao, 1996), such as an enlarged caudodorsal process of the premaxilla, a contact between the premaxilla and the lacrimal, a long rostral process of the nasal, an open canal on the lateral surface of the lacrimal, and fewer than ten maxillary teeth on each ramus. Although *Hongshanosaurus* is represented by a juvenile skull, it shows clearly many differences from the similar-sized *Psittacosaurus* skull (Cooms, 1982), such as an elliptical, and caudodorsally orientated orbit, a relatively long and low preorbital portion, and prominent jugal-quadratojugal caudoventral process below the maxillary tooth row. These suggest a new generic status is suitable.

Cladistic analysis (Table 1 and 2) including *Hongshanosaurus* confirms the monophyletic status of Marginocephalia; however, unlike most previous works (Sereno, 1986, 1999; Weishampel and Witmer, 1990), it puts *Heterodontosaurus* as the sister group to Marginocephalia (Fig. 2). The sister group relationship between *Heterodontosaurus* and Marginocephalia is strongly supported by a suite of features, including a short preorbital portion less than half of the skull length, lateral expansion of the jugal, and fewer than five premaxillary teeth.

Heterodontosaurus has long been considered as the most basal ornithopod. However, it lacks many key ornithopod features, which are present in *Hypsilophodon* and more

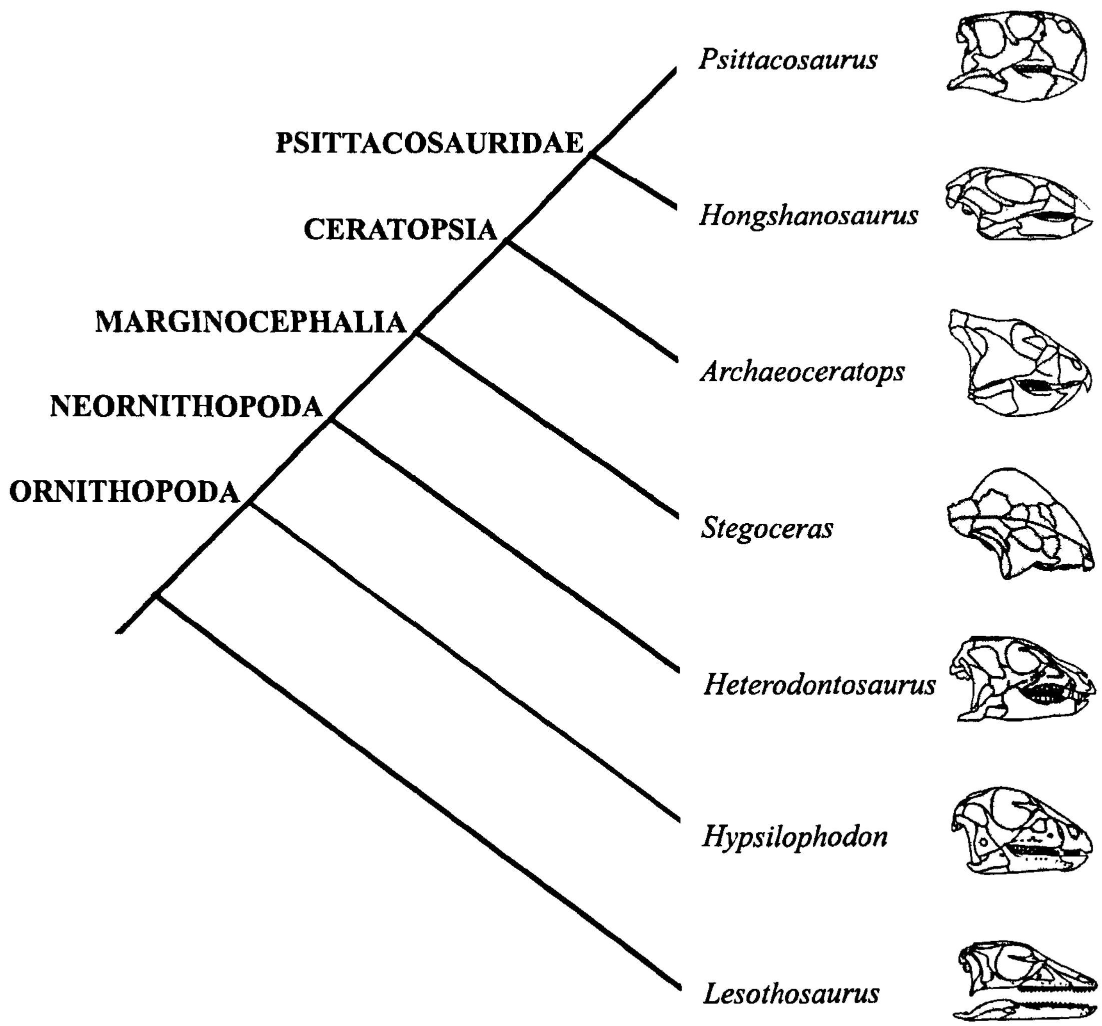

Fig. 2. Phylogenetic relationships of *Hongshanosaurus houi* gen. et sp. nov. based on a cladistic analysis from PAUP3.1.1 Branch-and-Bound search for seven taxa and 44 characters with all multi-state characters unordered. One most parsimonious tree is found at 61 steps with consistency index of 0.787 and retention index of 0.581.

derived forms, such as *Camptosaurus* and hadrosauriforms. These include an enlarged external naris, presence of a quadrate foramen, ventral placement of the premaxilla, presence of the rostral process of the maxilla, a rostrally elongated lacrimal, a rostrally reduced quadratojugal, a crescentic paroccipital process, and an enlarged bilobate predentary.

Our analysis confirms the monophyletic status for Marginocephalia, Ceratopsia, and Neoceratopsia. Marginocephalia is characterized by three derived cranial features: the presence of a parietosquamosal shelf, the caudally reduced quadratojugal, and the caudodorsally sloped quadrate. Ceratopsia possesses the following apomorphies: the presence of the rostral bone, a flat margin separating the narial fossa and the ventral margin of the premaxilla, absent of antorbital fenestra, and wide dorsoventral width of the jugal' s infraorbital ramus at least equal to its infratemporal ramus. Neoceratopsia evolved such derived features as the solid jugal-postorbital joint, caudally positioned jugal process, parietal dominated parietosquamosal shelf, pointed predentary rostral end, and bilobate and enlarged predentary.

The finding of the sister group relationship between *Heterodontosaurus* and Marginocephalia firmly stems the origin of Neornithopoda into the Early Jurassic, leaving the earliest Euornithopoda, the *Hypsilophodon*, to be Middle Jurassic. They two must originate no later than Early Jurassic.

4 Conclusions

Hongshanosaurus houi represented a new genus and species of Psittacosauridae. It is from the Lower Cretaceous Yixian Formation of Beipiao, Liaoning Province, China. Cladistic analysis including *Hongshanosaurus* confirms the monophyletic status for Marginocephalia, Ceratopsia, Neoceratopsia and Psittacosauridae. *Heterodontosaurus*, which is from the Lower Jurassic of Africa, is the sister taxon to Marginocephalia, rather than a basal Ornithopoda.

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