



Craniofacial Ontogeny of *Psittacosaurus mongoliensis* and *P. lujiatunensis* : Towards Evidence for the Developmental Underpinnings of Species Differences



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Introduction

The growth pattern of basal horned dinosaurs (Ceratopsia) are poorly understood, even though it has the potential to explain the developmental origins of evolutionary novelties (synapomorphies). The *Psittacosaurus* lineage is represented by multiple species, each having a growth series, and therefore is an ideal model for comparing patterns of growth with phylogeny. The model species investigated here include *P. mongoliensis* and *P. lujiatunensis*.

The growth of *P. mongoliensis* and *P. lujiatunensis* has been investigated in previous studies (Coombs, 1982; Hedrick et al., 2014; Sereno, 1990, 2010; Zhao et al., 2013; Zhou et al., 2006, 2007). The main shortcoming of these works is they are not focused on recovering growth series. The main objective of this study was to recover the growth series of *P. mongoliensis* and *P. lujiatunensis* following the work of Brochu (1996) by using cladistic analysis. Relevant developmental data were culled from the scientific literature and compiled into a cladistic data set of size-dependent and size-independent (Brinkman, 1988) skeletal characteristics of the skull and teeth. Secondary goals include characterization of each growth stage of each species and the comparison of the growth series to each other to identify shared growth changes.

Institutional Abbreviations

AMNH FARB, American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PKUP, Peking University Paleontological Collections, Beijing, China; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China; DMNH, Dalian Museum of Natural History, Dalian, Liaoning, China.

Materials and Methods

All available literature for *P. mongoliensis* and *P. lujiatunensis* was read (Bullar et al., 2019; Coombs, 1980, 1982; Hailu and Xing, 2005; Hedrick and Dodson, 2013; Hedrick et al., 2014; Osborn, 1923, 1924; Napoli et al., 2019; Sereno, 1990, 2010; Young, 1932; Zhao et al., 2013; Zhou et al., 2006, 2007) and relevant skull and tooth data were compiled into a character list (Appendix 1). The character list is uniform across all taxa for the purpose of efficient comparison of growth series *a posteriori*. Characters were scored 0 if they occurred in the least mature specimen, representing the least mature state, while states 1, 2, etc. represent states of increasing maturity (Brochu, 1996). Taxonomy of *P. mongoliensis* follows Sereno (1990); taxonomy of *P. lujiatunensis* follows Napoli et al. (2019).

The shared changes of the size of the orbit relative to the size of the skull is unclear based on the character description in Coombs (1982); it was included here assuming that despite ambiguity of exact ratios, a clear difference was observed.

Specimens and characters were compiled into data matrices (Tables 1, 2) in the software Mesquite (Maddison and Maddison, 2023). These data matrices were analyzed in the software PAUP (Swofford, 1998) using a Branch-and-Bound search. After a test search, three wildcard specimens were removed from *P. mongoliensis* to find optimal trees and increase resolution. No wildcard specimens were found in *P. lujiatunensis*. In analyses resulting in more than one tree, a strict consensus tree was obtained. Due to the small sample size ($n < 10$) for both species, a Spearman-Rank correlation test of size and maturity was not done. Once the growth series were obtained, homologous growth changes were identified between the two species.

Results

One growth series was recovered for *P. mongoliensis* (TL = 12; CI = 1.0; RC = 1.0), with three growth stages; synontomorphies are shown in Figure 1A. Three growth series with 16 steps were recovered for *P. lujiatunensis*. A strict consensus analysis of these trees was obtained (TL = 16; CI = 0.94; RC = 0.85) with six stages; synontomorphies are shown in Figure 1B. Comparison of the growth series identified three homologous growth changes; two occur in sequence, one occurs at different times between the two species (see Discussion).

Figure 1: Staff diagrams comparing the growth series of *P. mongoliensis* (A) and *P. lujiatunensis* (B). Growth stages are labeled at the nodes. Black dashed lines indicate shared synontomorphies that are out of sequence. Red dashed lines indicate shared synontomorphies in sequence. Orange text indicates a character reversal. Specimen images from (Bullar et al., 2019*; Osborn, 1924**; Sereno, 1990,*** 2010****; Zhou et al., 2006^X, 2007^{XX}). Skulls are not to scale.

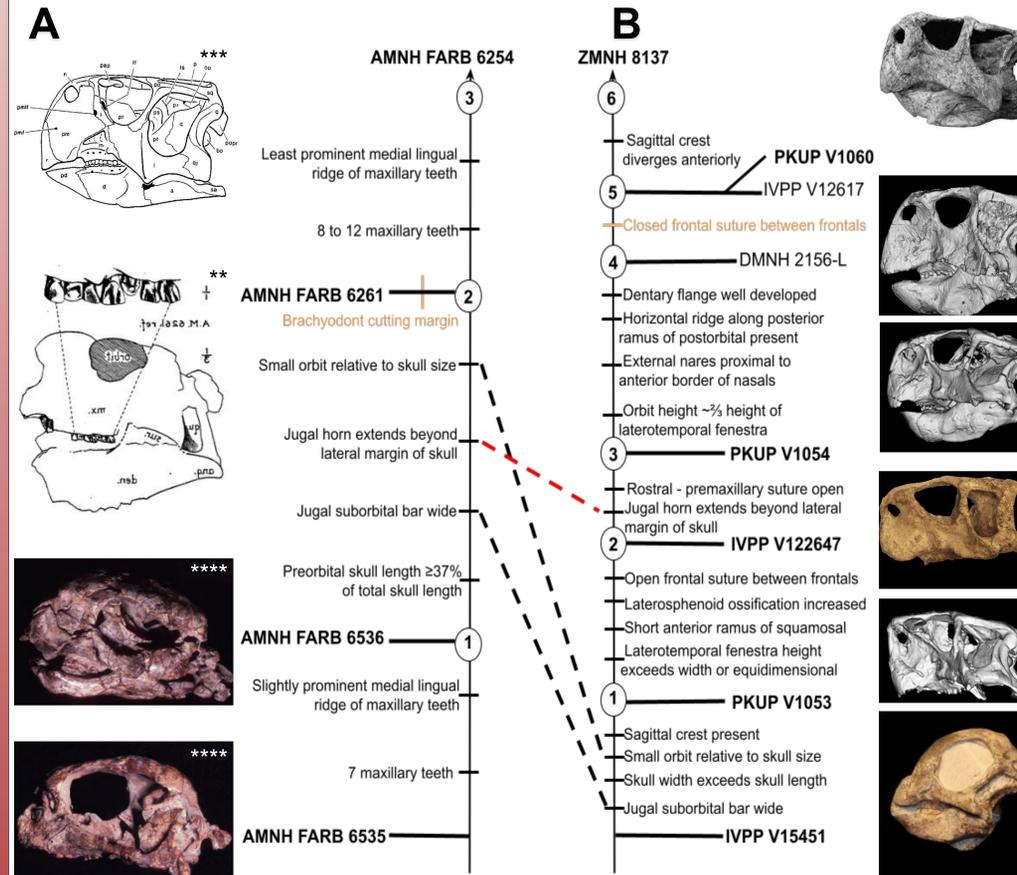


Table 1: Data matrix used to recover the ontogeny of *P. mongoliensis*.

Specimens	Characters						
	1	2	3	4	5	6	7
AMNH FARB 6254	1	1	1	2	1	1	2
AMNH FARB 6535	0	0	0	0	0	?	0
AMNH FARB 6536	0	0	0	1	0	1	?
AMNH FARB 6261	1	?	1	1	?	0	1

Table 2: Data matrix used to recover the ontogeny of *P. lujiatunensis*.

Specimens	Characters																		
	1	2	3	8	9	10	11	12	13	14	15	16	17	18	19				
ZMNH 8137	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0				
PKUP V1054	1	1	1	?	1	0	1	0	?	?	0	1	1	0	1				
PKUP V1053	?	0	1	?	?	0	0	0	1	0	0	0	0	?	0				
PKUP V1060	1	?	1	?	1	1	1	1	0	?	?	?	?	1	0				
DMNH 2156-L	?	1	?	1	1	1	1	?	1	?	?	?	?	?	1				
IVPP V15451	0	0	0	?	0	0	0	?	0	?	?	?	?	0	0				
IVPP V22647	1	0	1	0	1	0	1	0	1	?	?	?	?	?	1				
IVPP V12617	1	1	?	1	1	1	1	1	0	?	?	?	?	1	0				

Discussion

The two growth changes that occur in, presumably, the same order are evidence of the ancestral growth series of the *P. mongoliensis* and *P. lujiatunensis* clade. The growth change of a wide jugal horn in *P. mongoliensis* to occurs in the same growth stage with the two other shared growth changes, whereas in *P. lujiatunensis* it occurs in a later growth stage after those changes. If true, the growth series of a sister species of the *P. mongoliensis* and *P. lujiatunensis* clade is required to identify which timing event is ancestral for the lineage.

Alternatively, the early occurrence of the wide horn in *P. mongoliensis* is an artifact of undersampling of subadults. In contrast, more subadult specimens are sampled in *P. lujiatunensis* and so the characters are parsed with higher resolution; i.e., it shows that orbit size reduces before the jugal suborbital bar and horn changes. The undersampling hypothesis of *P. mongoliensis* can be tested by the addition of more subadults of that span the presumed gap in the growth series.

Although a single character list was used for both species, there is currently little overlap between the characters in the data matrices and, consequently, the optimized growth changes on the growth series. This deficit reflects the incomplete nature of the scientific literature, which can be rectified by first-hand study of the fossils.

The results for *P. lujiatunensis* show that the jugal horn lengthens after adult skull proportions are achieved. The same pattern is expected for *P. mongoliensis*.

Conclusions

- Two growth series were recovered, one for *P. mongoliensis* and one for *P. lujiatunensis*.
- Three homologous growth changes are shared between the two species; two co-occur in both growth series.
- One homologous growth character (jugal horn width) has a different timing between the two species, which is either a true difference or an artifact of a gap in the fossil record. Additional specimens of *P. mongoliensis* and a growth series of a sister species is required to test which hypothesis is defensible.

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Appendix 1: List of characters and characters states used to resolve the ontogeny of *P. mongoliensis* and *P. lujiatunensis*

- Orbit size relative to skull, lateral view (Coombs, 1980): large (0), small (1)
- Jugal horn prominence (Osborn 1923): incipient (0), extends beyond lateral margin of the skull (1)
- Jugal, suborbital bar, width (Coombs 1982): slender (0), wide (1)
- Maxilla, tooth count (Sereno 1990): 5 (0), 7 (1) 8-12 (2)
- Preorbital length relative to skull length (Sereno, 2010): ~30 - 35% (0), greater than ~37% (1)
- Tooth cutting margin (Osborn 1923): brachyodont (short crowned) (0), trilobed (1)
- Prominence of lingual median ridge of maxillary teeth (Osborn 1923): prominent (0), less prominent (1), least prominent (2)
- Rostral premaxillary suture, presence (Hedrick et al., 2014): obliterated (0), clear (1)
- Skull length relative to width (Hedrick et al., 2014): length exceeds width (0), width exceeds length (1)
- Orbit height relative to laterotemporal fenestra height: orbit height > 2/3 height of LTF (0), orbit height ~2/3 height of LTF (1)
- Laterotemporal fenestra, width relative to height (Sereno, 2010): width exceeds height (0), height exceeds width or equidimensional (1)
- Position of external nares, lateral view (You and Xu, 2005): deep to anterior border of nasals (0), proximal to anterior border of nasals (1)
- Parietals, sagittal crest, presence (Young, 1932): absent (0), present (1)
- Sagittal crest divergence anterior to supratemporal fenestra (Zhou et al., 2006): absent (0), present (1)
- Postorbital, presence of a horizontal ridge along posterior ramus (Zhou et al., 2006): absent (0), present (1)
- Squamosal, length of anterior ramus (Zhou et al., 2006): long (0), short (1)
- Laterosphenoid, degree of ossification (Zhou et al., 2006): poorly ossified (0), partially but incompletely ossified (1)
- Dentary, ventrolateral prominence of flange (Zhou et al., 2006): incipient (0), robust and well developed (1)
- Frontals, suture between frontals, presence (Hedrick et al., 2014): closed (0), open (1)

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