

New psittacosaurid highlights skull enlargement in horned dinosaurs

PAUL C. SERENO, ZHAO XIJIN, LORIN BROWN, and TAN LIN



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A new psittacosaurid is based on a nearly complete articulated skeleton from northeastern China that differs principally in skull size as compared to the most common and widespread species, *Psittacosaurus mongoliensis*. The skull of *Psittacosaurus major* sp. nov., is 25% larger despite very similar postcranial skeletal dimensions. Such selective skull enlargement is very unusual. Skull size in ceratopsians, in general, scales with positive allometry relative to body mass: species of greater mass have proportionately larger skulls. This pattern stands in marked contrast to that for other vertebrate herbivores, in which larger-bodied species either have proportionately similar or smaller skulls relative to body mass. Larger-bodied ceratopsians evolved skulls that are 50% or more of trunk length—as measured without their expansive cranial frill. Although contemporaneous duck-billed dinosaurs also exhibit some positive allometry in the skull, skull length remains approximately 35% of trunk length. The evolution of extraordinary absolute and relative skull size among ceratopsians appears to have been driven by sexual selection and involved the tandem evolution of reduced head mobility and an obligate quadrupedal posture.

Key words: Ornithischia, Marginocephalia, *Psittacosaurus*, Cretaceous, Yixian Formation, China.

Paul C. Sereno [dinosaur@uchicago.edu], Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, IL 60637, USA;

Zhao Xijin [zhaolu54@263.net], Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing 100044, China;

Lorin Brown [kidbones@sbcglobal.net], 1650 45th Street, Munster, IN 46321, USA;

Tan Lin [firsttan@sina.com], Long Hao Geologic and Paleontological Research Center, Bureau of Land and Resources, Hohhot 010010, Nei Mongol Autonomous Region, China.

Introduction

Comparison of skull length *versus* body mass in most tetrapods shows that larger animals of similar design have skulls that are proportionately the same or somewhat smaller in length. Skull length, in other words, scales isometrically or somewhat negatively in the vast majority of tetrapods (MacFadden 1986; Van Valkenburgh 1990). Across mammalian ungulates, skull length and body mass are so tightly correlated that the former often has been used as a proxy for the latter (Janis 1990).

Here we describe a very peculiar case among dinosaurs where one species has a skull some 25–30% larger than a closely related species despite similar postcranial dimensions. The case involves a new species of the Early Cretaceous-age parrot-beaked dinosaur *Psittacosaurus*. It highlights the unusual role played by skull size in ceratopsian evolution. Ceratopsids of Late Cretaceous age, in turn, evolved the largest skulls of any terrestrial herbivores, whether measured in relative or absolute dimensions. This trend in skull enlargement in larger-bodied species can be characterized quantitatively by plotting skull length as a function of estimated body mass.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; LH, Long Hao Institute for Stratigraphic Paleontology, Hohhot, Nei Mongol Autonomous Region, China.

Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Ceratopsia Marsh, 1890

Psittacosauridae Osborn, 1923

Genus *Psittacosaurus* Osborn, 1923

Psittacosaurus major sp. nov.

Derivation of the name: From the Latin, *major*, meaning greater.

Holotype: LH PV1, articulated skull and nearly complete postcranial skeleton (Figs. 1–3). The skull is nearly complete lacking only the right, and most of the left, palpebral, and portions of the right postorbital and squamosal. The postcranial skeleton lacks the left pubis, right radius and portions of the right manus, left tibia and fibula, and portions of the left pes.

Type locality: Near Beipiao City, Liaoning Province, China.

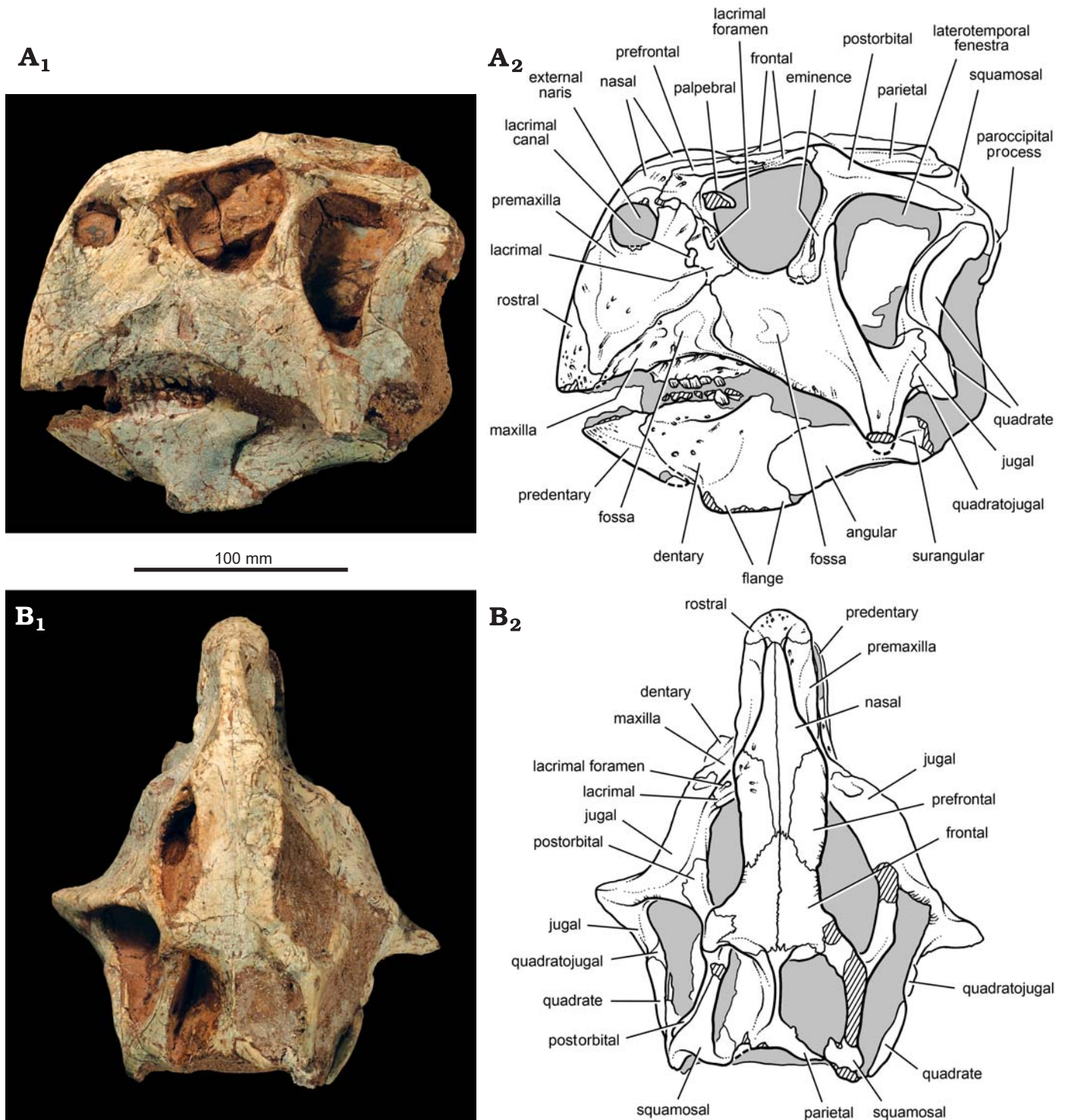


Fig. 1. Skull of *Psittacosaurus major* sp. nov., LHPV 1, Near Beipiao City, Liaoning Province, China, lower portion of the Lower Cretaceous Yixian Formation, in lateral (A) and dorsal (B) views. A₁ and A₂, photographs; A₂ and B₂, explanatory drawings of the same. In A₂ and B₂ the cross-hatching indicates the broken bone and the tone the matrix.

Type horizon: Lower portion of the Yixian Formation, Lower Cretaceous (Berriasian to Valanginian in age; Wang et al. 1998).

Diagnosis.—Psittacosaurid with a large skull relative to its postcranial skeleton (30% larger than *Psittacosaurus mongoliensis* and most other species); transversely narrow dor-

sal skull roof as a result of the narrowest proportions of the nasals and frontals among psittacosaur species; the most prominent dentary flanges of any psittacosaur species with a depth approximately one-third that of the mandibular ramus; ventrolaterally projecting jugal horn; absence (clo-

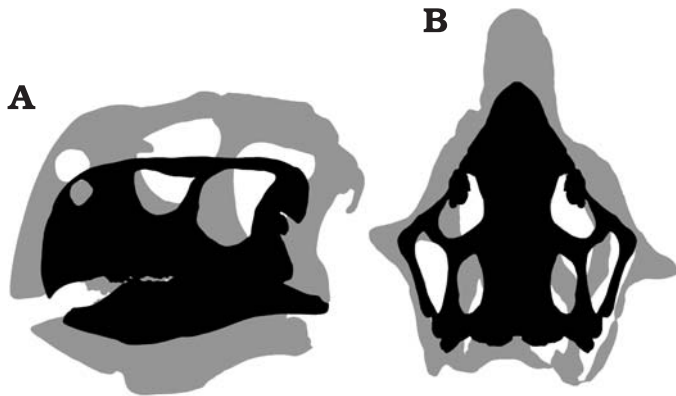


Fig. 2. Relative size of the skull of the adult holotypic specimens of *Psittacosaurus mongoliensis* (black) and *Psittacosaurus major* sp. nov. (grey) in lateral (A) and dorsal (B) views.

sure) of the external mandibular fenestra as in *Psittacosaurus sinensis* and *P. neimongoliensis*; seven sacral vertebrae (one dorsosacral added with rib attachment to the distal end of the preacetabular process), one more than in other psittacosaur species.

Description.—Almost all of the diagnostic features of *Psittacosaurus major* sp. nov. reside in the skull (Figs. 1, 2). In lateral view, the oval profile of the skull of *P. major* is the result of the relatively short snout and pronounced dentary flanges (Fig. 1A). Preorbital length is approximately 33% of skull length, similar to that in *P. sinensis* and intermediate between that in *P. meileyingensis* (27%) and *P. mongoliensis* (37%; Sereno 1987). In profile *P. major* most closely resembles *P. meileyingensis* (Sereno and Zhao 1988) as both species have pronounced, projecting mandibular flanges and an angular with very deep proportions (deeper than the surangular). In the posteroventral corner of the skull, the jugal and quadrate and the quadratojugal and squamosal approach each other more closely than in other species but do not establish sutural contact. The mandibular fenestra, which is retained as a small opening between the dentary, surangular and angular in all other psittacosaurid species, is closed in *P. major* as preserved on both sides of the skull.

In dorsal view, the skull is very similar to that of *P. mongoliensis* except for the narrow proportions of the nasals and frontals (Fig. 1B). Only a narrow median exposure of the nasals separates the prefrontals, and the sides of the snout are exposed to each side of the nasals in dorsal view. The frontals do not expand broadly posterior to the orbit. As a result, more of the laterotemporal region is exposed in dorsal view than in *P. mongoliensis*. The junction of the postorbital and frontal is swollen. Along the postorbital bar, the edge of the postorbital is everted but not swollen into a boss as in *P. sinensis*. The ventrolaterally projecting jugal horns are more prominently developed than in *P. mongoliensis* and *P. meileyingensis* and do not project as strongly laterally as in *P. sinensis* and *P. xingjiangensis* (Sereno et al. 1988). In lateral view, the tip of the jugal horn is situated ventral, rather than anterior, to the laterotemporal fenestra.

Table 1. Select measurements (cm) of *Psittacosaurus mongoliensis* (AMNH 6253; Sereno 1987) and *Psittacosaurus major* sp. nov. (LH PV1). Parentheses indicate estimate.

Measurement	<i>Psittacosaurus mongoliensis</i>	<i>Psittacosaurus major</i> sp. nov.
Skull		
Length in midline	15.2 ¹	20.3
Width across jugals	14.2 ¹	18.5
Axial column (centrum length)		
Cervical 2	2.4	2.4
Cervical 3	1.9	1.8
Cervical 4	1.8	1.8
Cervical 5	1.9	2.0
Cervical 6	(1.8)	2.2
Cervical 7	1.7	1.6
Cervical 8	1.9	1.8
Cervical 9	2.1	1.8
Dorsal 15	(2.1)	(2.2)
Caudal 6	1.8	1.8
Appendicular skeleton (maximum length)		
Scapula	14.8	17.1
Humerus	12.6	14.9
Radius	8.1	9.1
Metacarpal III	3.1	3.1
Femur	15.7	17.2
Tibia	18.1 ¹	19.7
Metatarsal III	7.9	8.6

¹ AMNH 6254

The maxillary and dentary crowns, as exposed in lateral view, are very similar to that in *Psittacosaurus mongoliensis* (Sereno and Zhao 1988). The lateral aspect of each maxillary crown is divided into three parts—a central low primary ridge and two lobes to either side. Low secondary ridges are present on the lobes, the anterior narrower than the posterior lobe. The lateral aspect of the dentary crowns is smooth. A bulbous primary ridge on the medial side is exposed along the apical wear facet in cross-section.

The vertebral column is nearly identical in form and size to that in *P. mongoliensis* (Table 1). The axis is not noticeably longer or more robust despite the relative increase in the size of the skull. The sacrum has incorporated an additional dorsal vertebra for a total of seven (Fig. 3). There are only six sacral vertebrae in other psittacosaurid species in which the sacrum is known. In these species, the rib of the first sacral contacts the base of the preacetabular process. In *P. major*, in contrast, the rib of the first sacral articulates with a raised articular facet close to the distal end of the preacetabular process, and the second sacral contacts the base of the process (Fig. 3). An additional dorsosacral, thus, appears to have been added in *P. major*. The centrum of this dorsosacral vertebra is fully coossified with that of the successive sacral.

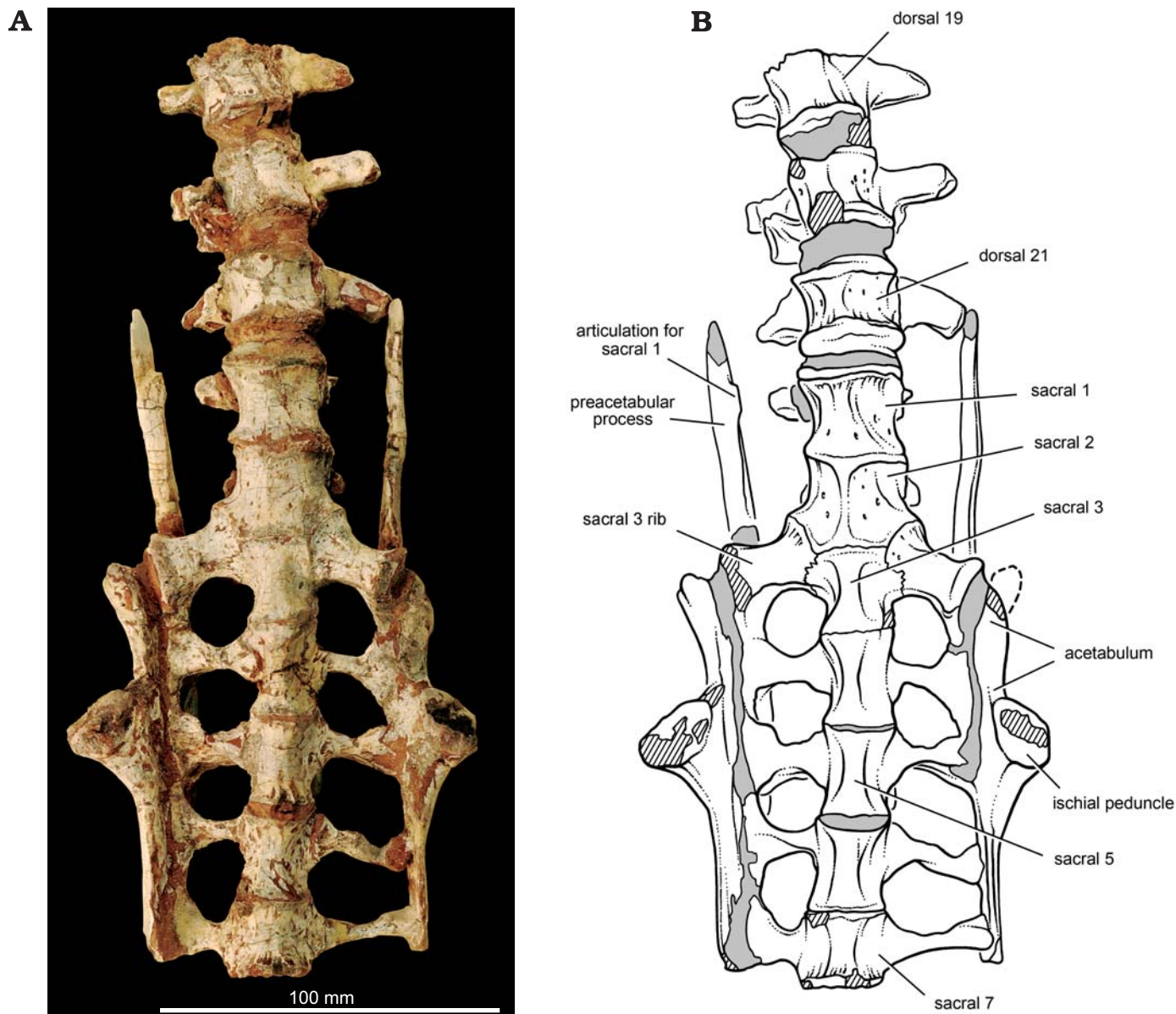


Fig. 3. Sacrum and articulated ilia of *Psittacosaurus major* sp. nov., LHPV 1, Near Beipiao City, Liaoning Province, China, lower portion of the Lower Cretaceous Yixian Formation. **A.** Photograph of in ventral view. **B.** Explanatory drawing of the same, showing broken bone (cross-hatching) and areas of matrix (tone).

The postcranial skeleton is remarkably conservative in species within the genus *Psittacosaurus*, and *P. major* is no exception. The major limb bones (proximal two segments) are approximately 10–15% longer than respective bones in the holotype of *Psittacosaurus mongoliensis* (Table 1). The additional length is matched by added girth, so the long bones have very similar internal proportions. The proportions of the major long bones within fore and hind limbs are also similar to that in *P. mongoliensis*. The unguals on the manus are intermediate in form between a recurved claw and flattened hoof, as is the case in other species of *Psittacosaurus*. Thus there is no evidence from the manual unguals to suggest that *P. major* emphasized quadrupedal posture any more than other psittacosaurids. The manual unguals in neoceratopsians, in contrast,

are usually broader and more hoof-shaped corresponding with an habitual quadrupedal stance (Fig. 4).

Materials and methods

Measurements.—The comparisons in this paper involve large-scale changes in the size and proportions of the skull in living and extinct tetrapods, changes that may be detected from reasonably accurate measurements, photographs, and skeletal reconstructions in the literature.

Skull length was used to estimate skull size rather than attempting to estimate skull volume or use another less intuitive proxy. Skull length was measured from the anterior tip

Table 2. Skull length, percentage of skull *versus* trunk length, and body mass in 26 dinosaurian herbivores for linear regression. Five frilled neoceratopsians are measured without, and with, the frill. Body mass estimates are from Seebacher (2001). Body mass of *Psittacosaurus major* sp. nov. was estimated by addition of 2 kg to that of *Psittacosaurus mongoliensis*.

No.	Species	Skull length (cm)	Skull/trunk length (%)	Body mass (kg)	References (skull, trunk lengths)
Ceratopsians					
1	<i>Psittacosaurus mongoliensis</i>	15	30	12.1	Sereno (1987)
2	<i>Psittacosaurus major</i> sp. nov.	20	39	14.1	this paper
3a	<i>Protoceratops andrewsi</i>	42	41	23.7	Brown and Schlaikjer (1940)
3b	<i>Protoceratops andrewsi</i> (with frill)	55	53	23.7	Brown and Schlaikjer (1940)
4a	<i>Centrosaurus apertus</i>	96	46	1,079.7	Brown (1914)
4b	<i>Centrosaurus apertus</i> (with frill)	157	76	1,079.7	Brown (1914)
5a	<i>Chasmosaurus belli</i>	88	50	1,658.7	Sternberg (1927)
5b	<i>Chasmosaurus belli</i> (with frill)	167	98	1,658.7	Sternberg (1927)
6a	<i>Triceratops horridus</i>	98	54	4,964.0	Ostrom and Wellnhofer (1986)
6b	<i>Triceratops horridus</i> (with frill)	113	86	4,964.0	Ostrom and Wellnhofer (1986)
7a	<i>Pentaceratops sternbergi</i>	130	63	4,846.0	Lehman (1998)
7b	<i>Pentaceratops sternbergi</i> (with frill)	243	118	4,846.0	Lehman (1998)
Ornithopods					
8	<i>Heterodontosaurus tucki</i>	12	36	1.8	Santa Luca (1980)
9	<i>Hypsilophodon foxii</i>	13	26	7.0	Galton (1974)
10	<i>Tenontosaurus tiletti</i>	64	32	242.9	Ostrom (1970)
11	<i>Camptosaurus browni</i>	40	31	268.4	Gilmore (1909)
12	<i>Iguanodon bernissartensis</i>	82	34	3,775.7	Norman (1980)
13	<i>Ouranosaurus nigeriensis</i>	65	32	1,120.4	Taquet (1976)
14	<i>Gryposaurus incurvimanus</i>	55	25	1,895.0	Horner (1992)
15	<i>Edmontosaurus annectens</i>	111	37	3,990.8	Lambe (1920), Lull and Wright (1942)
16	<i>Corythosaurus casuarius</i>	76	24	3,078.5	Ostrom (1961)
Thyreophorans					
17	<i>Scelidosaurus harrisonii</i>	19	20	64.5	Norman (2001)
18	<i>Sauropelta edwardsi</i>	46	30	902.9	Carpenter (1984)
19	<i>Euplocephalus tutus</i>	35	32	2,675.9	Coombs (1978), Carpenter (1982)
20	<i>Stegosaurus stenops</i>	39	19	2,610.6	Gilmore (1914)
Sauropodomorphs					
21	<i>Plateosaurus engelhardti</i>	36	17	1,072.6	Galton (1985)
22	<i>Shunosaurus lii</i>	44	18	4,793.5	Zhang (1988)
23	<i>Omeisaurus tiafuensis</i>	61	17	11,796.0	He et al. (1988)
24	<i>Apatosaurus louisae</i>	67	13	22,407.2	Berman and McIntosh (1978)
25	<i>Camarasaurus lentus</i>	51	17	11,652.2	Wilson and Sereno (1998), Madsen et al. (1995)
26	<i>Brachiosaurus brancai</i>	74	15	28,264.6	Janensch (1936)

of the snout to the posterior point on the occiput with the maxillary tooth row oriented horizontally. The posterior extremity was usually the paroccipital process or quadrate head. Posteriorly projecting cranial crests were not included unless indicated. The intention was to measure the length of the principal mass of the skull, irrespective of which cranial bone projected farther posteriorly. This measurement can be estimated in a straightforward manner when applied to skull figures in lateral view. For frilled ceratopsians, two measurements of skull length are provided, the larger value including the frill. The frill is the hypertrophied posterior margin of the

skull roof (composed of the parietal, squamosal, and often some marginal dermal ossicles) and was also measured by dropping a perpendicular to a horizontal aligned with the maxillary tooth row.

Trunk length was measured from the anterior to the posterior extremities of the pectoral and pelvic girdles, respectively. The anterior extremity is the anterior margin of the coracoid; the posterior extremity is the posterior tip of the ischium. These points span the volume occupied by the trunk. Trunk length, rather than postcranial length, may be the preferred proxy for estimating postcranial size, because it

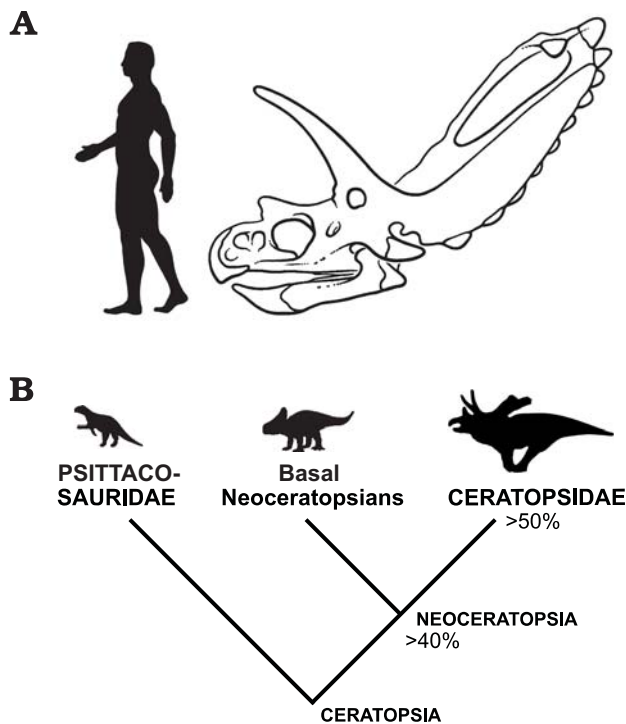


Fig. 4. Skull size in ceratopsians. **A.** Human silhouette (1.68 m) compared to an adult skull of the frilled ceratopsian *Pentaceratops sternbergi* (after Lehman 1998). **B.** Relationships among ceratopsians showing the shift to an obligate quadrupedal posture among neoceratopsians and stepwise increase in skull size (skull size shown as a percent of trunk length).

eliminates substantial variation in the length of cervical and caudal regions (e.g., sauropods).

Body mass estimates are based on the “polynomial” method that uses cross-sections to estimate axial volume and cylinders for limbs (Seebacher 2001). Although several alternative methods have been used to estimate body mass, most are in broad agreement for the majority of dinosaurs considered. The cited estimates are the most complete and methodologically-consistent set available. Finally, although the head is included in estimates of body mass, any correlation would only serve to lessen, rather than increase, the differential between skull length and body mass.

Statistical analysis.—We calculated two linear regressions (least squares) for body mass (x) against skull length and against cranial/postcranial length (y), respectively (Fig. 5). Body mass was plotted on a logarithmic scale to spread the data points for dinosaurs of small body mass. Original data, confidence intervals (95%) are shown, and slopes, y-intercepts, and coefficients of determination (r^2) are presented in Tables 2 and 3.

Discussion

Skull allometry in vertebrates.—There has been almost no quantitative exploration of scaling of skull size among dino-

saur. Positive allometry of the skull characterizes the largest terrestrial predators, which have large skulls relative to their body mass or to the length of their trunk. The skull in *Tyrannosaurus rex*, for example, measures 1.4 m in length, or about 40% of trunk length (Brochu 2002; Holtz 2004). Smaller-bodied basal tyrannosauroids with body lengths between 1–3 m (Xu et al. 2004, 2006), in contrast, have skulls that measure approximately 30% of trunk length, a more primitive and widespread proportion. Among dinosaurian herbivores, skull length only rarely exceeds 1 m in length and comprises a decreasing percentage of trunk length as body mass increases—with ceratopsians as the notable exception.

Living macropredators, such as *Varanus komodoensis* (Komodo dragon), tend to have relatively large skulls capable of ingesting or dismembering prey of large body mass. Varanids as a clade, however, still show little or no positive allometry in skull length (Emerson and Bramble 1993). In crocodylians, similarly, skull length scales isometrically with body size within and among species (Serenio et al. 2001). Although measurements tied to particular functional parameters may show significant positive allometry (Emerson and Bramble 1993), scaling of the skull in extant terrestrial vertebrates has not yielded markedly oversized skulls, especially among herbivores. Besides some birds with elongate snouts (specialized for piscivory, probing, or filter-feeding), marked positive allometry of the tetrapod skull is restricted to cetacean carnivores and filter-feeders in a marine habitat.

Several factors may play a role in constraining vertebrate skull size. First, interspecific brain volume scales with negative allometry (0.67–0.75 relative to body mass), and so the contribution by the neurocranium (*versus* the facial portion) almost invariably decreases as body size increases (Emerson and Bramble 1993). Second, inordinate head mass ultimately impedes locomotor speed and agility as well as trophic versatility on land. All large-bodied mammalian herbivores with proportionately large heads are quadrupeds with short necks and limited cranial mobility. Proboscideans, for example, rely on a muscular trunk for procurement of water and food-stuffs to compensate for limited cranial mobility.

Skull allometry in dinosaurian herbivores.—Trends in skull size were evaluated by linear regression of absolute and relative skull size across a sample of 26 herbivores ranging in body mass from about 2 to 30,000 kg (Fig. 5, Table 2). Skull

Table 3. Linear regression of skull length (cm) and skull/trunk length (%) *versus* body mass (kg) in 26 herbivorous dinosaur species.

Linear regression	Slope	y-Intercept	r^2
Skull length (cm) <i>versus</i> body mass (kg)			
Other dinosaurian herbivores (n = 19)	0.001	45.799	0.142
Ceratopsians (without frill) (n = 7)	0.017	39.986	0.692
Skull/trunk length (%) <i>versus</i> body mass (kg)			
Other dinosaurian herbivores (n = 19)	–0.001	28.215	0.377
Ceratopsians (without frill) (n = 7)	0.004	38.390	0.780

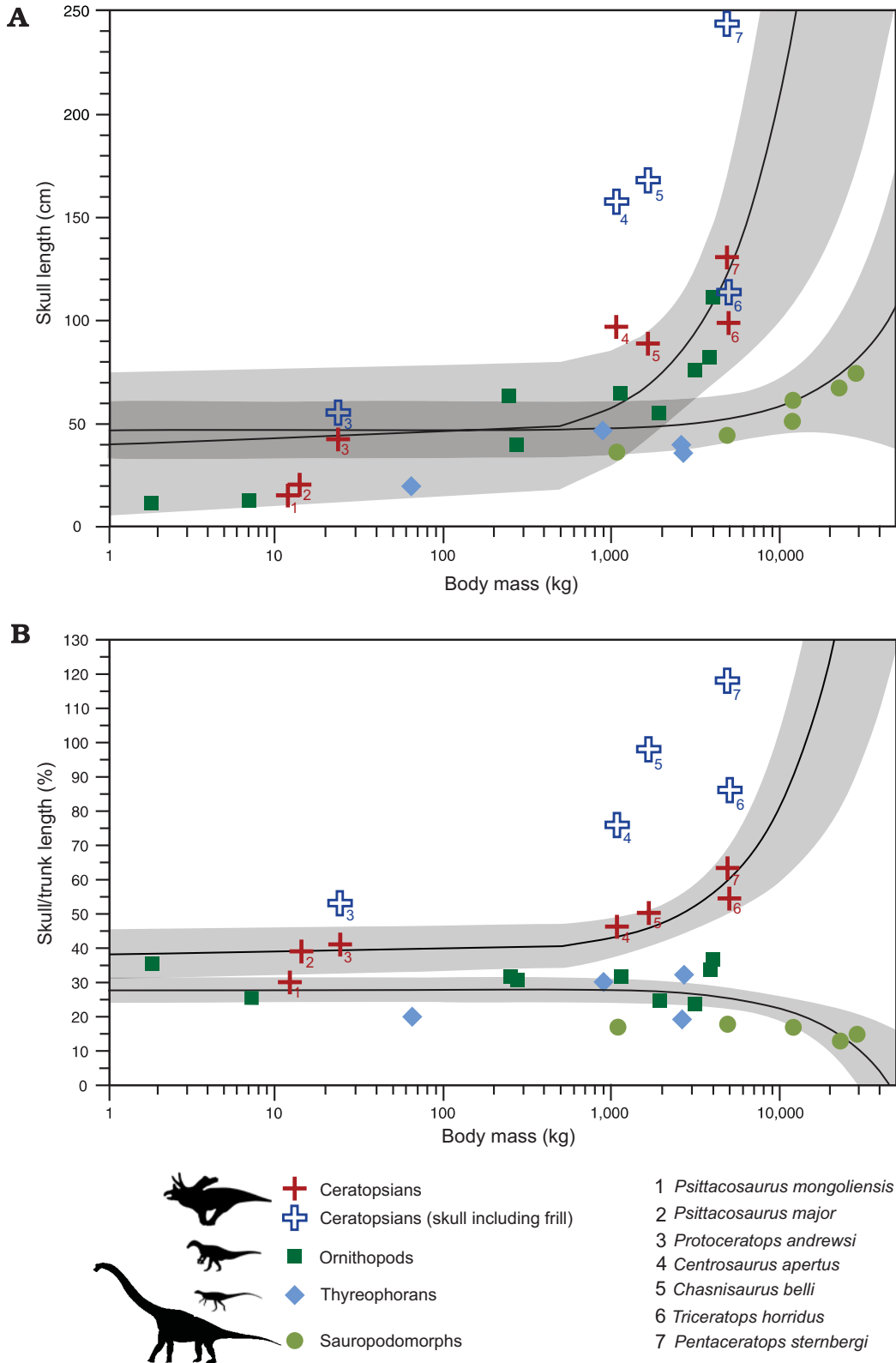


Fig. 5. Regression of skull dimensions (cm) against body mass (log kg) in dinosaurian herbivores. Seven ceratopsians are plotted (1–7); filled species (3–7) are plotted with, and without, the frill. **A.** Regression of skull length as a function of body mass shows that ceratopsians broadly overlap a comparable regression for other dinosaurian herbivores at body mass less than 100 kg. Larger-bodied ceratopsians (4–7; >1,000 kg), in contrast, have skulls approaching or exceeding a length of 1 m and plot outside the 95% confidence interval for other dinosaurian herbivores (lower curve). The largest ornithopods have comparable skull lengths to large-bodied ceratopsians. **B.** Regression of skull/trunk length as a function of body mass shows that ceratopsians have proportionately larger skulls even at moderate body masses between 10 and 100 kg broadly overlap a similar regression for other dinosaurian herbivores at body mass less than 100 kg. Larger-bodied ceratopsians (4–7; >1,000 kg), plot outside the 95% confidence interval for other dinosaurian herbivores including hadrosaurids (lower curve).

and trunk lengths were used as proxies for skull and trunk size, respectively, and regressed against body mass, as estimated by the "polynomial" method (see Materials and Methods). In order to better visualize data for smaller-bodied species, body mass was plotted on an exponential scale. Ceratopsians and nonceratopsians overlap at small body size but diverge at larger body size and were plotted separately.

In most ceratopsians, the posterior margin of the skull roof extends posterodorsally as an expanded frill of varying size, shape, orientation and ornamentation. Although composed almost entirely of typical roofing bones such as the parietal and squamosal, the frill is not directly comparable to the posterior margin of other skulls. Two skull lengths, thus, were measured and plotted for ceratopsians with frills: one with, and one without, the frill.

For 19 nonceratopsian herbivores, the absolute length of the skull ranged from 12 cm in the small-bodied ornithopod *Heterodontosaurus tucki* to 111 cm in the duckbill *Edmontosaurus annectens*. In stark contrast to mammalian ungulates, there is virtually no correlation between skull length and body mass (Fig. 5A, Table 3). The slope of this regression is near zero and the coefficient of determination (r^2 -value) is very low (0.142). Skull length increases most dramatically from about 12 to 60 cm while body mass increases from 10 to 100 kg. Above a body mass of 100 kg, skull length averages 60 cm (Fig. 5A, Table 2). Excluding the long-snouted hadrosauriform ornithopods, skull length in these moderate-to-large-bodied herbivores is remarkably constrained; absolute skull length varies by only a factor of two (from 35 to 74 cm) while body mass ranges 100-fold (from about 300 to 30,000 kg). Clearly there are severe constraints on maximum skull size in the vast majority of dinosaurian herbivores, such that skull length is kept well below 1 m for body mass that ranges across two orders of magnitude.

Hadrosauriform ornithopods, which include *Iguanodon*, *Ouranosaurus* and the duck-billed hadrosaurids, have relatively longer snouts and thus longer skulls than all other nonceratopsian herbivores. All hadrosauriforms lie above the 95% confidence interval for the regression of skull length against body mass (Fig. 5A). The longest hadrosauriform skull in the regression, pertaining to the hadrosaurid *Edmontosaurus annectens*, measures 111 cm. Hadrosaurids of even larger body size have been discovered; *Shantungosaurus* is among the largest and may have had a skull length approaching 150 cm (estimated from Hu 1973). Hadrosauriforms clearly have the longest skulls among nonceratopsian herbivores and completely overlap the size range for ceratopsians, as measured without the frill (Fig. 5A).

These two groups, nonetheless, are easily differentiated in a regression of skull size as a percentage of trunk size versus body mass (Fig. 5B). In hadrosauriforms, the skull is always less than 40% of trunk length; in all ceratopsians of comparable body mass, skull length always exceeds 45% of trunk length. Skull length approaching 40% of trunk length as in hadrosaurids and predators such as *Tyrannosaurus*, thus, may constitute a threshold, beyond which it may be impossible to

maintain even a facultative bipedal posture. Large-bodied ceratopsians, in contrast, are obligate quadrupeds and never attempt to balance body mass over hind limb supports alone.

The regression of skull size as a percentage of trunk size versus body mass also shows the virtual absence of correlation among nonceratopsian herbivores (Fig. 5B, Table 3). The slope of this regression is slightly negative and the coefficient of determination (r^2 -value) is very low (0.377). Herbivores up to 4000 kg, thus, show a fairly limited two-fold range of relative skull size, from about 19 to 37% of trunk length. The small ornithopod *Heterodontosaurus tucki* (1.8 kg) and the much larger hadrosaurid *Edmontosaurus annectens* (4000 kg), for example, both have skulls that are 37% of trunk length. Sauropodomorphs, which range well beyond 4000 kg in body mass, have proportionately smaller skulls that are only 15 to 20% of trunk length.

Skull allometry in ceratopsians.—Unusual cranial proportions first appear among psittacosaurids, the earliest and most basal ceratopsian clade (Fig. 4B). *Psittacosaurus mongoliensis* (Osborn 1923, 1924), one of the least modified of psittacosaurids, has the smallest skull of any ceratopsian relative to its postcranial skeleton. The skull is approximately 30% of trunk length, a proportion similar to that in other small dinosaurian herbivores. Skull length in *P. major* sp. nov. comprises approximately 40% of trunk length as in the frilled neoceratopsian *Protoceratops andrewsi* (as measured without the frill). The length differential between the skulls of the two psittacosaurid species, furthermore, would have been greater were it not for the longer snout proportions in *P. mongoliensis* (Fig. 2). When compared by volumetric displacement, the skull in *P. major* exceeds that in *P. mongoliensis* by 30%. This constitutes a significant increase in the mass of the head. The skull in *P. mongoliensis* may closely approximate the original cranial condition within the clade (Serenó 1990; You and Dodson 2004). If that is upheld, enlargement of the skull to 40% of trunk length may have occurred independently in psittacosaurids and neoceratopsians (Fig. 4).

Alone among all large terrestrial herbivores, neoceratopsians have evolved disproportionately large skulls, some of which approach 3 m in length (Fig. 4). In species such as *Pentaceratops sternbergi*, skull length actually exceeds trunk length (Lehman 1998). Ceratopsids have absolutely and relatively the largest skulls of any land vertebrate. Even when excluding the expansive posterior cranial frill, skull length in some species exceeds 1 m. Seven ceratopsians were evaluated including two psittacosaurids and a range of frilled neoceratopsians (Table 2).

The first regression compares absolute skull length and body mass (Fig. 5A). The slope is positive and the coefficient of determination (r^2 -value) higher than for nonceratopsians (0.692); large-bodied ceratopsians with body mass ranging from 1,000–4,000 kg have proportionately larger skulls, as measured without the frill (Table 3). In this regression, large-bodied ornithopods overlap the distribution of large-bodied ceratopsians. Separate regression of ornithopods (not shown)

parallels that for ceratopsians; large-bodied ornithopods, specifically the long-snouted hadrosauriforms, also exhibit positive allometry of skull size and lie outside the 95% confidence interval for other dinosaurian herbivores. Positive allometry of skull length relative to body mass in neoceratopsians and hadrosauriform ornithopods, thus, constitute notable exceptions among terrestrial herbivores.

The second regression plots relative skull length and clearly distinguishes neoceratopsians from hadrosauriform ornithopods and other dinosaurian herbivores (Fig. 5B). The slope is positive and the coefficient of determination ($r^2=0.780$) is higher than for nonceratopsians; large-bodied ceratopsians have proportionately larger skulls (as measured without the frill) relative to trunk length (Table 3). Skull length ranges from approximately 45–65% of trunk length. Positive allometry of skull/trunk proportions is unique to ceratopsians and yields striking proportions at large body size. In *Pentaceratops sternbergi*, for example, skull length including the frill (measured along a horizontal) actually exceeds trunk length (118%). Within ceratopsids, the ceratopsines (*Chasmosaurus belli*, *Triceratops horridus*, *Pentaceratops sternbergi*) appear to have longer skulls than centrosaurines (*Centrosaurus apertus*). Skull/trunk length percentage ranges from 50–63% in ceratopsines as compared to 46% for *Centrosaurus*. Although available data for centrosaurines are limited to a single species, several centrosaurine genera are remarkably similar and show species-specific traits only at maturity (Sampson et al. 1997).

Ceratopsian skull, neck and posture.—The ceratopsian skull was subject to marked sexual selection. Cranial horns and frills of variable size and shape appear late in growth, strongly suggesting that these structures functioned primarily as sexual characters in mate recognition and competition (Sampson et al. 1997). Many ceratopsian subgroups, such as psittacosaurids or centrosaurines, show little skeletal variation beyond species-specific features involving the shape, size, orientation or ornamentation of horns and frills. In ceratopsians, in addition, keratin extended from the horn or frill proper onto other bones of the skull, as shown by rugosities and impressed vascular tracts. Most of the external surface of the ceratopsid skull was enveloped in keratin, as evidenced by impressed vessels and surface texture (Horner 2002), which may have played a role in visual display. The overall size of the skull may well have been subject to sexual selection. In mammalian ungulates, in contrast, the keratin of horns is restricted to the bony horn core and does not extend over other cranial surfaces.

In neoceratopsians neck mobility was sacrificed for support, as relative skull size increased. The coossified anterior one-third of the cervical series in neoceratopsians prevented any intervertebral movement; the posterior two-thirds is composed of tall vertebrae with squat centra. Finally, the diameter of soft tissue attachment to the occiput and posterior aspect of the frill is very broad. Movement within the neck would have been extremely limited. Neoceratopsians, as a

consequence, are obligate quadrupeds with skulls positioned close to the ground for feeding. The transition from facultative biped to obligate quadruped is associated with an increase in skull size to more than 40% of trunk length (as measured excluding the frill; Fig. 4B).

Evolutionary constraint.—In closing, ceratopsians likely employed their cranial horns, frills and eventually much of the external skull surface in mate recognition and intraspecific rivalry (Sampson et al. 1997). Sexual selection, likewise, may well have driven the increase in absolute and relative size of the skull to dimensions not present elsewhere among terrestrial herbivores. Positive allometry of antlers in cervid mammals, by comparison, culminated in the enormous head armaments of *Megaloceras* (the so-called “Irish elk”). Yet in this case, antler enlargement had minimal impact on skull or other skeletal dimensions, as skull length in this cervid remained tightly correlated with body mass (Gould 1974). Dramatic skull size increase in ceratopsians, in contrast, evolved in tandem with a postural shift to obligate quadrupedality, the evolution of a unique cropping beak and slicing dentition, and the imposition of severe limitations on cervical and cranial mobility. Restriction of head movement during feeding constitutes a major trophic constraint and may explain the rarity of oversized skulls in large-bodied herbivores on land.

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