

Major cranial changes during *Triceratops* ontogeny

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This is the first cranial ontogenetic assessment of *Triceratops*, the well-known Late Cretaceous dinosaur distinguished by three horns and a massive parietal–squamosal frill. Our analysis is based on a growth series of 10 skulls, ranging from a 38 cm long baby skull to about 2 m long adult skulls. Four growth stages correspond to a suite of ontogenetic characters expressed in the postorbital horns, frill, nasal, epinasal horn and epoccipitals. Postorbital horns are straight stubs in early ontogeny, curve posteriorly in juveniles, straighten in subadults and recurve anteriorly in adults. The posterior margin of the baby frill is deeply scalloped. In early juveniles, the frill margin becomes ornamented by 17–19 delta-shaped epoccipitals. Epoccipitals are dorsoventrally compressed in subadults, strongly compressed and elongated in adults and ultimately merge onto the posterior frill margin in older adults. Ontogenetic trends within and between growth stages include: posterior frill margin transitions from scalloped to wavy and smooth; progressive exclusion of the supraoccipital from the foramen magnum; internal hollowing at the base of the postorbital horns; closure of the midline nasal suture; fusion of the epinasal onto the nasals; and epinasal expansion into a morphologically variable nasal horn. We hypothesize that the changes in horn orientation and epoccipital shape function to allow visual identity of juveniles, and signal their attainment of sexual maturity.

Keywords: dinosaurs; cranial ontogeny; *Triceratops*; Late Cretaceous

1. INTRODUCTION

Despite being one of the most common Late Cretaceous dinosaurs from North America, and known to science for over 100 years (Marsh 1889), only four non-adult *Triceratops* specimens are described in the literature: three postorbital horns (Brown & Schlaikjer 1940; Tokaryk 1997) and one partial skull (Goodwin *et al.* 2006). Historically, smaller *Triceratops* skulls and cranial elements were apparently overlooked, deemed highly incomplete or undesirable to collect. We report here on a *Triceratops* cranial growth series of 10 skulls (table 1) and over 28 partial skulls and individual cranial elements (table 2) from the Upper Cretaceous Hell Creek Formation, eastern Montana. Most have been collected since 1997. This assemblage provides an exceptional opportunity to document morphological characters and ontogenetic trends in four growth stages of *Triceratops*. Our sample of *Triceratops* was collected by the Museum of the Rockies (MOR) and the University of California Museum of Paleontology (UCMP), Berkeley field crews and prepared under our supervision. This is significant because many previously collected *Triceratops* skulls in museum collections have undergone extensive restoration, are composites or lack contextual field documentation, making their use unreliable (Ostrom & Wellnhofer 1986). Nonetheless, we reviewed the historically and scientifically important collection of *Triceratops* skulls in the Yale Peabody Museum (YPM). Each of the YPM skulls was determined to be an adult.

Most of the non-adult skulls in this study were found partially or completely disarticulated, allowing an exceptional view of the internal and external articulations of cranial elements. The skulls illustrated in figure 1 were

moulded and cast after the preparation was complete. The individual casts of the skull elements were reassembled and photographed. Reconstruction of missing elements is limited to the anterior portion of the youngest end member, UCMP 154452, and the nasal horn on the small juvenile skull, MOR 1199. The lower jaw of UCMP 154452 allows an accurate estimation of 38 cm for the length of this skull. The paired nasals in MOR 1199 preserve a rugose sutural surface dorsoanteriorly for articulation of an epinasal horn. Restoration was based on an isolated juvenile epinasal (MOR 1167). We use the term epinasal when this element is disarticulated from the skull and the term nasal horn when fusion occurs to the underlying nasals.

We identify a suite of cranial characters that are expressed in four growth stages of *Triceratops*. For convenience, we define and designate these four growth stages: baby, juvenile, subadult and adult. Each character suite is expressed in one specific growth stage represented by a skull or skulls listed in table 1. We also recognize a sequence of ontogenetic trends (see table 2). These ontogenetic trends are expressed within and across the sequence of growth stages. Table 2 lists the study set of specimens in growth stages with the ontogenetic trend(s) expressed.

Sixteen species of *Triceratops* have been described since the genus was first proposed by Marsh in 1889. Ostrom & Wellnhofer (1986) concluded that *Triceratops* was monospecific in their detailed assessment and revision of the genus. Forster (1996a) re-evaluated *Triceratops* and recognized two species: *Triceratops horridus* and *Triceratops prorsus*. We would expect the cranial ontogenetic characters identified in our study for *Triceratops* to be consistent, regardless of the number of species or genera accepted, because cranial ontogeny is conserved in closely related taxa. Furthermore, we propose that the sympatric and closely related ceratopsid *Torosaurus*, differentiated from

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Table 1. A growth series of 10 *Triceratops* skulls represents four growth stages: baby, juvenile, subadult and adult. (Abbreviations: d–v, dorsoventrally compressed; est, estimate; exo, exoccipital; np, not preserved; po, postorbital; so, supraoccipital; sq, squamosal.)

<i>Triceratops</i> skull	growth stage	po horn orientation (curvature)	po horn length above orbit (cm)	po horn diameter at base (cm)	nasal midline suture	nasal horn fusion to nasals	epoccipitals	caudal frill margin	braincase so between exo	skull length (cm)	basal skull length (cm)
UCMP 154452	baby	straight, no curvature	3.5	6.5	np	np		strongly scalloped	yes	38 (est)	28 (est)
MOR 1199	juvenile	posterior	19	20	open	np	delta-shaped	scalloped	yes	87	35.5
UCMP 136306	juvenile	posterior	40	29	np	unfused	delta-shaped	scalloped	yes	110	
MOR 1110	juvenile	posterior	50	39	open	unfused	np	scalloped	yes	135	61
UCMP 137263	subadult	anterior tip of horn	49	42	open	unfused	np	wavy	np	160 (est)	
MOR 1120	subadult	posterior anterior tip of horn	53	52	closed dorsally, open ventrally	fused dorsally, open ventrally	d–v	wavy	yes	165	69
MOR 699	subadult	anterior	np	np	np	np	d–v	wavy	np	165 (est)	
MOR 1604	subadult	anterior	60	54	closed	fused	np	smooth (sq only)	no	200 (est)	
MOR 004	adult	anterior	41	59	closed	fused	d–v, merged onto frill	smooth	np	208	94
UCMP 113697	adult	anterior	82	69	np	np	np	smooth	no	225	

Table 2. The study set of *Triceratops* and the ontogenetic trends expressed within and across four growth stages. (Abbreviations: MOR, Museum of the Rockies; UCMP, University of California Museum of Paleontology. A, parietal–squamosal frill with scalloped posterior margin; B, posterior frill margin less scalloped to wavy; C, epoccipitals merged onto smooth caudal frill margin; D, fan-shaped frill; E, posterior postorbital horn curvature; F, excavation of postorbital horn internally; G, fusion of nasals; H, fusion of nasal horn onto the nasals; I, supraoccipital present between the exoccipitals; J, anterior postorbital horn recurvature.)

<i>Triceratops</i>	element	growth stage	ontogenetic trends										
			A	B	C	D	E	F	G	H	I	J	
UCMP 154452	skull	baby	x									x	
MOR 652	squamosal	baby	x										
MOR 1098	postorbital horn	baby											
MOR 1053	postorbital horn	baby											
UCMP 158441	postorbital horn	baby											
UCMP 399749	postorbital horn	baby											
MOR 1199	skull	juvenile		x				x					
UCMP 136306	skull	juvenile		x				x					
MOR 1110	skull	juvenile		x				x	x				
UCMP 159233	partial skull	juvenile											
MOR 1129	partial skull	juvenile											
UCMP 139292	postorbital horn, maxillary, braincase	juvenile											
UCMP 150234	parietal	juvenile		x				x					
MOR 539	postorbital horns	juvenile						x					
UCMP 186583	epinasal	juvenile											
MOR 989	epinasal	juvenile											
MOR 1167	epinasal	juvenile											
UCMP 137263	skull	subadult		x		x							x
MOR 1120	skull	subadult		x	x	x			x	x	x	x	x
MOR 699	skull	subadult		x		x						x	x
UCMP 136092	skull	subadult		x		x						x	
UCMP 137266	partial skull and skeleton	subadult											x
UCMP 173739	postorbital horn	subadult											x
MOR 1604	skull	adult			x					x	x		x
MOR 004	skull	adult			x	x				x	x		x
MOR 1625	skull	adult			x					x	x		x
UCMP 113697	skull	adult			x	x			x	x			x
UCMP 174838	skull	adult			x					x	x		x
UCMP 136589	partial skull	adult			x								x
UCMP 140416	partial skull	adult					x						x
UCMP 129205	premaxillae, nasals, nasal horn	adult					x						

Triceratops on the basis of a fenestrated parietal–squamosal frill, possesses a similar cranial ontogeny to *Triceratops*. This hypothesis is supported by their shared adult morphology of anteriorly directed postorbital horns with hollow bases and dorsoventrally compressed epoccipitals merged onto the posterior edge of the parietal–squamosal frill.

2. RESULTS AND DISCUSSION

(a) Ontogenetic character stages

Baby growth stage characters are: short boxy frill (parietal + squamosal); deeply scalloped posterior frill margin; short, non-directional postorbital horns; and large orbit and foreshortened face. The baby growth stage and youngest end member is represented by UCMP 154452 (figure 1a), the smallest *Triceratops* skull yet known (Goodwin *et al.* 2006). The postorbital horn, American Museum of Natural History 5450, described by Brown & Schlaikjer (1940), and

the two left postorbital horns, Royal Saskatchewan Museum P2299.1 and P2623.1, described by Tokaryk (1997), are referable to this growth stage. Juvenile growth stage characters are posteriorly directed postorbital horns and delta-shaped epoccipitals. The juvenile growth stage is represented by two skulls: a small juvenile (MOR 1199, figure 1b) and a large juvenile (MOR 1110, figure 1c). Subadult growth stage characters are: postorbital horns reoriented anteriorly, while the tip of the horn preserves the prior posterior orientation; epinasal fused onto the underlying paired nasals; epoccipitals compressed dorsoventrally but maintain a triangular profile. The subadult growth stage is characterized by the *Triceratops* skull, MOR 1120 (figure 1d). Adult growth stage characters are: postorbital horns oriented strongly anteriorly; epoccipitals flattened dorsoventrally; and merge onto the posterior frill margin. The adult growth stage of *Triceratops* is exemplified by MOR 004 (figure 1e).

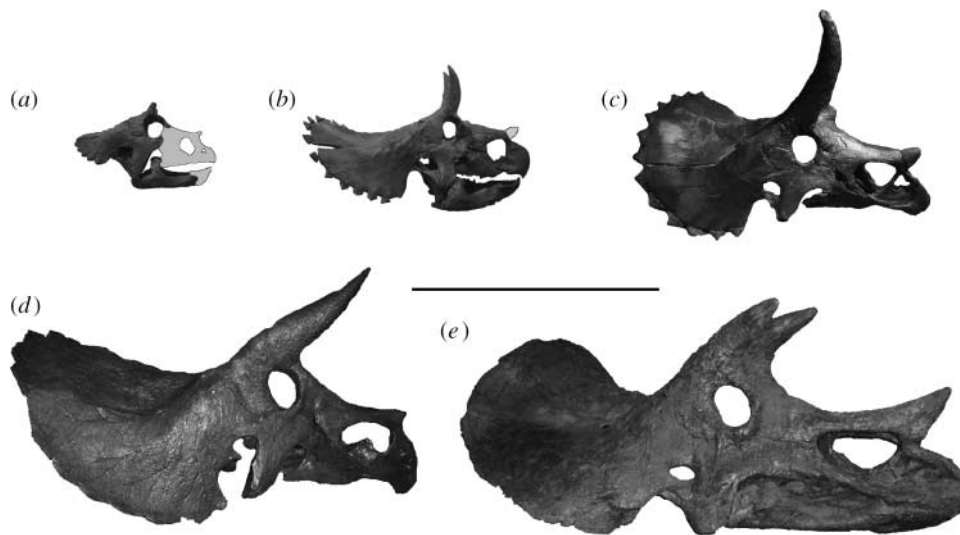


Figure 1. Five examples of the four cranial ontogenetic growth stages in *Triceratops* skulls in right lateral view. Skull length is given in parentheses. (a) UCM 154452, baby skull (38 cm); (b) MOR 1199, small juvenile skull (87 cm); (c) MOR 1110, large juvenile skull (135 cm); (d) MOR 1120, subadult skull (165 cm); and (e) MOR 004, adult skull (208 cm). Reconstructed area of (a) UCM 154452 and the epinasal in (b) MOR 1199 are drawn in white. Scale bar, 1 m.

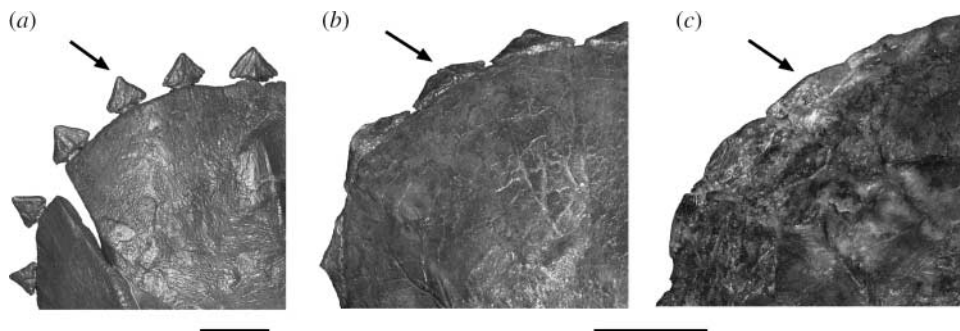


Figure 2. Anteroposterior view of three *Triceratops* parietal-squamosal frills showing the ontogenetic shape change of the epoccipitals. (a) MOR 1199, small juvenile; (b) MOR 1120, subadult and (c) MOR 004, adult skull. The arrow points to the epoccipital in each skull. Scale bar, 8 cm for (a) and 20 cm for (b) and (c).

(b) Ontogenetic trends

Ontogenetic trends occur within and between our four growth stages in *Triceratops*. These morphological developments are identified in selected skulls and cranial elements (table 2). Baby skulls have a parietal-squamosal frill with a scalloped posterior margin. These scallops decrease in depth ontogenetically and become more rounded in juveniles and wavy in subadults. Adult frills are almost smooth, when the epoccipitals merge onto the posterior frill late in ontogeny. The epoccipitals begin as equilateral delta-shaped triangles (figure 2a). The apex of the epoccipital is gradually compressed dorsoventrally, causing the lateral edges to nearly join or contact adjacent epoccipitals in subadults (figure 2b). The average epoccipital height to base ratio (H : B) of 0.14 for the small juvenile (MOR 1199), 2.3 for the large juvenile (MOR 1110) and 2.8 for the subadult (MOR 1120) supports this observation. Fusion to the posterior and lateral margin of the frill occurs in advanced adulthood (figure 2c). An H : B ratio is not measurable on the adult skulls, as the epoccipitals are severely compressed and fusion onto the frill margin obscures the contact between the ventral portion of the epoccipital with the underlying sculptured frill surface. The parietal-squamosal frill develops posterolaterally into a massive fan-like structure in adults. The parietal and squamosals remain unfused throughout ontogeny.

The postorbital horns start as stubs in babies (UCMP 154452, figure 1a) and grow nearly straight before curving posteriorly in juveniles (MOR 1199, figure 1b; MOR 1110, figure 1c). Older babies have straight horns of 5–12 cm long (Brown & Schlaikjer 1940; Tokaryk 1997) before posterior curvature begins. Posterior curvature of the postorbital horns is prominent in juvenile skulls (MOR 1199, figure 1b), before straightening (MOR 1110, figure 1c) and recurving strongly anteriorly in adults (MOR 004, figure 1e). A similar ontogenetic reorientation of the postorbital horn is documented in the Middle Cretaceous neoceratopsian, *Zuniceratops christopheri*, from an assemblage preserved in a bonebed (Wolfe & Kirkland 1998).

Internal excavation of the postorbital horns of *Triceratops* occurs within the juvenile ontogenetic stage. The youngest juvenile skull (MOR 1199, figure 1b) lacks this excavation, but it is present in the older juvenile skull (MOR 1110, figure 1c) in our growth series. Continued excavation progresses into adulthood.

The paired nasals and conical epinasal horn undergo significant alteration ontogenetically. Nasal fusion of the midline suture occurs between or within the juvenile and subadult growth stages. In juveniles, the nasals are paired, unfused elements with a broad, rugose sutural surface anterodorsally for contact with the epinasal. This sutural contact between the epinasal and underlying paired nasals is

confirmed in the large juvenile *Triceratops* skull MOR 1110 (figure 1c). The paired nasals become tightly fused along the midline suture in adulthood. Isolated, unfused epinasal horns are common in the Hell Creek Formation (see table 2). Ontogenetically, the nasal horn increases in size and mass, often extends over the anterodorsal sutural surface of the nasals. Fusion of the epinasal to the underlying paired nasals anterodorsally occurs in the subadult growth stage. The base of the horn becomes larger than the breadth of the paired nasal bones beneath it. The nasal horn may extend anteriorly over the premaxillae as it enlarges, becoming highly variable in size and profile in adult skulls.

In the baby *Triceratops*, the supraoccipital bisects the paired exoccipitals and forms the dorsal roof of the braincase and foramen magnum posteriorly (Goodwin *et al.* 2006). This arrangement is seen in the protoceratopsid *Protoceratops andrewsi* (Brown & Schlaikjer 1940). Contribution of the supraoccipital to the foramen magnum also occurs in the neoceratopsian, *Leptoceratops gracilis* (Sternberg 1951) and *Bagaceratops rozhdestvenskyi* (Maryanska & Osmólska 1975). A portion of the supraoccipital remains between the exoccipitals and contributes to the posterior foramen magnum at least through subadult ontogeny as observed in the skull of MOR 1120. In the adult *Triceratops* skull, UCMP 113697, the supraoccipital is completely excluded from the foramen magnum and overlies the exoccipitals, as described by Hatcher *et al.* (1907) and confirmed by Forster (1996b) and Dodson *et al.* (2004) as the adult condition.

3. CONCLUSIONS

This is the first analysis and description of an ontogenetic series of *Triceratops*, made possible by the recent discoveries of juvenile and subadult skulls from the Late Cretaceous Hell Creek Formation, Garfield and McCone Counties by the MOR and UCMP. The sample set consists of complete skulls, partial skulls and isolated cranial elements. Previous studies of *Triceratops* by Ostrom & Wellnhofer (1986) and Forster (1996a,b) are restricted to adult skulls.

We define four growth stages: baby, juvenile, subadult and adult based on observable and consistent morphological characters. A series of ontogenetic trends illustrate the range of morphological expression present in and between ontogenetic stages in this growth series. Previously unreported ontogenetic characters include: (i) reorientation of postorbital horn growth transforming from straight to posteriorly directed and finally recurving anteriorly; (ii) hollowing out of the postorbital horns ventrally; (iii) ontogenetic smoothing of the posterior frill margin; (iv) change in epoccipital morphology from delta-shaped, through dorsoventrally compressed and flattened in adults; and (v) removal of the supraoccipital from between the exoccipitals and the foramen magnum.

Posteriorly directed postorbital horns and delta-shaped epoccipitals in juveniles are probably visual cues of immaturity. We hypothesize that the recurvature of the postorbital horns from posterior to anterior curvature signals sexual maturity and adulthood (see Jarman 1983). No pattern or trend concerning the size or shape of the nasal horn was apparent.

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