THE SMALLEST KNOWN TRICERATOPS SKULL: NEW OBSERVATIONS ON CERATOPSID CRANIAL ANATOMY AND ONTOGENY

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ABSTRACT — The discovery of the smallest Triceratops skull (UCMP 154452) provides a new ontogenetic end member for the earliest stage of ceratopsid (Centrosaurinae plus Chasmosaurinae) cranial development. The lack of co-ossification among the parietal, squamosals, postorbitals, quadratojugal arch, and the braincase preserves sutural contacts and bone surfaces that later become obscured in adults. The ability to document the early development and morphology of the horns and frill in Triceratops allows a reevaluation of their functional roles. UCMP 154452 shows that the cranial ornamentation of the frill and the postorbital horns were not restricted to adults, but began at an early age in this species. This evidence supports the hypothesis that the function of ceratopsid horns and frills was potentially important for visual communication and species recognition because in this young form it could not have functioned in sexual display. Although some features of UCMP 154452 anticipate or mimic the adult character states, some braincase characters recapitulate the juvenile and adult stages of more basal neoceratopsians.

INTRODUCTION

Triceratops is one of the most familiar genera of Late Cretaceous dinosaurs; it is recognized by its distinctive skull, with three horns and massive frill made up of the parietal and paired squamosals. Previous assessments of ontogeny in Triceratops are based on an isolated juvenile postorbital horn (ca. 100 mm long) described over 60 years ago by Brown and Schlaikjer (1940a) from the Hell Creek Formation, Montana. Two supraorbital horn cores (95 mm and 65 mm long) from the Frenchman Formation of Saskatchewan were described by Tokaryk (1997) but could not be identified beyond Chasmosaurinae. Here we report the discovery of the smallest Triceratops skull, UCMP 154452, from the upper Hell Creek Formation (Maastrichtian), Garfield County, Montana. This new skull is identified as Triceratops by the presence of two 35-mm-long postorbital horns (outgrowths of the postorbital bones) and a highly scalloped, unfenestrated frill (Fig. 1).

This diminutive Triceratops is a mere 30 cm long and is the smallest ceratopsid skull known. Like the young other kinds of dinosaurs (Carpenter et al., 1994), UCMP 154452 has large orbits relative to skull size and a foreshortened face. The next smallest Triceratops skull is of a subadult over four times as long (Schlaikjer, 1935), and adult skulls are six to seven times longer (Hatcher, 1907). UCMP 154452 brings the known growth series of Triceratops to a new small extreme and shows that cranial ornamentation in the frill and the postorbital horns were not restricted to adult members, but began at an early age. UCMP 154452 provides important information on the morphology and development of the horns and frill in Triceratops and allows a reevaluation of their functional significance. A comprehensive assessment of Triceratops ontogeny based on a very complete cranial growth series in the collections of the MOR and UCMP (Goodwin and Horner, 2001) will follow this study (Horner and Goodwin, pers. observ.).

UCMP 154452 was discovered in strata of the Hell Creek Formation exposed in a small badland area located just north of the divide separating the drainages of Snow Creek, to the north, and Hell Creek (UCMP locality V97006, Garfield County, Montana). The skull was preserved in a bed of essentially unstratified, medium gray siltstone that weathers to light gray. Yellow, ferruginous streaks and globules as well as fragmentary plant remains occur throughout the sediment. Teeth and/or skeletal fragments of Tyrannosaurus, Triceratops, and Meniscoressus cf. robustus were discovered in outcrops in the immediate vicinity of the quarry at the same or slightly (ca. 2 m) higher stratigraphic levels and document the latest Cretaceous age of the locality (Lancian North American Land Mammal Age). The nearest exposures of the contact of the Hell Creek and overlying Tullock formations are approximately one mile (1.6 km) to the west and 2.5 miles (4.0 km) to the southeast. In both, the contact between these formations is at an elevation of ca. 2860 feet (875.2 m). The current elevation of V97006 is ca. 2770 feet (847.6 m). In the region of V97006 the strata of these formations appear to be essentially flat lying. The difference in current elevations of the formational contact and the fossil locality, ca. 90 feet (27.5 m), suggests that V97006 is within the upper third of the Hell Creek Formation, which is approximately 300 feet (91.8 m) thick in the valley of Hell Creek (see Wilson, 2004).


DESCRIPTION

The individual cranial elements of UCMP 154452 share an external bone texture that is striated and very porous, indicative of fast-growing tissue (Sampson et al., 1997). All sutures are patent and allow accurate articulation of this very young Triceratops skull. This early phase of cranial morphogenesis preserves sutural contacts and bone surfaces that become hidden in adults. The right side of the skull is more complete and the following elements, from the right side unless noted otherwise, are preserved: parietal, left and right squamosals, left and right postorbitals, prefrontal, jugal, quadrate, quadratojugal, occipital condyle, basicipital, left and right exoccipitals, surangular, and dentary. Less complete but identifiable fragments of the maxil-
lary, left quadrate, left jugal, vertebral centra, ossified tendons, and teeth were also found with the skull. Morphological descriptions are based on the right side.

Parietal

The parietal is nearly “square” (Figs. 2; 3B, E). It measures 124 mm in length along the midline and has a maximum width of 127 mm. The midline is ornamented by an undulating row of five raised bony prominences. This feature was also described by Dodson and Currie (1988) on a 210-mm-long parietal of the previously smallest known ceratopid, tentatively referred to *Monoclonius*. Rostrally, in UCMP 154452, each prominence becomes progressively narrower along the midline, but remains consistent in height, ca. 5 mm, above the surface of the parietal. Caudally, the parietal is about 5–7 mm thick and thins rostrally to less than 4 mm. This rostral thinning of the parietal is also observed in adult *Triceratops* skulls (Dodson and Currie, 1990). A prominent feature of UCMP 154452 is the “scalloped” caudal margin of the parietal. A series of three scallops on either side of the parietal midline is bordered caudally by a central scallop. These scallops continue onto the caudal margin of each squamosal and provide a distinctive appearance to the frill. These scallops are not separate ossifications but are formed by the parietal and squamosal. Consequently, they are not homologous with the epoccipitals that border the frill in subadult and adult *Triceratops* but merely mimic their shape. The dorsal and ventral surfaces of each scallop are smoother than the surrounding bone and were likely covered by hard keratin before the epoccipitals ossified. This scalloped edge becomes less pronounced and gently “wavy” in subadult *Triceratops* skulls when epoccipitals first appear and ossify along the frill margin (Goodwin et al., 1997).

Squamosal

The left and right squamosals (Fig. 3A, C, D, F) are nearly complete and are ca. 150 mm in maximum length. The squamosal thins rostrally from 6.3 mm to 3.0 mm. It articulates rostrolaterally with the jugal by an overlapping sutural contact. It also overlaps the caudal portion of the postorbital rostrodorsally. The medial edge of the squamosal forms the border for the supratemporal fenestra. The squamosal and parietal contribute to the frill along a fairly straight contact. The characteristic inward bend of the adult squamosal is expressed in the squamosals of UCMP 154452. This bend becomes greatly exaggerated in adult *Triceratops* (Dodson and Currie, 1990; Dodson, 1993). The medial edge of the squamosal curves slightly and does not appear to overlap with the parietal rostrally as in subadult and adult skulls. The caudal border of the squamosal has five distinct scallops. A longitudinal series of raised prominences radiate rostrolaterally onto the dorsal surface of the postorbitals. Ventrally, a bifurcating prominent ridge of bone serves as the articular surface for the exoccipital and quadrate where these bones form a prominent buttress beneath the frill (Fig. 4B).

Postorbital

The most distinctive feature of the left and right postorbitals is the 35-mm-long postorbital horns (Fig. 5). The postorbital horns...
are oriented rostrally at ca. 10° and do not show the caudally directed curvature of older juvenile and subadult Triceratops postorbital horns (Goodwin et al., 1997). Indented vascular grooves on the exterior surface of the postorbitals indicate that they were covered by a keratinous sheath (Horner and Marshall, 2002). The grooves are deepest on the surface of the horns. A row of raised prominences radiates caudolaterally and continues onto the squamosals. The right postorbital confirms that the ventral part of the cornual sinus at the basal region of the horn core formed early (Fig. 5B). The rostral face of the postorbital horn (Fig. 5C) has a prominent rugose sutural surface for the prefrontal. This roughened sutural surface covers nearly the entire rostral surface of the postorbital horn. Laterally, the caudodorsal region continues as a thin wedge of bone that articulates with the squamosal by sliding beneath its rostral edge.

Prefrontal

We identify a 39.6 mm long semi-lunate bone as the right prefrontal (Fig. 6). It is ca. 7 mm thick. The medial and caudal edges are dominated by a rugose sutural surface. Caudally, the prefrontal thickens where it meets the rostral face of the postorbital. Three prominent foramina are on the anterodorsal surface and a single central foramen penetrates the prefrontal. The prefrontal forms the anterodorsal margin of the orbit and enables the reconstruction of the front of the skull.

Jugal

The jugal (Fig. 7A, B) forms the ventral border of the orbit and the dorsal rim of the lateral temporal fenestra. This sutural pattern of the jugal bordering the rim of the lateral temporal fenestra dorsally is considered plesiomorphic by Forster (1996a: 261, character 1; also see Fig. 1). In the derived state, the squamosal forms the dorsal rim of the lateral temporal fenestra and does not extend across the top of the jugal in adult Triceratops. In UCMP 154452, the squamosal remains excluded from most of the dorsal margin of the lateral temporal fenestra by a caudally directed jugal spur. Individual variation may be the cause of this slight anatomical difference, but it could also be an expression of the primitive condition retained in the adult Triceratops and at this early stage of ontogeny. In all ceratopsids, the jugal expands caudally and the squamosal enlarges caudoventrally. As a result, the infratemporal fenestra is compressed and reduced in size. The jugal-squamosal contact excludes the postorbital from the infratemporal fenestra in adult Triceratops (Dodson and Currie 1990:600). This is also observed in UCMP 154452. A squamosal process ventral to the temporal opening is undeveloped at this early stage of ontogeny. Deep vesicle grooves are present around the ventral rim of the orbit and become shallower on the remaining jugal dorsally. A prominent feature of the jugal is the ventrally directed “wedge” of bone that covers the anterolateral surface of the quadratojugal along an overlapping sutural con-

FIGURE 3. The fill of UCMP 154452, Triceratops, in dorsal (A–C) and ventral (D–F) views. Right squamosal (A, F), parietal (B, E), and left squamosal (C, D). The caudal margin of the frill is highly scalloped.
tact. Ventrally, the sutural surface of the jugal is slightly concave and thinner (ca. 4 mm) compared to 6 mm in overall thickness. The distal tip of the jugal is flared but does not show any evidence for an epijugal, which evidently forms later in ontogeny.

**Quadrate**

The quadrate (Fig. 8) is 98 mm in maximum length dorsoventrally and is nearly totally excluded from the caudal margin of the infratemporal fenestra by the overlapping quadratojugal. The quadrate articulates with the quadratojugal along a vertical axis laterally. This articulation is further supported by a spur of bone that rises from the ventral sutural surface of the quadrate to meet a gentle depression on the lower medial surface of the quadratojugal. The quadrate expands transversely dorsally, a precursor to the significant dorsal expansion in adult *Triceratops* (Forster, 1996b). The flange of bone meets the underside of the squamosal along a pronounced V-shaped ridge of bone (see Fig. 4B). It is overlain by the squamosal and underlain by the exoccipital. This arrangement is also observed in adult skulls (Hatcher, 1907; Ostrom and Wellnhofer, 1986). The surface for articulation with the lower jaw lies at the rostral-most region of the quadrate. It is robust and round, but does not form a transverse articular surface or distinct double condyle, bisected by a trough, for articulation with the mandible of adults (Hatcher, 1907; Ostrom and Wellnhofer, 1986). This ventral condyle is rostral to the more caudally directed dorsal flange.

**Quadratojugal**

The quadratojugal (Fig. 8) is wedged between the quadrate and the overlapping ventral jugal flange. The quadratojugal is thick ventrally, thin dorsally, and wrapped around the caudal portion of the quadrate. The medial ventral condyle is slightly concave where it contacts the quadrate. Laterally, the quadratojugal is marked by a ridge and faceted surface where the jugal flange overlaps it. This arrangement is consistent with the adult condition (Ostrom and Wellnhofer, 1986). All of the sutural surfaces are open and overlapping. The quadratojugal forms nearly the entire ventral and caudal border of the lateral temporal fenestra. In adult *Triceratops*, the squamosal forms this caudal border of the infratemporal fenestra (Dodson and Currie, 1990). In lateral view the quadratojugal is largely obscured by the jugal in most adult skulls but not in UCMP 154452, particularly adjacent to the infratemporal opening.

**Lateral Temporal Fenestra**

The lateral temporal fenestra (Fig. 1) lies beneath and caudal to the orbit. The opening is nearly oval and bordered by the jugal...
The braincase of UCMP 154452 (Fig. 9) is well preserved and reveals the substantial amount of ontogenetic transformation that takes place into adulthood. The bones of the braincase are unfused and are loosely coalesced by overlapping rugose or tongue-and-groove sutures. Important differences with the adult ceratopsid braincase in the arrangement and articulation of the basioccipital, exoccipitals, and supraoccipital are noted below.

**Occipital Condyle**—The occipital condyle is 31.9 mm mediolaterally and 28.9 mm vertically. It is nearly oval and unfused and is formed by a one-third contribution from the basioccipital and one-third from each ventral exoccipital (Fig. 9). This arrangement is typical of all ceratopsids but is often obscured by fusion in adult skulls (Lehman, 1989; Chinnery, 2004). The dorsal sutural surface is irregularly grooved where it accepts the exoccipital. The short pedunculate neck of the condyle is constricted dorsoventrally and transversely.

**Basioccipital**—The basioccipital is 48 mm long and 26.5 mm wide. Caudally it is dominated by its contribution to the occipital condyle. A median ridge divides the basioccipital. A distinctive midline hourglass-shaped ridge and grooved sutural surface for the alisphenoid are preserved. The rostrodorsal surface is rugose where it articulates with the descending process of the exoccipital. Well-developed basioccipital tubera extend rostrolaterally. The basioccipital is excluded from the foramen magnum by the paired exoccipitals. A small portion of the left basisphenoid is preserved in close contact along the rostroventral surface of the basioccipital. The foramen magnum is 23.6 mm wide.
Supraoccipital—In all adult ceratopsids, the supraoccipital is excluded from the foramen magnum by the exoccipitals, which unite above the foramen magnum (Hatcher, 1907; Dodson and Currie, 1989; Forster, 1996b). UCMP 154452 does not share this condition. At this very early stage of ontogeny, UCMP 154452 exhibits the primitive state in which the supraoccipital articulates between the exoccipitals dorsomedially. The occipital condyle is formed by a one-third contribution from the basioccipital and one-third from each exoccipital. Exit foramen for cranial nerves IX–XI and XII are noted. Abbreviations: bo, basioccipital; exo, exoccipital; fm, foramen magnum; oc, occipital condyle; so, supraoccipital.

Exoccipital—The exoccipitals extend as a “wing” of bone laterally from the foramen magnum, forming a buttress that contacts the ventral surface of the squamosal (see Fig. 4B). According to Ostrom and Wellnhofer (1986:123), this configuration provides major support for the entire frill along this junction of the quadrates and squamosal contact. This arrangement remains consistent into adulthood. The right exoccipital is more complete than the left and preserves the relatively large exit foramina for cranial nerves IX–XI and XII with a septum of bone between the foramina (Fig. 9).

Surangular

The right surangular (Fig. 10) is 62.5 mm in length. It varies in thickness from 3.5 mm at the most rostral edge where it meets the dentary to 10.7 mm caudally along the articular surface for the quadrate. Rostromedially, the surface is striated where it articulates with the dentary. The mandibular foramen is preserved along the upper portion of the dorsal surface. The surangular is laterally convex and slightly concave medially. The surangular thickens and develops a flat curved shelf caudally. This shelf is deflected laterally, flattened dorsally, and articulates with the quadrate. Caudomedially, the surangular is sharply concave where it meets the articular.

Dentary

The dentary (Fig. 11) is 160 mm long and allows determination of the maximum skull length and restoration of the skull in Fig. 1. The coronoid process is robust, offset laterally, and curves rostrally. Ostrom and Wellnhofer (1989) interpreted the sturdy coronoid process as a critical attachment site for powerful adductor musculature. The dentary is straight, convex laterally and concave medially except for the dental battery, which is nearly vertical. The rostral edge is relatively thicker (6.5–10.4 mm) where it meets the predentary bone. Caudally it is 4.4 mm thick. Medially, the symphyseal surface is indicated by horizontal striations on the thickened bony facet. Vertically, the coronoid process is offset about 30 degrees to the axis of the dentary. A strong lateral ridge runs along the length of the dentary ventrolaterally. Below this ridge, the ventral surface of the dentary is flattened and striated where the splenial would lie longitudinally. A deep adductor fossa is present caudomedially below the coronoid process. Even at this young age, the fossa is relatively large and sufficient as a major insertion site for the M. adductor posterior (Ostrom and Wellnhofer, 1989). The Meckelian groove extends ca. 48 mm along the rostromedial surface of the adductor fossa from the caudal edge of the dental battery. A shallow longitudinal groove lies along the ventral border of the fossa caudally, indicating the place of attachment for the M. intramandibularis (Ryan and Currie, 1998). The dental battery is 107 mm long and
occupies a large extent of the dentary. At least 20 alveoli are present along the length of the dental battery. No teeth are preserved in the jaw. Laterally, the dentary bears two rows of foramina. According to Lehman (1989), these foramina probably communicate with the mandibular fossa, carrying branches of the mandibular ramus of the trigeminal nerve, the mandibular artery, and veins to the tissues of the cheek and predentary. Rostrally, an upper third row of foramina is present.

Maxillary
A 55.3-mm-long left maxillary fragment was recovered with the skull. Seven dental grooves are preserved on the interior surface. No maxillary teeth are preserved in position. The dental magazine is relatively delicate, and the bone becomes more robust along the caudodorsal margin.

Teeth
Isolated leaf-shaped teeth were found associated with the skull. They are double-rooted with a strong median ridge and a lingual covering of enamel.

Vertebrae
At least three isolated, fragmentary vertebrae were recovered with the skull. Fragments of their centra reveal a very spongy interior surrounded by a relatively thin periosteal exterior. Toothed sutures remain open on the dorsal surface of the centra, indicating that the neural spines are unfused. This is not unexpected in such a small, young individual.

Ossified Tendons
Fragments of ossified tendons were closely associated with the skull. The largest piece is 38.1 mm long and ca. 4 mm in diameter. The medial surface is incompletely striated and the remaining surface is smooth. One fragment is triangular and broad cranially, like the adult tendon.

DISCUSSION
In adult Triceratops, the large, solid, saddle-shaped frill is 65–70% of the basal skull length (= caudal surface of basioccipital to tip of rostral bone; Forster, 1996b). In UCMP 154452, the frill is only 48% of the estimated basal skull length. Although it already has small postorbital horns and a solid, scalloped frill that closely resembles the epicic平al-bordered adult skull, UCMP 154452 had proportions very different from those of the adult skull. The parietosquamosal frill is short and square, whereas in adults it is elongate, fan-like, and more concave. Features of the braincase in UCMP 154452 recall the adult condition of more basal neoceratopsians (Brown and Schlaikjer, 1940b). Here, the exoccipitals unite below but not above the foramen magnum, allowing the supraoccipital to form the dorsal margin of the foramen magnum and contribute to the roof of the braincase (Fig. 9). This condition is shared with Protoceratops, even as adults (Brown and Schlaikjer, 1940b, Dodson and Currie, 1990c), but is lost in adult Triceratops where the exoccipitals unite above the foramen magnum, excluding the supraoccipital (Hatcher et al., 1990; Brown and Schlaikjer, 1940b). In this sense, some juvenile features of Triceratops recapitulate a character state of more basal neoceratopsians as might be expected. Evidence pre-
sented by Gilmore (1917) and more recently by Lehman (1988) suggests that this arrangement of the supraoccipital may be a juvenile ceratopsid character. Gilmore (1917:fig. 11) determined that the supraoccipital of the type of Brachyceratops montaneus (USNM 7951) contributes to the formation of the foramen magnum in this immature ceratopsid. Lehman (1989:fig. 6B, C) observed that the supraoccipital forms at least the caudal root of the endocranial cavity in an incomplete juvenile braincase referred to Chasmosaurus mariscalensis (UTEP P.37.7.068).

In contrast, certain juvenile features appear to anticipate the structural condition of the adult Triceratops skull. First, although no teeth were preserved in place in the dentary or the small fragment of the maxillary, isolated teeth recovered from the sediment around the tiny skull share the crown pattern and double-rooted form of adults (contra Carpenter, 1982). Second, the lateral wings of the exoccipital expand from either side of the occipital condyle into broad flanges that contact the ventral surface of each squamosal. As in adults, this portion of the exoccipital forms an expansive brace that provides primary support for the overlying frill (Ostrom and Wellnhofer, 1986; Forster, 1996b). Third, a parasagittal row of low bosses ornaments the superior surfaces of the postorbitals, squamosals, and the parietal midline. The number of scallops on the caudal margin of the squamosals and parietal equals the number of epipatals that border the adult frill (Hatcher, 1907; Forster, 1996b). Finally, the epipatural ornamentation of the adult frill and postorbital horns served as an important visual sign in species communication, then perhaps the scalloped frill and horns of very young individuals served the same function.

It has often been suggested that the ornamental skull features of ceratopsids (horns and frills) reflect a role in mate competition or species recognition (Forster and Sampson, 2002). Dimorphism can be recognized in adequate population samples of taxa by a divergence of biometric characters during ontogeny (Darwin, 1871). Among non-avian dinosaurs, sexual dimorphism has been suggested in theropods (Colbert, 1990; Raath, 1990), hadrosaurids (Dodson, 1975; Hopson, 1975; Molnar, 1977), and ceratopsians (Ostrom and Wellnhofer, 1986; Dodson, 1996; Forster, 1996b) but in each case it is not extreme and has not been demonstrated statistically. Only the basal ceratopsian Protoceratops shows statistically significant dimorphism (Dodson, 1976), but it is minor. Sexual dimorphism has been inferred for various centrosaurines and chasmosaurines (Lehman, 1990; Forster, 1996b; Sampson et al., 1997; Ryan et al., 2001), but again, this variation has not been established statistically and has not been differentiated from ontogenetic or within-normal-populational variation (Padian et al., 2004). Dimorphism can be expressed early in ontogeny, or as a late pulse that reflects maturity and agonistic sexual behavior, usually among males, resulting in an extended growth trajectory (Weckerly, 1998). This by itself does not confirm sexual display or associated mating behavior as the principal function of low-level dimorphism; the morphology of horns and frills may have served different functions at different times in an individual's life. We suggest visual communication and species recognition, perhaps involving complex signaling (Ord et al., 2001) as an alternative but not exclusive function of these cranial ornaments.

In general, dinosaurian cranial display features, such as horns, spikes, and bony pads in ceratopsids (Forster, 1996a, Sampson et al., 1997), crests on hadrosaurid skulls (Horner and Currie, 1994), and the frontoparietal domes of pachycephalosaurids (Goodwin et al., 1998; Williamson and Carr, 2002; Goodwin and Horner, 2004) did not appear until later stages of development. Immature centrosaurines of different genera have similar horn-core ontogenies (Sampson et al., 1997); adult features of horns and frills appear only late in ontogeny, suggesting a function in sexual display or species/mate recognition. Sexual dimorphism has also been inferred for some chasmosaurines (Dodson, 1996), but is not generally accepted for either chasmosaurines or centrosaurines (Dodson et al., 2004). The new tiny Triceratops shows that the normally late-developing features often associated (if dimorphic) with sexual display began to be expressed at a very early age. This pattern appears likely for Chasmosaurus (Lehman, 1989; 1990), though at relatively larger size and presumably later age. This clearly derived condition within chasmosaurines, given current knowledge of ceratopsian phylogeny and phylogeny, suggests a heterochronic shift of the expression of these characters. However, hypotheses of heterochrony can only be tested by comparative ontogenies, which at present are insufficient.

The basal neoceratopsian Protoceratops expresses some features, such as a nasal boss and a vertical tilt to the frill, only late in life, suggesting that the centrosaurine pattern may be primitive. However, specimens referred to Zuniceratops (Wolfe and Kirkland, 1998) appear to show long-developing horns that are present in juveniles, like chasmosaurines but unlike centrosaurines. The phylogenetic placement of cf. Zuniceratops outside Ceratopsidae (see Dodson et al., 2004) suggests that the function of cranial structures in species recognition may have preceded the divergence of centrosaurines and chasmosaurines. If so, then the late-developing structures of centrosaurines would be derived, heterochronically shifted features and could perhaps be exclusively linked to sexual display (Lehman, 1990; Ryan et al., 2001), if significant dimorphism can be established.

A function in sexual display (Farlow and Dodson, 1975; Molnar, 1977; Sampson, 1997) or resisting predators (Colbert, 1948, 1961; Molnar, 1977) has long been the dominant model for cranial ornamentation in dinosaurs, despite little evidence for sexual dimorphism. However, it is difficult to support a hypothesis of sexual display when the sexes show little or no evidence of discrete morphological features apart from size (Darwin, 1871); even so, hypotheses of a function in sexual display must be tested by evidence beyond simple morphologic difference. Conversely, species recognition is simply tested by the presence of low sexual dimorphism with species-specific morphology that is apparent to intra- and interspecific individuals (Vrba, 1984). Non-directional morphologic trends in phylogeny and the presence of several related sympatric or parapatric species are two tests of species recognition as a factor that structures morphological diversity (Padian et al., 2004). Ceratopsids pass these tests.

Low sexual dimorphism in ceratopsians supports our hypothesis that the early ontogenetic expression of horn and frill morphology in some ceratopsids reflects a visual cue for communication and species recognition; clearly these features appeared well before sexual maturity in UCMP 154452. Extant African bovids use an effective visual communication system that involves horn morphology and body color (Vrba, 1984). These explicit species differences have long histories of divergence and sorting in bovid subclades (Vrba, 1984). Similar visual cues based on horn and frill morphology may have stimulated greater species diversity earlier in ceratopsian evolutionary history. Farlow and Dodson (1974), Hopson (1975), and Sampson (1997) have acknowledged the potential importance of species recognition in dinosaur diversity.

The many forms of sexual dimorphism among birds are conventionally split into body size and overall plumage-color attributable to melanins, carotenoids, and structural colors (Owens and Hartley, 1998). Structural colors arise from the scattering of ultraviolet light by collagen fibers. Prum et al. (1994, 1999) report how skin color in the face and head is used by an assortment of extant birds for visual communication. Deep vesicle grooves in the face of each squamosal. As in adults, this portion of the exoccipital projects the occipital condyle into broad flanges that contact the ventral surface of each squamosal. The basal neoceratopsian Protoceratops expresses some features, such as a nasal boss and a vertical tilt to the frill, only late in life, suggesting that the centrosaurine pattern may be primitive. However, specimens referred to Zuniceratops (Wolfe and Kirkland, 1998) appear to show long-developing horns that are present in juveniles, like chasmosaurines but unlike centrosaurines. The phylogenetic placement of cf. Zuniceratops outside Ceratopsidae (see Dodson et al., 2004) suggests that the function of cranial structures in species recognition may have preceded the divergence of centrosaurines and chasmosaurines. If so, then the late-developing structures of centrosaurines would be derived, heterochronically shifted features and could perhaps be exclusively linked to sexual display (Lehman, 1990; Ryan et al., 2001), if significant dimorphism can be established.

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Low sexual dimorphism in ceratopsians supports our hypothesis that the early ontogenetic expression of horn and frill morphology in some ceratopsids reflects a visual cue for communication and species recognition; clearly these features appeared well before sexual maturity in UCMP 154452. Extant African bovids use an effective visual communication system that involves horn morphology and body color (Vrba, 1984). These explicit species differences have long histories of divergence and sorting in bovid subclades (Vrba, 1984). Similar visual cues based on horn and frill morphology may have stimulated greater species diversity earlier in ceratopsian evolutionary history. Farlow and Dodson (1974), Hopson (1975), and Sampson (1997) have acknowledged the potential importance of species recognition in dinosaur diversity.
explaining the diversity of horn and frill structures in Ceratopsidae (Centrosaurinae plus Chasmosaurinae) and their near relatives, and that substantial sexual dimorphism has not yet been established in ceratopsids.

Nearly all anatomical and behavioral studies of Triceratops have been based on adult skulls. The development of larger, more visible postorbital horns, a massive nasal horn, and the ossification of ocipiopals along the frill margin may have signaled sexual maturity and the onset of mating in adult Triceratops. Functional analyses of these cranial features in adult Triceratops have often restricted their role to sexual display and mating behavior, based on the presumption that these features were not present in very young individuals and did not express themselves until adulthood (Sampson et al., 1997; Dodson and Currie, 1990; Sampson, 2001; but see Farke, 2004). To the contrary, UCM 154452 demonstrates that in very young Triceratops, these species-specific cranial characters began to be formed early in life—ostensibly earlier than in centrosaurine ceratopsids—and may have been important for visual communication and species recognition even at this early stage.

CONCLUSION

UCMP 154452 documents the youngest ontogenetic stage of Triceratops and illuminates a great transformation in size, shape, and rearrangement of cranial elements that occurred in the skull during growth into adulthood. As the smallest ceratopsid skull known, it provides a new end member for the youngest stage of cranial ontogeny in Triceratops. The patent cranial sutures reveal morphology that is often concealed in adult skulls. Juvenile features of the braincase in UCM 154452 recapitulate the primitive character state of more basal neoceratopsians. On the other hand, cranial ornamentation in the frill and the postorbital horns of Triceratops were not restricted to adult members, but began at an early age. The appearance of horns and a scalloped frill at this small size and early age is support for the hypothesis that cranial ornaments in ceratopsids were at least as important as a visual organ for species communication as they may have been for sexual display or agonistic encounters.

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