Evolutionary trends in *Triceratops* from the Hell Creek Formation, Montana

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Edited by Gene Hunt, Smithsonian Institution, Washington, DC, and accepted by the Editorial Board June 1, 2014 (received for review July 16, 2013)

The placement of over 50 skulls of the well-known horned dinosaur *Triceratops* within a stratigraphic framework for the Upper Cretaceous Hell Creek Formation (HCF) of Montana reveals the evolutionary transformation of this genus. Specimens referable to the two recognized morphospecies of *Triceratops*, *T. horridus* and *T. prorsus*, are stratigraphically separated within the HCF with the *T. prorsus* morphology recovered in the upper third of the formation and *T. horridus* found lower in the formation. Hypotheses that these morphospecies represent sexual or ontogenetic variation within a single species are thus untenable. Stratigraphic placement of specimens appears to reveal ancestor–descendant relationships. Transitional morphologies are found in the middle unit of the formation, a finding that is consistent with the evolution of *Triceratops* being characterized by anagenesis, the transformation of a lineage over time. Variation among specimens from this critical stratigraphic zone may indicate a branching event in the *Triceratops* lineage. Purely cladogenetic interpretations of the HCF dataset imply greater diversity within the formation. These findings underscore the critical role of stratigraphic data in deciphering evolutionary patterns in the Dinosauria.

The Hell Creek Project (1999–2010), a multiinstitutional survey of the fauna, flora, and geology of the Upper Cretaceous Hell Creek Formation (HCF), provides insights into the paleobiology and evolution of the last nonavian dinosaurs (1). *Triceratops* (Ceratopsidae: Chasmosaurinae) is the most abundant dinosaur in the HCF; >50 skulls, including previously unknown or rare growth stages, have been collected throughout the entire formation (spanning ~1–2 million y) (2) over the course of the Hell Creek Project (1, 3–5). The combination of a stratigraphically controlled robust sample from the entire ~90-m-thick HCF and identification of ontogenetic stages makes *Triceratops* a model organism for testing hypotheses proposed for the modes of dinosaur evolution (e.g., refs. 6–8).

Since its initial discovery (9), as many as 16 species of *Triceratops* were named based on variations in cranial morphology (10, 11). Forster (12) recognized only two species, *Triceratops horridus* and *Triceratops prorsus*, based on cranial features including differences in relative length of the postorbital horn cores (long in *T. horridus* and shorter in *T. prorsus*), morphology of the rostrum (elongate in *T. horridus* and shorter in *T. prorsus*), and closure of the frontoparietal fontanelle (sensu Farke) (13) (open in *T. horridus* and closed in *T. prorsus*). Marsh initially distinguished these two species by the morphology of the nasal horn (14); the type specimen of *T. horridus* possesses a short, blunt nasal horn whereas the nasal horn in *T. prorsus* is elongate. Whether or not these taxa were largely biogeographically separated or represented ontogenetic variants or sexual dimorphs within a single species has remained unresolved (8, 10, 12, 15–18). A record of the stratigraphic distribution of *Triceratops* from the Upper Cretaceous Lance Formation of Wyoming compiled by Lull (19, 20) suggested that these taxa overlap stratigraphically. However, this assessment was likely based on limited stratigraphic data (15) and “the precise stratigraphic placement of these specimens can no longer be established” (ref. 10, p. 155). As such,

consideration of morphological variation in a detailed stratigraphic context is necessary to reassess systematic hypotheses.

Results

Stratigraphic placement of *Triceratops* specimens within the HCF reveals previously undocumented shifts in morphology. The HCF is divided into three stratigraphic units: the lower third (L3), middle third (M3), and upper third (U3) (1, 21). The stratigraphic separation of *Triceratops* morphospecies is apparent with specimens referable to *T. prorsus* (following Forster) (12) found in U3 and *T. horridus* recovered only lower in the HCF. Specimens from the upper part of M3 exhibit a combination of *T. horridus* and *T. prorsus* features (Fig. 1, *SI Text*, and Fig. S1).

L3 *Triceratops*. *Triceratops* from the lowermost 15–30 m of the HCF (L3) possess either a small nasal horn (Fig. 24 and *Dataset S1*) or a low nasal boss. The boss morphology appears in a large individual that histologically represents a mature specimen [= “*Torosaurus*” ontogenetic morph (ref. 3; but see also refs. 22–24)] [Museum of the Rockies (MOR) specimen 1122] (*SI Text*). The nasal process of the premaxilla (NPP) in L3 *Triceratops* is narrow (Fig. 2B and Fig. S2) and strongly posteriorly inclined; a pronounced anteromedial process is present on the nasal (Fig. S3). The frontoparietal fontanelle remains open until late in ontogeny (MOR 1122). Specimens from the lower unit of the HCF bear a range of postorbital horn-core lengths (ranging from ~0.45 to at least 0.74 basal-skull length) (Fig. 2D and *Dataset S1*).

Significance

The deciphering of evolutionary trends in nonavian dinosaurs can be impeded by a combination of small sample sizes, low stratigraphic resolution, and lack of ontogenetic (developmental) details for many taxa. Analysis of a large sample ($n > 50$) of the famous horned dinosaur *Triceratops* from the Hell Creek Formation of Montana incorporates new stratigraphic and ontogenetic findings to permit the investigation of evolution within this genus. Our research indicates that the two currently recognized species of *Triceratops* (*T. horridus* and *T. prorsus*) are stratigraphically separated and that the evolution of this genus likely incorporated anagenetic (transformational) change. These findings impact interpretations of dinosaur diversity at the end of the Cretaceous and illuminate potential modes of evolution in the Dinosauria.

Author contributions: J.B.S., D.W.F., M.B.G., and J.R.H. designed research; J.B.S., D.W.F., M.B.G., and J.R.H. performed research; J.R.H. contributed new reagents/analytic tools; J.B.S. and D.W.F. analyzed data; and J.B.S., D.W.F., and M.B.G. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. G.H. is a guest editor invited by the Editorial Board.

Data deposition: Nexus files are available at Morphobank.org (project number 1099).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1313334111/-DCSupplemental.

Fig. 1. Stratigraphic placement of HCF *Triceratops* reveals trends in cranial morphology including elongation of the epinasal and change in morphology of the rostrum. (A) HCF stratigraphic units. (B) Magnetostratigraphic correlation (45, 46). NS, no signal, so precise position of C29r-C30n boundary is unknown. (C) Stratigraphic positions of *Triceratops* specimens within a generalized section. Specimens plotted by stratigraphic position, not by facies. Relative position of specimens from different areas is approximate at the meter scale (5). See refs. 1 and 5 for further specimens for which more precise position (beyond HCF unit) is to be determined. Scale in meters. (D) MOR 2702 nasal horn from U3. (E) UCMP 113697 nasal horn from upper part of M3; black arrow indicates epinasal-nasal protuberance. (F) MOR 2982 nasal horn from lower part of M3 (image mirrored). (G) MOR 1120 nasal horn from L3. (H) MOR 004 young adult *Triceratops* skull from U3 (cast; image mirrored). Postorbital horn cores reconstructed to approximate average length of young adult specimens from this unit. (I) UCMP 113697 late-stage subadult/young adult *Triceratops* skull from the upper part of M3. (J) MOR 1120 (cast) subadult *Triceratops* skull from L3. Figure modified from ref. 5. f, fine sand; m, medium sand. (Scale bars: 10 cm.)

M3 *Triceratops*. The mean nasal-horn length increases through M3 (Figs. 1 E and F and 24). The University of California Museum of Paleontology (UCMP) specimen 113697 (collected ~6 m below the base of U3) possesses a nasal horn that is elongate (length/width: 2.12) (Dataset S1) but retains a broad posterior surface, giving the horn a subtriangular cross-section. Forster (12) noted that UCMP 113697 exhibits a small nasal boss posterior to the nasal horn. Disarticulated specimens (e.g., MOR 3027 and MOR 3045) reveal that this protuberance posterior to the epinasal appears to be formed by the combination of a posterior projection on the epinasal (Fig. S4) and the anteriormost nasal. A homologous morphology is observed in specimens from L3 and the lower half of M3 (MOR 1120, MOR 2982, and MOR 3010). UCMP 128561, from the upper half of M3, exhibits a low nasal boss (25, 26) (SI Text). The anteromedial process of the nasal is pronounced in *Triceratops* from M3, and the NPP is more vertically inclined in specimens from upper M3, producing a more convex rostrum morphology, which was previously found to characterize *T. prorsus* (12, 23). The frontoparietal fontanelle is open in late-stage subadults/young adults (UCMP 113697).

U3 *Triceratops*. Specimens from U3 exhibit the features Forster (12) found to characterize *T. prorsus*. U3 *Triceratops* possess an elongate, relatively narrow nasal horn (average length/width > 2) (Fig. 24 and Dataset S1). The NPP is more vertically inclined, producing a convex rostrum lacking the low, elongate profile noted in *T. horridus* [although the largest, and presumably oldest, known specimens (e.g., MOR 004 and MOR 1625) exhibit proportionally longer rostra] (Fig. 2E and Dataset S1). The NPP is

anteroposteriorly expanded, and the anteromedial process of the nasal is greatly reduced (Fig. S3) (27). The frontoparietal fontanelle becomes constricted and eventually closed in late-stage subadults/young adults (e.g., MOR 2923 and MOR 2979), ontogenetically earlier than in L3 and M3. The postorbital horn cores are short (<0.64 basal-skull length) (Fig. 2D). Further, U3 *Triceratops* seem to exhibit nasals that are more elongate than *Triceratops* from the lower half of the HCF (Fig. 2F and Dataset S1).

Shifts in Morphology over Time. Epinasals exhibit a directional morphologic trend; average length increases throughout the formation (Fig. 24 and Dataset S1) (Spearman's rank coefficient = 0.824, $P = 4.15E-07$). A protuberance just posterior to the epinasal, observed in specimens from L3 and M3 (Fig. 1), is particularly pronounced in UCMP 113697 from the uppermost M3 (Fig. 1E). U3 *Triceratops* either do not exhibit this feature or express only a subtle ridge in the homologous location. Concurrent with elongation of the epinasal was an expansion of the NPP (Fig. 2B) (Spearman's rank coefficient = -0.969, $P = 3.74E-06$) and an increase in the angle between the NPP and the narial strut of the premaxilla (Fig. 2C and Dataset S1) (Spearman's rank coefficient = 0.802, $P = .000186$). Nasals also become more elongate relative to basal skull length (although only three specimens with complete nasals have thus far been recorded from the lower half of the formation) (Fig. 2F and Dataset S1) (Spearman's rank coefficient = 0.804, $P = 0.00894$).

Postorbital horn-core length appears to be variable throughout L3 and M3 and is consistently short in U3 *Triceratops* (Fig. 2D and Dataset S1) [Spearman's rank coefficient is negative (-0.197)

Fig. 2. Stratigraphic variation in cranial morphology. Each unit of the HCF is divided into upper and lower sections. For L3, the upper part is here designated as strata above the basal sandstone. For M3, the upper part is here considered the upper 15 m of the unit. The 10-m sandstone and above is here considered the upper section of U3. (A) Epinasal length/width. MOR 3011 denoted by a gray diamond as the fragmentary nature of this specimen obscures its ontogenetic status. Square represents UCMP 128561. Results of Spearman's rank correlation analysis in white box. (B) Nasal process of the premaxilla (NPP) height/width. (C) Angle between the NPP and the narial strut of the premaxilla. (D) Postorbital horn core length/basal skull length. Estimated total lengths are used here for postorbital horn core length (Dataset S1). (E) Rostrum length/basal skull length. (F) Nasal length/basal skull length. Vertical lines denote the mean (not including juvenile or taphonomically deformed specimens) (Dataset S1). Dark gray bars represent SE. Black rings denote juveniles. Gray ring represents Royal Tyrrell Museum (RTMP) specimen 2002.57.7. Spearman's rank correlation analyses exclude juveniles and taphonomically distorted specimens (indicated by diamonds). Asterisks indicate statistically significant P values. Scale on x axes are logarithmic.

and not statistically significant ($P = 0.392$)]. Large juvenile U3 *Triceratops* (e.g., MOR 1110) can possess more elongate post-orbital horn cores (0.64 basal-skull length). Whereas U3 post-orbital horn core length falls within the range of variation observed lower in the formation (Fig. 2D), elongate postorbital horn cores have thus far not been found in post-juvenile stage *Triceratops* from U3. Many large *Triceratops* (e.g., MOR 1122 and MOR 3000) (3) exhibit evidence of postorbital horn-core resorption, suggesting that maximum length is reached earlier in ontogeny. Maximum postorbital horn-core length may have been expressed later in development (or for a longer duration) in *Triceratops* from lower in the formation.

Triceratops from the upper half of the HCF exhibit a more vertically inclined NPP (Fig. 2C), which contributes to a rostrum that appears shorter and more convex in lateral profile (a feature Forster noted in *T. prorsus*) (12). However, we note that a Spearman's rank correlation test found apparent reduction in rostrum length to be statistically insignificant (Spearman's rank coefficient 0.018, $P = 0.966$). Large specimens from U3 (e.g., MOR 004) possess a more elongate rostrum relative to basal-skull length (Fig. 2E and Dataset S1); however, the shape of U3 rostra appears to be consistently convex.

Eotriceratops xerinsularis, found in the stratigraphically older uppermost Horseshoe Canyon Formation (~68 Ma) (28), expresses morphologies (elongate postorbital horn cores, small nasal horn) consistent with its stratigraphic position relative to *Triceratops*.

Cladistic and Stratocladistic Analyses. Initial cladistic analyses recovered a polytomy of all HCF specimens, with the 50% majority tree producing a succession of *Triceratops* that largely correlates with stratigraphic placement (Fig. S5 and SI Text). Removal of the more fragmentary material recovered *Torosaurus* specimens as basal to a stratigraphic succession of *Triceratops*, including a polytomy of specimens from the upper half of the formation (Fig. 3A). A similar topology was recovered when specimens not exhibiting codeable features of the parietal squamosal frill were removed from the analysis (Fig. 3B). Removal of MOR 2924, a specimen from the base of U3 that does not preserve post-orbital horn cores (SI Text), recovers specimens from the upper part of M3 as basal to U3 *Triceratops*.

In the analysis of the most reduced dataset, UCMP 113697 and MOR 3027 cluster together (Fig. 3C). These specimens exhibit a combination of characters found in *Triceratops* from L3 and M3. The epinasal of UCMP 113697 is morphologically intermediate between L3 and U3 *Triceratops* (the epinasal of MOR 3027 is incomplete). These specimens each exhibit large post-orbital horn cores (a feature expressed in some L3 *Triceratops*) and a more vertically inclined NPP (found in U3 *Triceratops*). MOR 3045 is recovered as being more derived than UCMP 113697 and MOR 3027 (Fig. 3) based on its possession of relatively short postorbital horn cores, a more expanded NPP, and a pronounced step bordering the "incipient fenestrae" (sensu ref. 3) (SI Text). This specimen exhibits the basal condition of the anteromedial nasal process and expresses a pronounced upturn of the posterior surface of the epinasal, suggesting the presence of a protuberance in life. MOR 3045 exhibits a fairly elongate epinasal (estimated length/width, ~1.88), with a posterior surface that is broader than is seen in most U3 specimens and, like UCMP 113697, MOR 3027, and U3 *Triceratops*, exhibits a more vertically inclined NPP.

Stratocladistic analyses, in which specimens were grouped into operational units based on stratigraphic position, were performed in the program StrataPhy (29). *Torosaurus* specimens were initially considered separately from other specimens (SI Text). Initial results suggested that specimens from the upper half of the HCF represented a sequence of ancestors and descendants but differed on the position of operational units from the lower half of the formation (Fig. S6A). This result was likely influenced by missing data for specimens from the lower half of the formation; no specimens from lower M3 preserve frill characters that can distinguish them from the *Torosaurus* morphology. When *Torosaurus* specimens were incorporated into *Triceratops* operational units, three topologies were produced: a strictly cladogenetic result, a topology in which all operational units except lower M3 were recovered in a transformational sequence, and a topology in which the HCF operational units were recovered in two lineages (an upper L3/lower M3 lineage and an upper M3/U3 lineage) that had diverged at some point in the deposition of L3 (Fig. S6B). Pruning of *Torosaurus* specimens from the dataset produced two topologies that incorporated morphological transformation: one topology in which all HCF operational units fell into a single lineage and another topology presenting two HCF lineages that diverged either in L3 or before deposition of the HCF (Fig. S6C).

Discussion

Evolutionary Patterns. One of the principle questions in evolutionary biology regards the modes of evolution: what evolutionary patterns are preserved in the fossil record and how prominent are these patterns (30–32)? Small sample sizes for most nonavian dinosaur taxa complicate the investigation of evolutionary modes in this group. As such, it is unknown how prominent a role anagenesis (the transformation of lineages over time) (Fig. 4A) (33–37) played in their evolution or whether the majority of morphologies recorded in the fossil record were a product of

Fig. 3. Results of cladistic analysis of HCF *Triceratops*. (A) Strict consensus tree produced by analysis of HCF specimens using a heuristic search and multistate coding once the most fragmentary specimens were removed (See [SI Text](#) and [Fig. S5](#) for additional results). Bootstrap support values below nodes. Bremer support values greater than 1 above nodes. *Torosaurus* specimens are recovered as basal to a stratigraphic succession of specimens. MOR 3011 does not preserve characters of the parietal-squamosal frill. (B) Analysis (multistate coding, branch-and-bound search) excluding specimens that could not be coded for at least 10 cranial characters or characters of the frill. (C) Analysis (multistate coding, branch-and-bound search) after removal of MOR 2924 ([SI Text](#)).

cladogenesis (evolution via branching events) (Fig. 4 *B–D*) (8, 32, 33, 37, 38).

Horner et al. (6) presented evidence for anagenesis in several dinosaur clades within the Cretaceous Two Medicine Formation of Montana. It has been suggested that the ceratopsid sample size presented in that study was too small and that cladogenesis was a more conservative interpretation of the data (7). A combination of large sample size, ontogenetic resolution, and detailed stratigraphic data makes *Triceratops* an ideal taxon for testing hypotheses regarding evolutionary mode in a nonavian dinosaur.

Restriction of the full *T. prorsus* morphology to U3 renders untenable hypotheses that *T. horridus* and *T. prorsus* represent sexual or ontogenetic variation within a single taxon. *Triceratops* from the upper part of M3 exhibit a combination of features found in L3 and U3 *Triceratops*. This pattern suggests that the evolution of *Triceratops* incorporated anagenesis.

Strict consensus trees produced by cladistic analyses either recover upper M3 specimens in a polytomy with all HCF specimens, in a polytomy of HCF *Triceratops* from the upper half of the formation, or UCMP 113697 and MOR 3027 cluster together whereas MOR 3045 shares more features with U3 *Triceratops* (Fig. 3 and [Fig. S5](#)). We will consider four alternative hypotheses for the morphological pattern recorded in the HCF:

- T. prorsus* evolved elsewhere and migrated into the HCF, eventually replacing the incumbent HCF *Triceratops* population by the beginning of the deposition of U3. Upper M3 specimens represent early members (or close relatives of) this group that would come to dominate the ecosystem.
- Variation between MOR 3045, MOR 3027, and UCMP 113697 represents intraspecific (or intrapopulation) variation. As the HCF *Triceratops* lineage evolved, some individuals expressed more of the features that would eventually dominate the population. Over time, these traits were selected for and characterized U3 *Triceratops*. This is a purely anagenetic scenario.
- A bifurcation event is recorded in the HCF and occurred at some point before the deposition of U3, resulting in two lineages that differ primarily in the morphology of the epinasal and rostrum (consistent with Forster's diagnoses for *T. horridus* and *T. prorsus*). MOR 3045 represents an early member of a lineage that evolved into U3 *Triceratops*. This scenario incorporates anagenesis (38) and is presented in some trees produced by the stratocladistic analysis ([Fig. S6](#)).
- The evolution of *Triceratops* was characterized by a series of cladogenetic events that produced at least five taxa over the course of the deposition of the HCF (the L3 clade, the lower M3 clade, the MOR 3027 clade, the MOR 3045 clade, and the U3 clade). This strictly cladogenetic scenario suggests that no *Triceratops* found lower in the HCF underwent evolutionary transformation into forms found higher in the formation.

A Biogeographic Signal? The Hell Creek Project's stratigraphic record of *Triceratops* is primarily restricted to northeastern Montana. It has been hypothesized that *T. horridus* and *T. prorsus* were largely biogeographically separated, with *T. prorsus* generally restricted to the Hell Creek and Frenchman Formations and *T. horridus* commonly found in the more southern Lance, Laramie, and Denver Formations (15, 17). However, this suggested biogeographic segregation may represent an artifact of the stratigraphic record. Specimens that have thus far been described from neighboring coeval formations exhibit morphologies consistent with their stratigraphic position relative to the HCF (39, 40) ([SI Text](#)).

premaxilla. J. Sertich provided access to specimens at the Denver Museum of Nature and Science. P. Sheehan provided access to, and locality data for, Milwaukee Public Museum (MPM) specimen VP6841. R. Scheetz and B. Britt provided access to a cast of Museum of Western Colorado (MWC) specimen 7584 at Brigham Young University Museum of Paleontology; W. Clemens shared stratigraphic data for this specimen. The Bureau of Land Management, Charles M. Russell National Wildlife Refuge, and the Department of Natural Resources and Conservation provided access to land under their management and provided collection permits. We are grateful to the Twitchell, Taylor, Trumbo, Hohen, and Isaacs families for land access. We thank Museum of the Rockies (MOR) volunteers, staff, and

all participants in the Hell Creek Project. We thank the MOR and the University of California Museum of Paleontology (UCMP) for support of this research. Funding for the Hell Creek Project was provided by donations from J. Kinsey, C. B. Reynolds, H. Hickam, and Intellectual Ventures. The Windway Foundation and the Smithsonian Institution provided grants (to J.R.H.). UCMP provided funding (to M.B.G.). The Theodore Roosevelt Memorial Fund of the American Museum of Natural History, the Fritz Travel Grant of the Royal Ontario Museum, and the Jurassic Foundation provided grants (to J.B.S.). The Evolving Earth Foundation and the Doris O. and Samuel P. Welles Research Fund of the UCMP provided grants (to J.B.S. and D.W.F.).

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