

NEW INSIGHTS ON THE FRILL ORNAMENTATIONS OF PROTOCERATOPSIDS

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ABSTRACT *Protoceratops andrewsi* is a small-bodied, non-ceratopsoid ceratopsian dinosaur found in the Upper Cretaceous Djadokhta Formation in Mongolia. Although it has a well-developed parietosquamosal frill, the frill margin has been thought to be unadorned, unlike ceratopsids. On ceratopsids, especially centrosaurines, the subadult frill margin in dorsal view is typically undulated, with the apex of each undulation providing a locus onto which an epiparietal can potentially fuse and mature into a frequently modified shape that can aid in the identification of species. This study explicitly notes that the frill margin of *P. andrewsi* frill is undulated. Although virtually all *P. andrewsi* and a limited number of specimens of other protoceratopsids examined in this study have frill margin undulations, their development is variable and generally quite subtle; the size, number, and position of the processes are highly plastic among individuals and do not exhibit a consistent pattern related to the size of individuals. There is no sign that the undulations of *P. andrewsi* were associated with epiossifications. Due to the subtlety and inconsistency of the frill undulations, the potential functions of the frill margin undulations are currently not obvious. We also report several previously underappreciated protoceratopsid features that may have taxonomic utility within marginocephalians and important implications for understanding the evolution of the integumentary structures within Ceratopsia.

KEYWORDS Dinosauria, Marginocephalia, Ceratopsia, *Protoceratops*, Parietosquamosal

INTRODUCTION

Protoceratops is a non-ceratopsoid ceratopsian and one of the most abundant taxa found in the Upper Cretaceous Djadokhta Formation and contemporaneous strata distributed in the Gobi Desert of Mongolia and Inner Mongolia, China. Hundreds of specimens of this genus have been collected since its discovery in 1922 (Granger and Gregory, 1923), and new specimens are still being collected (Chen, 2017; Ishigaki et al., 2018; Chen et al., 2022). The huge sample size presented by the *Protoceratops* specimens has allowed for the investigations of morphological variations, growth, sexual dimorphism, and ecology in this genus (e.g., Brown and

Schlaikjer, 1940; Dodson, 1976; Fastovsky et al., 1997, 2011; Hone et al., 2014, 2016; Maiorino et al., 2015; Fostowicz-Frelik and Słowiak, 2018), with implications for its function and the selection pressures related to its evolution (e.g., Brown and Schlaikjer, 1940; Kurzanov, 1972; Dodson, 1976; Maiorino et al., 2015; Hone et al., 2016; Knapp et al., 2021). The parietosquamosal frill of *Protoceratops* is well developed compared to other non-ceratopsoid ceratopsians but has generally been thought to be unadorned (Gregory and Mook, 1925; Brown and Schlaikjer, 1940), unlike ceratopsids whose parietosquamosal frills can have processes composed of either the frill margin, epiossifications, or both (Sampson et al., 1997; Ryan et al., 2001; Mallon et al., 2023). The initial

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suggestion that *Protoceratops* has frill margin undulations (Serenó, 2000) was later questioned, with the putative undulations being instead considered to be preservational artifacts (Makovicky, 2002). Here we report data supporting the presence of the frill undulations in *Protoceratops* along with some underappreciated anatomical features of *Protoceratops* that may have implications for the evolution of the ceratopsian frill.

MATERIALS AND METHODS

We examined 62 *Protoceratops* specimens housed in the American Museum of Natural History, the Institute of Paleontology of the Mongolian Academy of Sciences, and the former Hayashibara Museum of Natural Sciences. There are two known *Protoceratops* species, *P. andrewsi* and *P. hellenikorhinus*; the former is only known from Mongolia, and the latter from Inner Mongolia, China. Only Mongolian specimens were examined due to logistical constraints, and, therefore, we could not examine *P. hellenikorhinus* specimens.

Most of the specimens examined here are from two localities: Bayn Dzag, the type locality of *P. andrewsi* (Granger and Gregory, 1923), and Tugrikin Shire, where the famous “Fighting Dinosaurs” (*P. andrewsi* MPC-D 100/512 and *Velociraptor mongoliensis* MPC-D 100/25) were found (Kielan-Jaworowska and Barsbold, 1972). We also examined specimens of *P. andrewsi* and *Protoceratops* sp. from Udyn Sayr (Handa et al., 2012), *Protoceratops* sp. from the adjacent locality of Bor Tolgoi (Saneyoshi et al., 2010; Tsogtbaatar and Chinzorig, 2010) and *Bagaceratops* sp. from Udyn Syar (Czepeński, 2020).

Additionally, we briefly describe MPC-D 100/555, a nearly complete articulated skeleton of *Protoceratops* (field number 949726 TSGT-Ts-IV), which was found at Tugrikin Shire during the Hayashibara Museum of Natural Sciences-Mongolian Paleontological Center Joint Paleontological Expedition in 1994. Unfortunately, the specimen was damaged during preparation, so our observations of this specimen are based on the original specimen stored at IP-MAS and from photographs taken in the field during the collection of the specimen.

Institutional Abbreviations — AMNH, American Museum of Natural History, New York, United States; HMNS, Hayashibara Museum of Natural Sciences, Okayama, Japan;

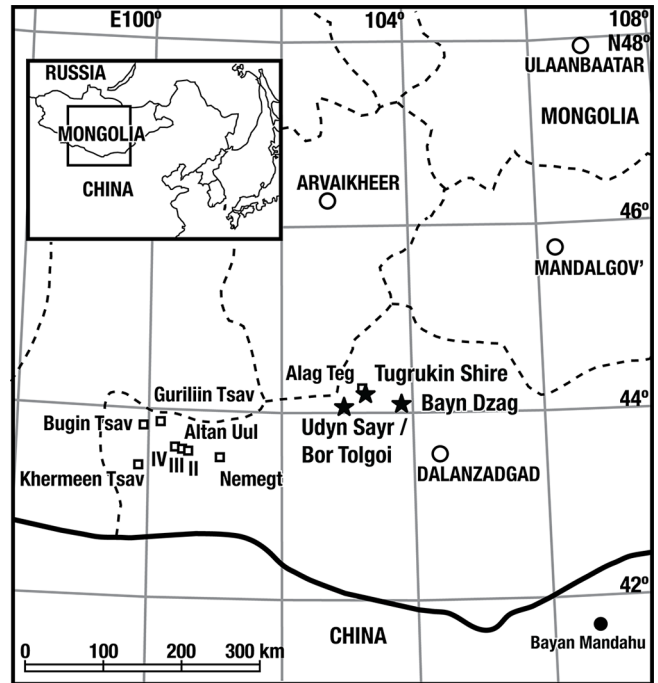


FIGURE 1. Locality map of central and western Gobi Desert. Stars represent the localities yielding *P. andrewsi*, a black circle indicates the locality of *P. hellenikorhinus*, and open squares indicate representative dinosaur fossil localities of this area. The map was modified from Watabe et al. (2010).

IP-MAS; the Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MPC, Mongolian Paleontological Center, Ulaanbaatar, Mongolia (currently IP-MAS)

RESULTS

Description of MPC-D 100/555

MPC-D 100/555 was, when collected, a well-preserved, nearly completely articulated skeleton (Fig. 2A), but it was extensively damaged during preparation. The skull was almost complete but lacked the right posterior bar of the parietal when found (Fig. 2B and C). Although small fragments of the frill are still available, it is impossible to know their relative original positions in the frill. A well-defined, dorsally convex longitudinal ridge on the lateral surface of the maxilla, the curved anterior margin of the predentary, and the curved ventral edge of the dentaries all indicate that this specimen belongs to *Protoceratops andrewsi* rather than to *P. hellenikorhinus* (Lambert et al., 2001). This is congruent with

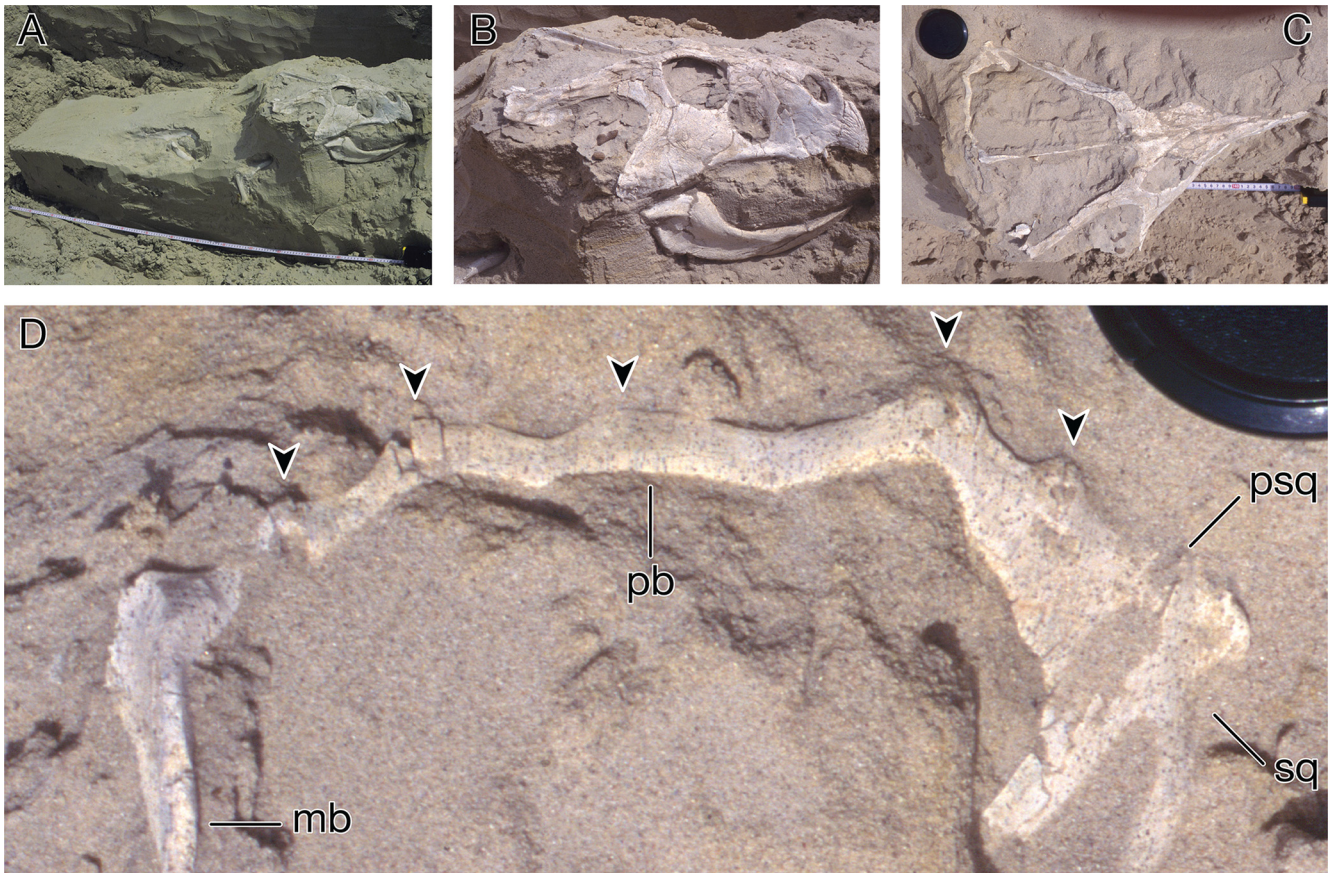


FIGURE 2. Field photographs of MPC-D 100/555, a *Protoceratops andrewsi* specimen with strong undulations. **A**, right lateral view of the whole skeleton in sediments; **B**, right lateral view of the skull; **C**, dorsal view of the skull; **D**, close-up of the posterior portion of the parietosquamosal frill in the dorsal view. Black arrows indicate the processes. **Abbreviations:** **mb**, midline bar of parietal; **pb**, posterior bar of parietal; **psq**, parietal-squamosal contact; **sq**, squamosal.

the fact that, to date, only *P. andrewsi* has been reported from the locality. Based on the field photographs and the fragmented specimen, the total (390 mm) and basal (250 mm) skull lengths, frill length (160 mm), and half-width (123 mm) can be reliably estimated. The basal skull length is approximately 70% of the longest reported *Protoceratops andrewsi* basal skull length (AMNH 6466, 357 mm; Dodson, 1976; Maiorino et al., 2015; Hone et al., 2016). The field photographs clearly show that the frill margin of this specimen is strongly undulated compared to typical *Protoceratops* specimens (Fig. 2D), although none of the frill fragments in the collection preserve the undulated frill margin. There appear to be five processes located on the convex posterior margin of the parietal. The size and shape of the processes are not consistent, and they are unevenly distributed; the second and third processes lateral to the midline bar have wide bases, but the

first, fourth, and fifth processes have relatively narrower bases, giving the latter three more triangular-shaped. There are no epioassifications associated with the processes or indications that they were ever present.

Additional Protoceratopsid Specimens with Undulated Frill Margins

Undulated *Protoceratops* frill margins were noted by Sereno (2000), who included “low tab-shaped processes on the frill margin (three on the squamosal and four or five on the parietal)” as one of the potential autapomorphies of *P. andrewsi*, and illustrated by drawings of AMNH 6408 (Sereno 2000: Fig. 25.6). Four tab-shaped flanges on the left and five on the right posterior parietal bar are indicated in the figure, but processes on the squamosals are not indicated. AMNH 6408 is currently on display but inaccessible for

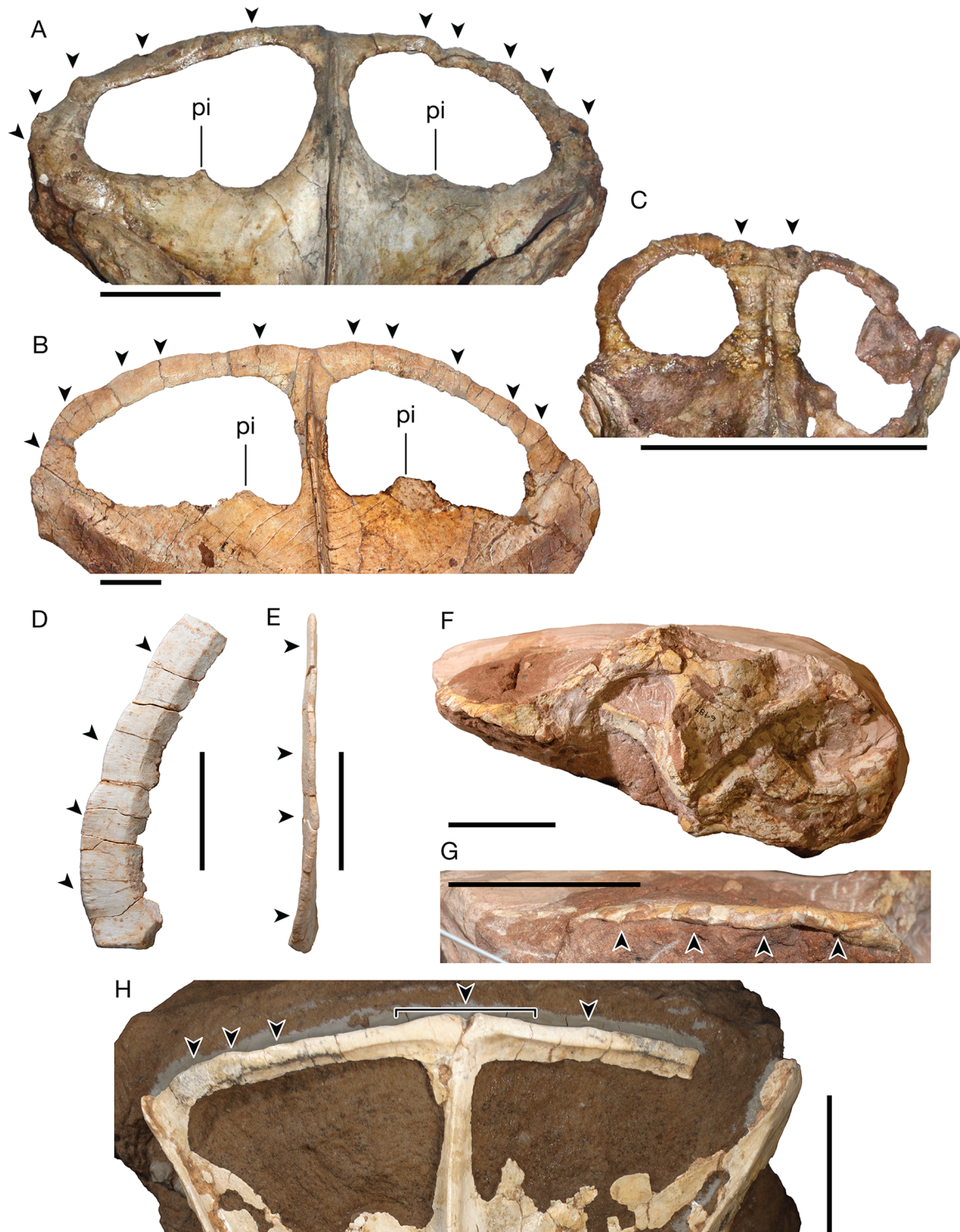


FIGURE 3. *Protoceratops andrewsi* specimens showing frill margin undulations. **A**, dorsal view of AMNH 6408 parietosquamosal frill; **B**, dorsal view of AMNH 6466 parietosquamosal frill; **C**, dorsal view of AMNH 6419 parietosquamosal frill; **D**, dorsal view of MPC-D 100/554; **E**, lateral view of MPC-D 100/554, right side of the photograph is dorsal side; **F**, right lateral view of AMNH 6487 (a partial skull); **G**, ventral oblique posterolateral view of right posterior parietal bar of AMNH 6487; **H**, dorsal view of MPC-D 100/537 parietosquamosal frill. Note that the matrix and modeling clays supporting some parts of this specimen are shaded since the color of the clay obscures the frill margin. **Abbreviation:** pi, process projecting inward to the parietal fenestra. Black arrows indicate the processes. Scale bars equal 5 cm. Scale bars of A-C are produced based on the frill width reported in Hone et al. (2016).

TABLE 1. Summary of measurements and degrees of undulation development of selected protoceratopsid specimens in this study. * indicates the measurements are estimated. **Abbreviations:** TSL, total skull length; BSL, basal skull length; FL, frill length; FHW, frill half-width.

Specimen number	Taxon	Locality	TSL	BSL	FL	FHW	Source of measurement	Development of undulations	Figure numbers
AMNH 6419	<i>Protoceratops andrewsi</i>	Bayn Dzag	115	76	52	34	Hone et al. (2016)	moderately	Fig. 3C
AMNH 6487	<i>Protoceratops andrewsi</i>	Bayn Dzag	-	149*	97*	-	this study	moderately	Fig. 3F and G
MPC 100/534	<i>Protoceratops andrewsi</i>	Tugrikin Shire	222	157	153	144	this study	slightly	Fig. 8 in Hone et al. (2014)
MPC-D 100/537	<i>Protoceratops andrewsi</i>	Udyn Sayr	274*	168*	163	119	this study	slightly	Fig. 3G
AMNH 6408	<i>Protoceratops andrewsi</i>	Bayn Dzag	314	235	152	121	Hone et al. (2016)	moderately	Fig. 3A
MPC-D 100/555	<i>Protoceratops andrewsi</i>	Tugrikin Shire	360*	250*	160*	123*	this study	highly	Fig. 2D
MPC-D 100/554	cf. <i>Protoceratops andrewsi</i>	Bayn Dzag	-	-	-	160*	this study	moderately	Fig. 3D and E
AMNH 6425	<i>Protoceratops andrewsi</i>	Bayn Dzag	469	313	264	236	Hone et al. (2016)	slightly	not figured
AMNH 6466	<i>Protoceratops andrewsi</i>	Bayn Dzag	491	357	262	233	Hone et al. (2016)	moderately	Fig. 3B
MPC-D 100/540	<i>Protoceratops</i> sp.	Udyn Sayr	-	-	-	338	this study	slightly	Fig. 4A and B
MPC-D 100/551	<i>Bagaceratops</i> sp.	Udyn Sayr	140*	230*	90	146	this study	slightly	Fig. 4C

close observation; however, at least some of the processes are visible (Fig. 3A). Based on the figure in Sereno (2000) and observation of the displayed specimen, the lateralmost processes are the most prominent. Although the squamosal frill margin is not preserved on the right, the left squamosal seems to have at least two processes. AMNH 6466, also on display, also appears to have frill margin undulations, although their development is less pronounced (Fig. 3B). The shapes of these processes are more elliptical in dorsal view than those of AMNH 6408. There seem to be five processes on both sides, but their relative positions do not seem to be symmetrical. The squamosal frill margins of AMNH 6466 also have slightly developed processes, three on the right and at least one on the left. Another gallery specimen, AMNH 6419, with a basal skull length of only 76 mm (Table 1), also appears to have weakly developed processes including at least one process close to the midline on both sides of the posterior parietal bar (Fig. 3C). Although it is difficult to confirm, the frill margin undulations of these three AMNH gallery specimens appear to be real features of the frill and can not be attributed to breakage or postmortem modification

by scavenging by insects or mammals, the latter frequently observed on *Protoceratops* specimens from the aeolian Djadokhta and Barun Goyot formations (Kirkland and Bader, 2010; Matsumoto and Saneyoshi, 2010; Saneyoshi et al., 2011).

Frill undulations were also observed on MPC-D 100/554 from Bayn Dzag (field number IPG-OUS18Sep-038, Ishigaki et al., 2018) that we tentatively assign to cf. *Protoceratops andrewsi* based on the shape of the parietal (Makovicky and Norell, 2006; Chinnery and Horner, 2007). The specimen preserves four processes (Fig. 3D). The lateralmost process is associated with short ridges that run perpendicular to the outer margin of the frill. Although it is very subtle, these processes appear to be imbricated (Fig. 3E), a feature that is characteristic of Centrosaurinae (Dodson et al., 2004). The imbrication of the processes is also seen on AMNH 6487, a partial skull preserving a partial right parietal and a right squamosal (Fig. 3F and G). The degree of imbrication tends to be most pronounced on the lateralmost processes.

Three specimens of *P. andrewsi* have been observed to have a process spanning the posterior margin of the midline

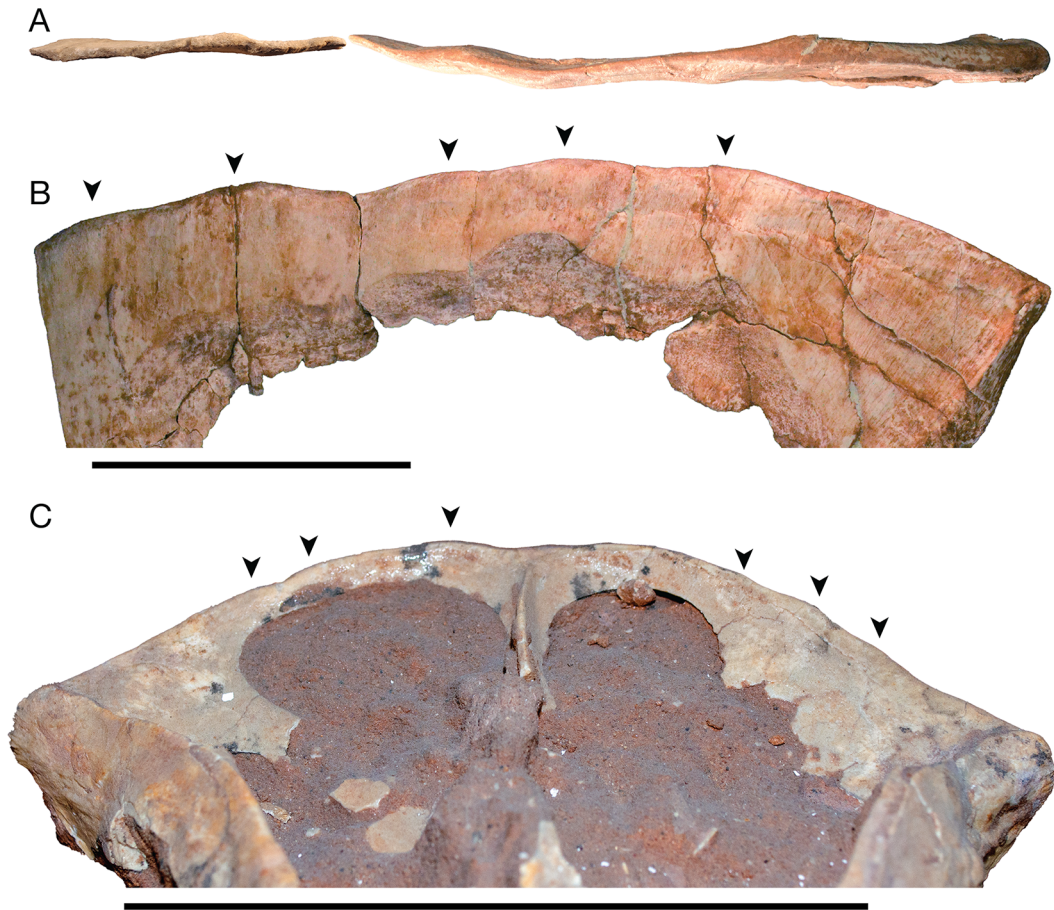


FIGURE 4. Protoceratopsid specimens showing frill margin undulations. **A**, *Protoceratops* sp., MPC-D 100/540 parietosquamosal frill in posterolateral view; **B**, in dorsal view; **C**, *Bagaceratops* sp., MPC-D 100/506, parietosquamosal frill in anterodorsal view. Black arrows indicate the processes. Scale bars equal 10 cm.

parietal bar (Fig. 3H). It is distinct on MPC-D 100/537 from Udyn Sayr (Handa et al., 2012) but only subtly developed on MPC-D 100/534, an almost complete skeleton and skull from Tugrikin Shire (Hone et al., 2014). AMNH 6425, an almost complete skull (Brown and Schlaikjer, 1940), is also interpreted as having this feature, but its identification is equivocal due to the poor preservation of this portion of the skull.

The undulations along the posterior parietal margins are also present on protoceratopsid specimens that are not assigned to *P. andrewsi*. MPC-D 100/540, a partial skull of *Protoceratops* sp., includes the left half of the parietal (Handa et al., 2012) that has at least five imbricated processes along the posterior margin (Fig. 4B and C). Although the specimen is fragmentary, the surface preservation is pristine, and there are no signs of postmortem damage along the posterior margin of the parietal, allowing us to

confidently identify this feature. The *Bagaceratops* sp. parietal (MPC-D 100/551, mislabeled as MPC-D 100/551B in Czepiński, 2020) also has at least three processes, but their development is quite subtle (Fig. 4C).

Additional Observations on Protoceratopsid Frills

Several protoceratopsid specimens show a region of rugose texture and eminences on the lateral side of the squamosals (Fig. 5A) adjacent to the dorsoposterior margin of the infratemporal fenestra. Both rugosities and eminences co-occur in many individuals, but one feature or the other can be variably expressed. The rugosity on the squamosal is like the texture developed on the posterior part of the jugals and the postorbitals of some *Protoceratops* specimens, typically near the posterodorsal margin of the orbit (Fig. 5B). The eminences are typically expressed as elongated bumps. When multiple bumps co-occur, they are aligned in parallel.

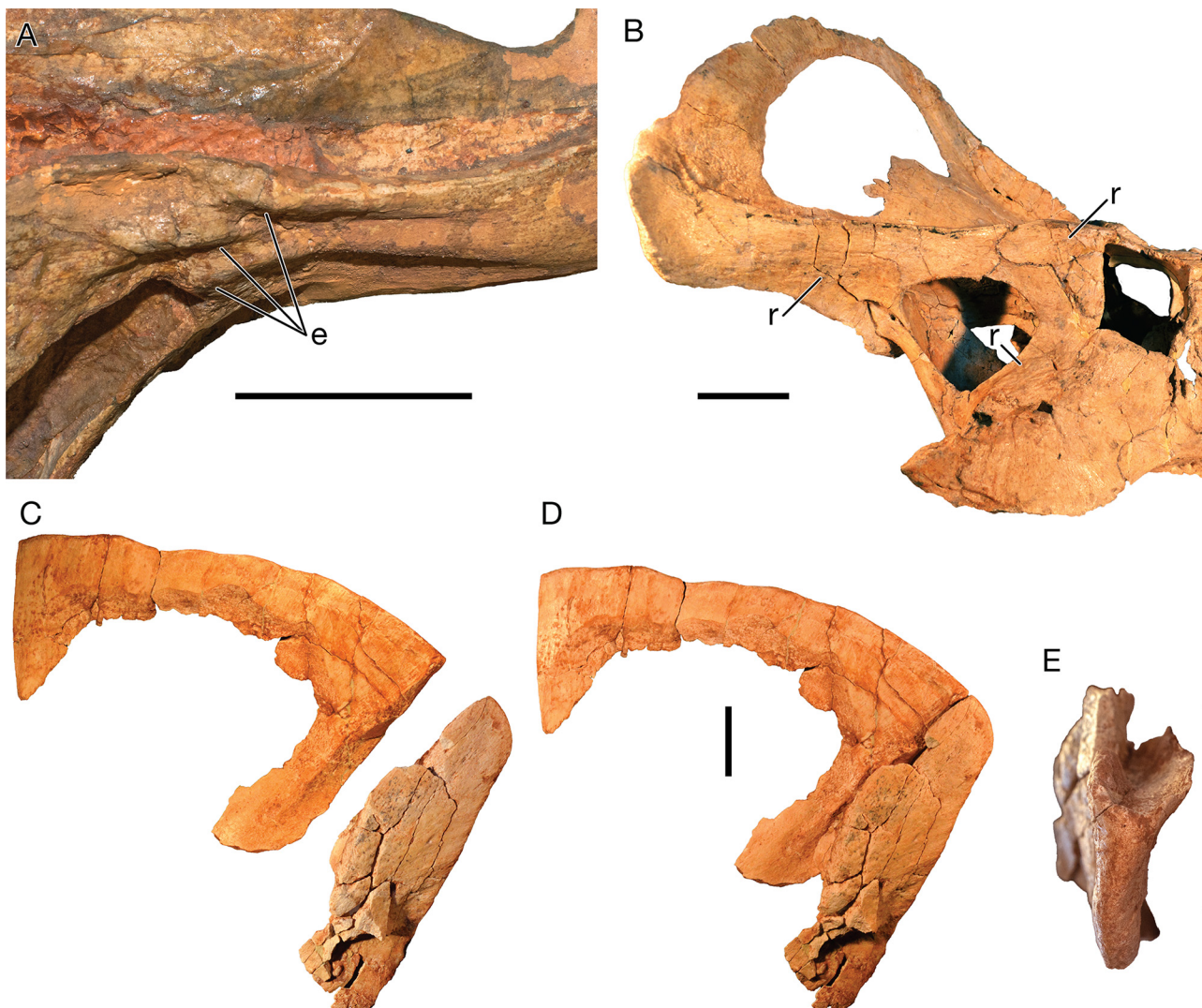


FIGURE 5. Protoceratopsid specimens showing some anatomical features that have been underappreciated in previous studies. **A**, dorsally obliques anterolateral view of ridges on the lateral surface of left squamosal of AMNH 6433, *P. andrewsi*, note the posterior parts of squamosal including ridges are not preserved and sculpted; **B**, right lateral view of the skull of MPC-D 100/530, *P. andrewsi* showing rugosity on squamosal, postorbital, and jugal; **C-E**, parietosquamosal frill of MPC-D 100/540; **C**, disarticulated parietal and squamosal; **D**, articulated parietal and squamosal; **E**, posterior view of squamosal, showing deeply concave parietal contact. **Abbreviations:** e, eminence; r, rugosity. Scale bars equal 5 cm.

Although the superb articulated preservation of many *Protoceratops* specimens allows for the detailed investigation of their anatomy, the information on the articular surface of individual skull bones is poorly understood. The disarticulated partial skull of MPC-D 100/540 (*Protoceratops* sp.) presents the unique opportunity to observe the parietosquamosal contact of this genus in detail, revealing that the convex parietal inserts into the deeply concave articulating surface of the squamosal (Fig. 5C-E).

DISCUSSION

Evolution of Frill Margin Undulations of Protoceratopsids

In this study, we confirm the presence of marginal frill undulations in *Protoceratops andrewsi*, a feature that is common in ceratopsids. This feature on *P. andrewsi* was first noted by Sereno (2000) but subsequently discounted by Makovicky (2002). The presence of frill margin undulations on *Protoceratops* sp. and *Bagaceratops* sp. suggests that the

undulated frill margin is not an autapomorphy of *P. andrewsi* as suggested by Sereno (2000) but is rather potentially a synapomorphy for Protoceratopsidae. In Ceratopsoidea, a similar feature was reported by Nessov (1995) on a squamosal of *Turanoceratops* with a “slightly serrated or unserrated along the posterolateral margin”. Unfortunately, the squamosal is now missing (Sues and Averianov, 2009), so its presence cannot be confirmed. A frill margin undulation has not been reported in *Zuniceratops* (Wolfe et al., 2010); however, the frill margin is poorly represented in the known specimens. Additional frill specimens of non-ceratopsid ceratopsoids will be critical to our understanding of the evolution of frill margin undulations and their associated ornamentations.

Although the protoceratopsid frill itself likely functioned as a display structure either intra-, interspecifically or both (Dodson, 1976; Maiorino et al., 2015; Hone et al., 2016; Knapp et al., 2021), the subtlety of undulations and the lack of systematic patterns relative to size increase or sexual dimorphism in the undulation morphology among the examined individuals (Table 1) do not provide unequivocal support for the hypothesis that the undulations contributed to a display function in this group. This interpretation could be rejected if the processes were in some way exaggerated by soft tissues. However, we did not find any signs of epiossifications on the examined protoceratopsid specimens or evidence (e.g., neurovascular grooves) for attachment points for overlying cornified sheaths (Hieronymus et al., 2009), although rugose texturing or small bumps were occasionally observed on some processes, which cannot be discounted as being associated with overlying soft tissues. Even if the undulations were not associated with enlarged soft tissue structures, they may still have been covered with pronounced scales as suggested by bumps on parietal midline bars, squamosals, and supraorbital regions as well as epiparietals and episquamosals of centrosaurines (Hieronymus et al., 2009). Further detailed observations on the surface texture and osteohistological analyses of protoceratopsid parietosquamosal frills that are beyond the scope of this study are necessary to elucidate the possible presence of soft tissue on these processes during life. Based on the dataset of VanBuren et al. (2015), the ratio of total skull length/basal skull length of *P. andrewsi* is exceptionally high among non-ceratopsid ceratopsians and within the range of ceratopsids (*P. andrewsi* 2.13; non-ceratopsid ceratopsians except *P. andrewsi* 1.01-1.32; ceratopsids

1.87-2.56). Our observations, therefore, suggest that frill undulations occur when the frill is enlarged in the ceratopsian evolution, such as seen in *Protoceratops*.

The imbrications of parietal frill margin undulations have been regarded as a synapomorphy of centrosaurines (e.g., Dodson et al., 2004). Although the imbricated processes seen on some protoceratopsid specimens are generally very subtle compared to centrosaurines, the pattern of the imbrications (the anterior margins of processes shift ventrally, and the posterior margins dorsally) is the same as that observed in centrosaurines, suggesting that the frill margin undulations in these clades are not independently acquired, but are homologous.

Chiba et al. (2017) suggested that epiparietal morphology was highly plastic in non-eucentrosauran centrosaurines (e.g., *Xenoceratops* [Ryan et al., 2012] and *Wendiceratops* [Evans and Ryan, 2015]) and became relatively fixed in eucentrosaurans. The degree of plasticity seen in the morphology, number, and location of protoceratopsid frill processes is even higher than that of non-eucentrosauran centrosaurines, suggesting that the plasticity of this feature was present in the common ancestor of Coronosauria and decreased during the evolution of Ceratopsoidea.

As frill margin imbrications are potentially a shared feature between protoceratopsids and centrosaurines, the morphology of the parietosquamosal contact of protoceratopsids is also similar to that of centrosaurines. The parietosquamosal contact is a buttress-like structure made of the convex contact surface of the parietal and the concave squamosal contact. Chasmosaurines differ from centrosaurines in having a contact that is relatively flat in cross-section (Ryan and Russell, 2005; Longrich, 2013). The parietosquamosal contact of *Protoceratops* was previously coded as the chasmosaurine-like condition (Ryan and Russell, 2005), but our observations clearly indicate that protoceratopsids have a deeply concaved centrosaurine-type parietosquamosal contact (Fig. 5E). Additionally, some *Protoceratops andrewsi* have a short process projecting posteriorly from the anterior margin of the parietal fenestra (e.g., AMNH 6466 and AMNH 6408 in Fig. 3A and B) which has been listed as one of three diagnostic characters for *Protoceratops andrewsi* (Makovicky, 2002). However, similar processes are reported in many centrosaurine specimens (e.g., Holmes et al., 2019; Brown et al., 2020), suggesting that this structure may also be a shared feature between protoceratopsids and centrosaurines.

Comments on the Cranial Features Shared within Marginocephalia

In reference to the bumps or ridges on the lateral surface of *Protoceratops* squamosals, similar structures are often reported in centrosaurines (Penkalski and Dodson, 1999; Sampson et al., 2013; Rivera-Sylva et al., 2016; Chiba et al., 2017) and have been suggested to be associated with overlying scales (Hieronymus et al., 2009). Similar structures to the eminences and rugosities on squamosals, postorbitals or jugals seen on protoceratopsids can also be seen on these elements of basal ceratopsians such as *Yinlong* (Xu et al., 2006; Han et al., 2015), *Archaeoceratops* (You and Dodson, 2003), and *Auroraceratops* (Morschhauser et al., 2019). Furthermore, the similarities have been pointed out between the nodes on supraorbitals, postorbitals, and squamosals of pachycephalosaurs and the bumps in corresponding locations of centrosaurines (Hieronymus et al., 2009). Although the homology of ornamentations on the circumorbital regions and the lateral surface of squamosals have not been thoroughly investigated, the potential integumentary traces on *Protoceratops* squamosals imply the deeply nested homology of facial integumentary structures in various marginocephalians.

CONCLUSION

We regard that undulated frill margins exist in virtually all examined protoceratopsid specimens unless the feature has been taphonomically altered. The location of each process is variable within an individual bilaterally and among individuals. The degree of undulations is also variable among the specimens examined and does not appear to exhibit a systematic pattern relative to size increase or sexual dimorphism. Our examination of *Protoceratops andrewsi* and protoceratopsid frills has brought insights regarding the morphology and evolutionary implications of frill margin undulations in Ceratopsia. Our findings indicate that *P. andrewsi* has frill margin undulations, contrary to most of the previous studies. Furthermore, the undulated frill margin is not a unique characteristic of *P. andrewsi* but may be a shared feature in protoceratopsids or even Coronosauria. Frill margin undulations seem to have evolved when the frill itself was enlarged in the ceratopsian evolutionary history. Due to the subtlety of the frill undulations in protoceratopsids, it is plausible that these undulations, first a by-product of an enlarged frill, were later augmented by epiossifications in the ceratopsids for signaling

functions. Several other anatomical features, such as imbrications of frill margins and the parietal contact of the squamosals, highlight the similarity between protoceratopsids and centrosaurines that have not been previously documented. Detailed observations, including osteohistological analyses of frill and other skull elements on other non-ceratopsid ceratopsians, as well as discoveries of more non-ceratopsid ceratopsid specimens, will be critical to further elucidating the frill and facial integumentary structures in the ceratopsian evolution.

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AUTHOR CONTRIBUTIONS

KC and MJR designed the project and drafted the manuscript. KC, YY, and SK gathered and interpreted the data. All authors edited the manuscript.

LITERATURE CITED

Brown, B. & Schlaikjer, E. M. (1940). The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences*, 40(3),

- 133–266. <https://doi.org/10.1111/j.1749-6632.1940.tb57047.x>
- Brown, C., Holmes, R., & Currie, P. (2020). A subadult individual of *Styracosaurus albertensis* (Ornithischia: Ceratopsidae) with comments on ontogeny and intraspecific variation in *Styracosaurus* and *Centrosaurus*. *Vertebrate Anatomy Morphology Palaeontology*, 8(1), 67–95. <https://doi.org/10.18435/vamp29361>
- Butler, R. J., Upchurch, P., & Norman, D. B. (2008). The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology*, 6(1), 1–40. <https://doi.org/10.1017/s1477201907002271>
- Chen, X. (2017). The discovery and significance of the protoceratopsid dinosaur from the Lower Cretaceous of Ordos region, Inner Mongolia. *Acta Geoscientica Sinica*, 1–5. <https://doi.org/10.3975/cagsb.2017.02.08>
- Chen, X., Tan, K., Lu, L., & Ji, S. (2022). Occurrence of *Protoceratops hellenikorhinus* (Ceratopsia: Protoceratopsidae) in Alxa region, western Inner Mongolia, China. *Acta Geologica Sinica*, 96(11), 3722–3732. <https://doi.org/10.19762/j.cnki.dizhixuebao.2022302>
- Chiba, K., Ryan, M. J., Fanti, F., Loewen, M. A., & Evans, D. C. (2017). New material and systematic re-evaluation of *Medusaceratops lokii* (Dinosauria, Ceratopsidae) from the Judith River Formation (Campanian, Montana). *Journal of Paleontology*, 92(2), 272–288. <https://doi.org/10.1017/jpa.2017.62>
- Chinnery, B. J. & Horner, J. R. (2007). A new neoceratopsian dinosaur linking North American and Asian taxa. *Journal of Vertebrate Paleontology*, 27(3), 625–641. [https://doi.org/10.1671/0272-4634\(2007\)27\[625:anndln\]2.0.co;2](https://doi.org/10.1671/0272-4634(2007)27[625:anndln]2.0.co;2)
- Czepeński, Ł. (2020). New protoceratopsid specimens improve the age correlation of the Upper Cretaceous Gobi Desert strata. *Acta Paleontologica Polonica*, 65. <http://www.app.pan.pl/article/item/app007012019.html>
- Dodson, P. (1976). Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. *Journal of Paleontology*, 50(5), 929–940.
- Dodson, P., Forster, C. A., & Sampson, S. D. (2004). Ceratopsidae. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria* (pp. 494–513). University of California Press. <https://doi.org/10.1525/9780520941434-029>
- Evans, D. C. & Ryan, M. J. (2015). Cranial anatomy of *Wendiceratops pinhornensis* gen. et sp. nov., a centrosaurine ceratopsid (Dinosauria: Ornithischia) from the Oldman Formation (Campanian), Alberta, Canada, and the evolution of ceratopsid nasal ornamentation. *PLOS ONE*, 10(7), e0130007. <https://doi.org/10.1371/journal.pone.0130007>
- Fastovsky, D. E., Badamgarav, D., Ishimoto, H., Watabe, M., & Weishampel, D. B. (1997). The paleoenvironments of Tugrikin-shireh (Gobi Desert, Mongolia) and aspects of the taphonomy and paleoecology of *Protoceratops* (Dinosauria: Ornithischia). *PALAIOS*, 12(1), 59–70. <https://doi.org/10.2307/3515294>
- Fastovsky, D. E., Weishampel, D. B., Watabe, M., Barsbold, R., Tsogtbaatar, K. H., & Narmandakh, P. (2011). A nest of *Protoceratops andrewsi* (Dinosauria, Ornithischia). *Journal of Paleontology*, 85(6), 1035–1041. <https://doi.org/10.1666/11-008.1>
- Fostowicz-Freluk, L. & Słowiak, J. (2018). Bone histology of *Protoceratops andrewsi* from the Late Cretaceous of Mongolia and its biological implications. *Acta Palaeontologica Polonica*, 63(3), 503–517. <https://doi.org/10.4202/app.00463.2018>
- Granger, W. & Gregory, W. K. (1923). *Protoceratops andrewsi*, a pre-ceratopsian dinosaur from Mongolia. *American Museum Novitates*, 72, 1–9.
- Gregory, W. K. & Mook, C. C. (1925). On *Protoceratops*, a primitive ceratopsian dinosaur from the Lower Cretaceous of Mongolia. *American Museum Novitates*, 156, 1–9.
- Han, F.-L., Forster, C. A., Clark, J. M., & Xu, X. (2015). Cranial anatomy of *Yinlong downsi* (Ornithischia: Ceratopsia) from the Upper Jurassic Shishugou Formation of Xinjiang, China. *Journal of Vertebrate Paleontology*, 36(1), e1029579. <https://doi.org/10.1080/02724634.2015.1029579>
- Handa, N., Watabe, M., & Tsogtbaatar, K. (2012). New specimens of *Protoceratops* (Dinosauria: Neoceratopsia) from the Upper Cretaceous in Udyn Sayr, southern Gobi area, Mongolia. *Paleontological Research*, 16(3), 179–198. <https://doi.org/10.2517/1342-8144-16.3.179>
- Hieronymus, T. L., Witmer, L. M., Tanke, D. H., & Currie, P. J. (2009). The facial integument of centrosaurine ceratopsids: morphological and histological correlates of novel skin structures. *The Anatomical Record*, 292(9), 1370–1396. <https://doi.org/10.1002/ar.20985>
- Holmes, R. B., Persons, W. S., Rupal, B. S., Qureshi, A. J., & Currie, P. J. (2019). Morphological variation and asymmetrical development in the skull of *Styracosaurus albertensis*. *Cretaceous Research*, 104308. <https://doi.org/10.1016/j.cretres.2019.104308>
- Hone, D. W. E., Farke, A. A., Watabe, M., Shigeru, S., & Tsogtbaatar, K. (2014). A new mass mortality of juvenile *Protoceratops* and size-segregated aggregation behaviour in juvenile non-avian dinosaurs. *PLOS ONE*, 9(11), e113306. <https://doi.org/10.1371/journal.pone.0113306>
- Hone, D. W. E., Wood, D., & Knell, R. J. (2016). Positive allometry for exaggerated structures in the ceratopsian dinosaur *Protoceratops andrewsi* supports socio-sexual signaling. *Palaeontologia Electronica*, 19(1), 1–13. <http://palaeo-electronica.org/content/2016/1369-sexual-selection-in-ceratopsia>
- Ishigaki, S., Tsogtbaatar, K., Toyoda, S., Mainbayar, B., Noumi, Y., Takahashi, A., Buyantegsh, B., Byambaa, P., Zorig, E., Bayardorj, C., Ochirjantsan, E., Saneyoshi, M., Hayashi, S., & Chiba, K. (2018). Report of the Okayama University of Science – Mongolian Institute of Paleontology and Geology Joint Expedition in 2018. *Bulletin of Research Institute of Natural Sciences, Okayama University of Science*, 44, 19–32.
- Kielan-Jaworowska, Z. & Barsbold, R. (1972). Narrative of the Polish-Mongolian Palaeontological Expeditions 1967–1971. *Palaeontologia Polonica*, 27, 5–13.
- Kirkland, J. I. & Bader, K. (2010). Insect trace fossils associated with *Protoceratops* carcasses in the Djadokhta Formation (Upper Cretaceous), Mongolia. In M. J. Ryan, B. J. Chinnery-Allgeier, & D. A. Eberth (Eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium* (pp. 509–519). Indiana University Press.
- Knapp, A., Knell, R. J., & Hone, D. W. E. (2021). Three-dimensional geometric morphometric analysis of the skull of *Protoceratops andrewsi* supports a socio-sexual signalling role for the ceratopsian frill. *Proceedings of the Royal Society B: Biological Sciences*, 288(1944), 20202938. <https://doi.org/10.1098/rspb.2020.2938>
- Kurzanov, S. M. (1972). Sexual dimorphism in protoceratopsians. *Palaeontological Journal*, 1, 91–97.
- Lambert, O., Godefroit, P., Li, H., Shang, C.-Y., & Dong, Z.-M. (2001). A new species of *Protoceratops* (Dinosauria, Neoceratopsia) from the Late Cretaceous of Inner Mongolia (P. R. China). *Bulletin de l'Institut royal des Sciences naturelles de Belgique. Sciences de la Terre, Supplement* 71, 5–28.
- Maiorino, L., Farke, A. A., Kotsakis, T., & Piras, P. (2015). Males

- resemble females: re-evaluating sexual dimorphism in *Protoceratops andrewsi* (Neoceratopsia, Protoceratopsidae). *PLOS ONE*, 10(5), e0126464-22. <https://doi.org/10.1371/journal.pone.0126464>
- Makovicky, P. (2002). *Taxonomic revision and phylogenetic relationships of basal Neoceratopsia (Dinosauria: Ornithischia)*. Columbia University.
- Makovicky, P. J. & Norell, M. A. (2006). *Yamaceratops dorn gobiensis*, a new primitive ceratopsian (Dinosauria: Ornithischia) from the Cretaceous of Mongolia. *American Museum Novitates*, 3530, 1–42. [https://doi.org/10.1206/0003-0082\(2006\)3530\[1:ydanpc\]2.0.co;2](https://doi.org/10.1206/0003-0082(2006)3530[1:ydanpc]2.0.co;2)
- Mallon, J. C., Holmes, R. B., & Ruffolo, S. J. (2023). Development and homology of the medial parietal ornamentation in centrosaurine ceratopsids (Dinosauria, Ornithischia). *Journal of Vertebrate Paleontology*, 42(5), e2211637. <https://doi.org/10.1080/02724634.2023.2211637>
- Matsumoto, Y. & Saneyoshi, M. (2010). Bored dinosaur skeletons. *The Journal of the Geological Society of Japan*, 116(1), I–II. https://doi.org/10.5575/geosoc.116.1.i_ii
- Morschhauser, E. M., Li, D., You, H., & Dodson, P. (2019). Cranial anatomy of the basal neoceratopsian *Auroraceratops rugosus* (Ornithischia: Ceratopsia) from the Yujingzi Basin, Gansu Province, China. *Journal of Vertebrate Paleontology*, 38(sup1), 36–68. <https://doi.org/10.1080/02724634.2017.1399136>
- Nessov, L. A. (1995). *Dinozavry Severnoy Yevrazii: novyye dannyye o sostave kompleksov, ekologii i paleobiogeografii* [Dinosaurs of Northern Eurasia: New data on the composition of assemblages, ecology, and paleobiogeography]. Izdatelstvo Sankt-Peterburgskogo universiteta, St.-Petersburg.
- Ryan, M. J., Evans, D. C., & Shepherd, K. M. (2012). A new ceratopsid from the Foremost Formation (middle Campanian) of Alberta. *Canadian Journal of Earth Sciences*, 49(10), 1251–1262. <https://doi.org/10.1139/e2012-056>
- Ryan, M. J., Russell, A. P., Eberth, D. A., & Currie, P. J. (2001). The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. *PALAIOS*, 16, 482–506. <https://doi.org/10.2307/3515564>
- Sampson, S. D., Ryan, M. J., & Tanke, D. H. (1997). Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. *Zoological Journal of the Linnean Society*, 121(3), 293–337. <https://doi.org/10.1111/j.1096-3642.1997.tb00340.x>
- Saneyoshi, M., Watabe, M., Suzuki, S., & Tsogtbaatar, K. (2011). Trace fossils on dinosaur bones from Upper Cretaceous eolian deposits in Mongolia: Taphonomic interpretation of paleoecosystems in ancient desert environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 311(1–2), 38–47. <https://doi.org/10.1016/j.palaeo.2011.07.024>
- Saneyoshi, M., Watabe, M., Tsubamoto, T., Tsogtbaatar, K., Chinzorig, T., & Suzuki, S. (2010). Report of the HMNS-MPC Joint Paleontological Expedition in 2007. In T. Tsubamoto (Ed.), *Hayashibara Museum of Natural Sciences Research Bulletin Vol. 3* (pp. 19–28). Hayashibara Museum of Natural Sciences.
- Sereno, P. C. (2000). The fossil record, systematics and evolution of pachycephalosaurs and ceratopsians from Asia. In M. J. Benton, M. A. Shishkin, D. M. Unwin, & E. N. Kurochkin (Eds.), *The age of dinosaurs in Russia and Mongolia* (pp. 480–516). Cambridge University Press.
- Sues, H.-D. & Averianov, A. (2009). *Turanoceratops tardabilis*—the first ceratopsid dinosaur from Asia. *Naturwissenschaften*, 96(5), 645–652. <https://doi.org/10.1007/s00114-009-0518-9>
- Tsogtbaatar, K. & Chinzorig, T. (2010). Fossil specimens prepared in Mongolian Paleontological Center: 2002–2008. In T. Tsubamoto (Ed.), *Hayashibara Museum of Natural Sciences Research Bulletin Vol. 3* (pp. 155–166). Hayashibara Museum of Natural Sciences.
- VanBuren, C. S., Campione, N. E., & Evans, D. C. (2015). Head size, weaponry, and cervical adaptation: Testing craniocervical evolutionary hypotheses in Ceratopsia. *Evolution*, 69(7), 1728–1744. <https://doi.org/10.1111/evo.12693>
- Watabe, M., Tsogtbaatar, K., Suzuki, S., & Saneyoshi, M. (2010). Geology of dinosaur-fossil-bearing localities (Jurassic and Cretaceous: Mesozoic) in the Gobi Desert: Results of the HMNS-MPC Joint Paleontological Expedition. In T. Tsubamoto (Ed.), *Hayashibara Museum of Natural Sciences Research Bulletin Vol. 3* (pp. 41–118). Hayashibara Museum of Natural Sciences.
- Wolfe, D. G., Kirkland, J. I., Smith, D., Poole, K., Chinnery-Allgeier, B., & McDonald, A. (2010). *Zuniceratops christopherei*: the North American ceratopsid sister taxon reconstructed on the basis of new data. In M. J. Ryan, B. J. Chinnery-Allgeier, & D. A. Eberth (Eds.), *New perspectives on horned dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium* (pp. 91–98). Indiana University Press.
- Xu, X., Forster, C. A., Clark, J. M., & Mo, J. (2006). A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. *Proceedings of the Royal Society B: Biological Sciences*, 273(1598), 2135–2140. <https://doi.org/10.1098/rspb.2006.3566>
- You, H. L. & Dodson, P. (2003). Redescription of neoceratopsian dinosaur *Archaeoceratops* and early evolution of Neoceratopsia. *Acta Palaeontologica Polonica*, 48(2), 261–272.