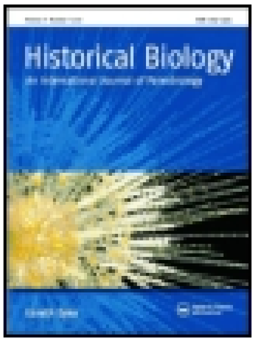

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Ontogeny and variation of a protoceratopsid dinosaur *Bagaceratops rozhdestvenskyi* from the Late Cretaceous of the Gobi Desert

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ABSTRACT
Bagaceratops rozhdestvenskyi is a ceratopsian dinosaur from the Late Cretaceous Baruungoyot Formation of the Gobi Desert, closely related to *Protoceratops* spp. Several *Bag. rozhdestvenskyi* skulls demonstrate a wide range of variation in their morphology and size. Here I argue that the observed variability is most likely of intraspecific nature. Specimens classified in a few allegedly distinct species from the same or near-contemporary sediments, namely *Gobiceratops minutus*, *Lamaceratops tereschenkoi* and *Platyceratops tatarinovi* from Baruungoyot Formation, and *Magnirostris dodsoni* from Bayan Mandahu, are younger subjective synonyms of *Bag. rozhdestvenskyi*. They plausibly represent an ontogenetic series within the latter. *Breviceratops kozlowskii* is a distinct taxon. The evolutionary relationships within Protoceratopsidae are complicated by the mosaic distribution of plesiomorphic and derived features in distinct species. I suggest that taxa distribution and observed changes in morphology are an evidence for the ancestral position of *Protoceratops andrewsi* among protoceratopsids. It implies possible temporary separation between the geological formations of the Gobi Desert yielding distinct protoceratopsid species. The novel evolutionary scenario suggests number of convergences that occurred in Protoceratopsidae and Ceratopsoidea (reduction of the premaxillary dentition, fusion of nasals, development of the accessory antorbital fenestra). Present study reveals the significance of the intraspecific and ontogenetic variation in the study of the neoceratopsian taxonomy.

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Dinosauria; Ceratopsia; Protoceratopsidae; Mongolia; intraspecific variation; ontogeny

Introduction

Ceratopsia is a greatly diversified group of ornithischian dinosaurs, especially abundant in the Upper Cretaceous sediments of the Northern Hemisphere (Makovicky 2012). The taxonomical richness of the derived ceratopsians (Ceratopsidae) from North America is well known, given of dozens of recognised species. However, the early evolution of the non-ceratopsid ceratopsians remains poorly understood. Recent discoveries from Asia and North America are filling the gap in the ceratopsian fossil record, making clear that diversity of that group was significantly greater than thought earlier (Kurzanov 1992; Lambert et al. 2001; Makovicky and Norell 2006; Xu et al. 2006; Sereno 2010; Morschhauser 2012; Farke et al. 2014; Zheng et al. 2015)

Protoceratopsidae is a group of non-ceratopsid ceratopsian dinosaurs that significantly contributed to the Late Cretaceous vertebrate fossil assemblages of the Gobi Desert (Figure 1). *Protoceratops andrewsi* Granger and Gregory 1923 was the first protoceratopsid dinosaur to be described, coming from the rocks of the Djadokhta Formation. It is known from number of specimens coming from several localities (Brown and Schlaikjer 1940; Dodson 1976) that enabled research on the para-populational level. Many studies were performed regarding ontogeny (Brown and Schlaikjer 1940; Handa et al. 2012; Hone et al. 2016; Saneyoshi et al. 2017), sexual dimorphism (Kurzanov 1972; Dodson 1976; Maiorino et al. 2015), and social behaviour (Fastovsky et al. 2011; Hone et al. 2014) of this species. However, other protoceratopsids attracted less attention.

Bagaceratops rozhdestvenskyi Maryańska and Osmólska 1975 was described from the Baruungoyot Formation, based on the material collected by the Polish-Mongolian Paleontological Expeditions in the 1970s, along with *Breviceratops kozlowskii* (Maryańska and Osmólska 1975) Kurzanov 1990. The Sino-Canadian Expeditions to Bayan Mandahu in Inner Mongolia provided material of other taxa, *Protoceratops hellenikorhinus* Lambert et al. 2001 and *Magnirostris dodsoni* You and Dong 2003. Material collected from the Baruungoyot and Djadokhta Formations by the Russian Expeditions led to the erection of four other species, *Lamaceratops tereschenkoi* Alifanov 2003, *Platyceratops tatarinovi* Alifanov 2003, *Bainoceratops efremovi* Tereschenko and Alifanov 2003 and *Gobiceratops minutus* Alifanov 2008. Description of these taxa suggested a high diversity of the protoceratopsid dinosaurs from the Gobi Desert, but the validity of some of them seemed to be questionable (Makovicky 2002; Makovicky and Norell 2006; Morschhauser 2012).

Here I re-examine both the published and yet undescribed material of the protoceratopsid dinosaurs from the Baruungoyot Formation. The main purpose of this study is to recognise the ontogenetic and intraspecific variation in the sample and to determine the real taxonomical diversity within the Protoceratopsidae.

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Supplemental data for this article can be accessed here.

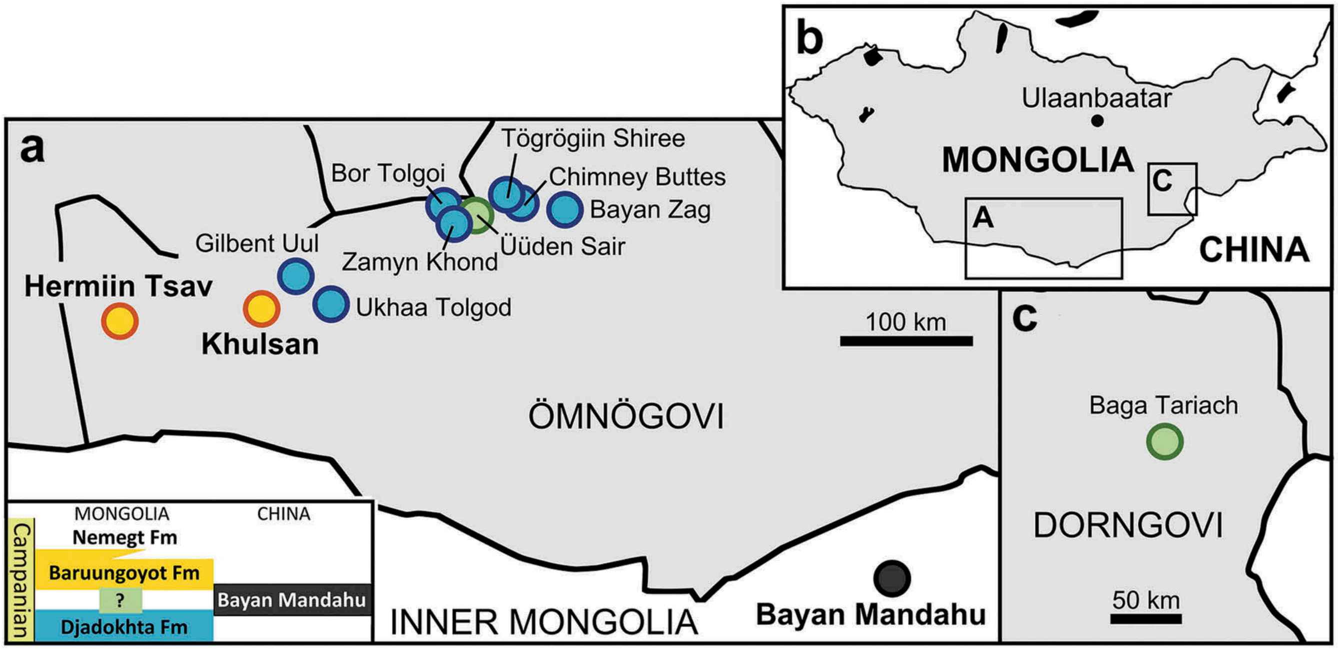

Figure 1. Late Cretaceous localities with protoceratopsid remains of the Baruungoyot (orange), Djadokhta (blue) and Bayan Mandahu (black) Formations and localities of ambiguous age (green) in the Ömnögovi Province and Inner Mongolia Region (a), and the Dorngovi Province (c), and their position within the Gobi Desert (b). Names of localities with confirmed *Bagaceratops rozhdestvenskyi* remains are in bold. At the lower left stratigraphic coordinates of the formations are presented. Geographic and stratigraphic data from Jerzykiewicz and Russell (1991); Norell and Makovicky 1999; Saneyoshi et al. 2010; Dingus et al. 2008.

Material and methods

I examined 59 protoceratopsid specimens from the Baruungoyot Formation (Table 1; Supplementary Information), including the holotype of *Bagaceratops rozhdestvenskyi* (ZPAL MgD-I/126) and 31 specimens referred to this taxon by Maryańska and Osmólska (1975); the holotypes of *Platyceratops tatarinovi* (PIN 3142/4), *Gobiceratops minutus* (PIN 3142/299) and *Lamaceratops tereschenkoi* (PIN 4487/26); the holotype of *Breviceratops kozlowskii* (ZPAL MgD-I/117) and 7 specimens referred by Maryańska and Osmólska (1975) and Kurzanov (1990); and 15 specimens of protoceratopsids from the Baruungoyot Formation, previously not mentioned in the literature.

Eight protoceratopsid specimens from the Baruungoyot Formation have not been examined personally. MPC-D 100/535, a nearly complete, articulated skeleton from Hermiin Tsav assigned to *Bagaceratops rozhdestvenskyi* (Matsumoto and Saneyoshi 2010) and four not-described in the literature, fragmentary specimens collected at Hermiin Tsav in 1973

Table 1. Material of the protoceratopsid dinosaurs from the Baruungoyot Formation examined during this study.

Specimens	Locality	Previous identification	References	This study
ZPAL MgD-I/126	Hermiin Tsav	*Bagaceratops rozhdestvenskyi* (holotype)	Maryańska and Osmólska 1975	*Bagaceratops rozhdestvenskyi*
ZPAL MgD-I/123–125, 127–133a, 134, 135, 137, 138, 140, 144, 145, 148, 149, 150, 152, 153	Hermiin Tsav	*Bagaceratops rozhdestvenskyi*	Maryańska and Osmólska 1975	*Bagaceratops rozhdestvenskyi*
PIN 3142/3	Hermiin Tsav	*Breviceratops kozlowskii*	Kurzanov 1990	*Bagaceratops rozhdestvenskyi*
PIN 3142/4	Hermiin Tsav	*Platyceratops tatarinovi* (holotype)	Alifanov 2003	*Bagaceratops rozhdestvenskyi*
PIN 3142/299	Hermiin Tsav	*Gobiceratops minutus* (holotype)	Alifanov 2008	*Bagaceratops rozhdestvenskyi*
MPC-D 100/506; IGM 100/1817; ZPAL MgD-I/301, 302, 306, 307, 310	Hermiin Tsav			*Bagaceratops rozhdestvenskyi*
ZPAL MgD-I/133b, 136, 139a, 139b, 141, 142, 143, 146, 147, 151, 154	Hermiin Tsav	*Bagaceratops rozhdestvenskyi*	Maryańska and Osmólska 1975	Protoceratopsidae indet.
ZPAL MgD-I/155, 303, 305, 308, 309, 312, 316	Hermiin Tsav			Protoceratopsidae indet.
PIN 4487/26	Khulsan	*Lamaceratops tereschenkoi* (holotype)	Alifanov 2003	*Bagaceratops rozhdestvenskyi*
IGM 100/3653	?Khulsan			*Bagaceratops rozhdestvenskyi*
ZPAL MgD-I/118, 120	Khulsan	*Breviceratops kozlowskii*	Maryańska and Osmólska 1975	*Bagaceratops rozhdestvenskyi*
ZPAL MgD-I/117	Khulsan	*Breviceratops kozlowskii* (holotype)	Maryańska and Osmólska 1975	*Breviceratops kozlowskii*
ZPAL MgD-I/116	Khulsan	*Breviceratops kozlowskii*	Maryańska and Osmólska 1975	*Breviceratops kozlowskii*
ZPAL MgD-I/119, 121, 122	Khulsan	*Breviceratops kozlowskii*	Maryańska and Osmólska 1975	Protoceratopsidae indet.
ZPAL MgD-I/304	Khulsan			Protoceratopsidae indet.

(MPC-D 100/507, 508, 509, 510) were not available for study during my visit to MPC (Mongolian Paleontological Center of the Mongolian Academy of Sciences) in October 2016. Photographs of some of these specimens were kindly provided by A. Knapp, M. Saneyoshi and D. Hone. Specimens PIN 3142/1 and PIN 3142/2 from Hermiin Tsav, referred to *Breviceratops kozlowskii* by Kurzanov (1990) are lost from PIN (Paleontological Institute of the Russian Academy of Sciences) since the 1990s (Abbott 1996; V. Alifanov pers. comm. 2015). PIN 3142/5, a nearly complete skull lacking the tip of the snout from Hermiin Tsav was not available to study during my visits to PIN in November 2015 and November 2016. This specimen was described by Kurzanov (1990) as a very large *Br. kozlowskii* with the catalogue number PIN 3142/4, that is actually the holotype number of *Platyceratops tatarinovi*. My observations of PIN 3142/1 and PIN 3142/5 are based on the drawings provided by Kurzanov (1990). The braincase of the specimen ZPAL MgD-I-133 was unavailable to study, being on loan to the Institute of Geology and Palaeontology, Charles University in Prague since 2001. During my visit to MPC in October 2016, only a cast of MPC-D 100/506 was available for study.

I examined also the material of protoceratopsid dinosaurs from Bayan Mandahu including the holotype of *Magnirostris dodsoni* (IVPP V12513) housed in IVPP (Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences), and the material of *Protoceratops hellenikorhinus* (three specimens and two casts) housed in RBINS (Royal Belgian Institute of Natural Sciences). For comparison, I examined a total of 149 specimens referred to *Protoceratops andrewsi* from the Djadokhta Formation, housed in the collections of ZPAL (Institute of Paleobiology of the Polish Academy of Sciences), MPC, PIN, AMNH (American Museum of Natural History) and IGM (Institute of Geology, Ulaanbaatar, Mongolia).

Measurements taken from most of the studied specimens follow Dodson (1976), however a few measurements, describing details of the nasal horncore, rostral and maxilla were added (Figure 2). Measurements data for unavailable specimens were taken from the literature (Dodson 1976; Lambert et al. 2001; Handa et al. 2012; Hone et al. 2014; Maiorino et al. 2015) and unpublished photographs provided by the authors. Measurements from the pictures were taken using the Fiji software (Schindelin et al. 2012).

Due to the fragmentary preservation of numerous specimens, the partial basal length (measured from the rostral margin of the maxilla to the caudal margin of the quadrate; measurement 3 at Figure 2) was used as the main skull size discriminant, instead of the basal length (measured from the rostral margin of the rostral to the caudal margin of the quadrate). There is a strict correlation between the partial basal length and the basal length (R^2 = 0.9606–0.9994 for different species; Supplementary Information). For even more fragmentary specimens, the length of the maxilla was used, which is well correlated with the partial basal length (R^2 = 0.8919–0.9611). For isolated mandibles, the dentary length (measured from the rostral margin of the dentary to the rostral margin of the coronoid process; measurement 10 at Figure 2) was used to estimate the complete size of the individual skull. The dentary length is well correlated with the overall length of the mandible (R^2 = 0.7856–0.9698). The total length of the mandible correlates well with the partial basal length (R^2 = 0.9245–0.9326) and the basal length of the skull (R^2 = 0.7582–0.9855). However, as seen in some specimens of *Protoceratops andrewsi*, the basal length is not always correlated with the total skull length, because of intraspecific variation in the development of the parietosquamosal frill (Maiorino et al. 2015; Hone 2016). For details and plots, see Supplementary Material.

In order to separate the putative ontogenetic changes from the population variability, all of the available cranial material of protoceratopsid dinosaurs from the Baruungoyot Formation (Hermiin Tsav and Khulsan localities; Figure 1) previously referred to as *Bagaceratops rozhdestvenskyi, Breviceratops kozlowskii, Gobiceratops minutus, Lamaceratops tereschenkoi*

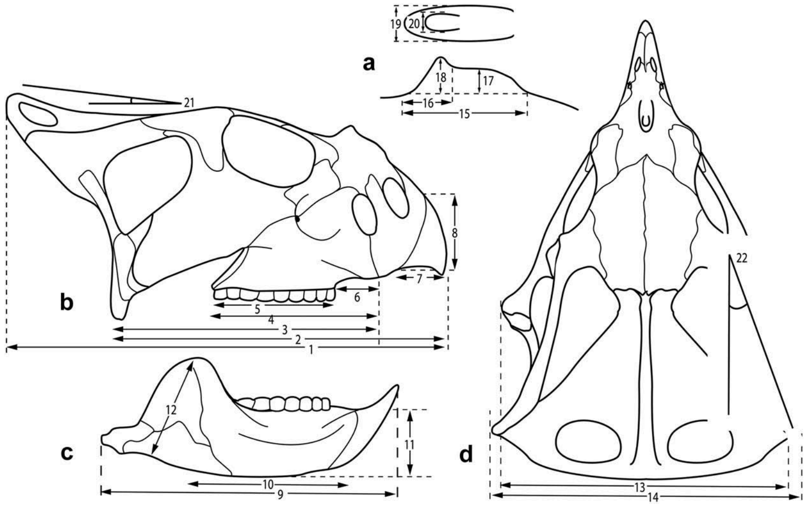

Figure 2. Measurements taken from specimens, including the nasal horncore in dorsal and lateral views (a), skull in lateral (b) and dorsal (d) views and the mandible in lateral view (c). 1) total length of the skull, 2) basal length of the skull, 3) partial basal length of the skull, 4) length of the maxilla, 5) teeth row length, 6) length of the maxillary diastema, 7) rostral length, 8) rostral height, 9) mandible length, 10) dentary length, 11) dentary height, 12) coronoid height, 13) width across the jugals, 14) parietosquamosal width, 15) basal horncore length, 16) spike length, 17) basal horncore height, 18) spike height, 19) basal horncore width, 20) spike width, 21) dorsal and 22) lateral inclination of the parietosquamosal frill.

and *Platyceratops tatarinovi*, was united together and subdivided into four size classes, in relation to the estimated partial basal skull length:

(1) Very small individuals (estimated partial basal skull length up to 4 cm)
(2) Small individuals (estimated partial basal skull length up to 9 cm)
(3) Medium-sized individuals (estimated partial basal skull length up to 15 cm)
(4) Large individuals (estimated partial basal skull length more than 15 cm)

For the detailed description of the examined material, see Supplementary Information. Transcriptions of the Mongolian locality names follow Benton (2000).

Institutional abbreviations: AMNH – American Museum of Natural History, New York, USA; IGM – Institute of Geology, Ulaanbaatar, Mongolia; IMM – Inner Mongolia Museum, Hohhot, China; IVPP – Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China; MPC – Mongolian Paleontological Center (Institute of Paleontology and Geology) of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MSM – Mesa Southwest Museum, Mesa, Arizona, USA; MTM – Hungarian Natural History Museum, Budapest, Hungary; PIN – Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium; UMNH – Natural History Museum of Utah, Salt Lake City, Utah, USA; ZPAL – Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland

Description

Very small individuals

The smallest specimens have a short skull with a tiny parietosquamosal frill (Figures 3 and 4(a–f)). The orbits are relatively large, comprising up to 50% of the partial basal length of the skull. The preorbital portion is short and narrow in dorsal view.

The rostral bone is poorly preserved in the smallest specimens and only in ZPAL MgD-I/123 its fragment is visible (Figure 3(a,c,d,f)). However, the rostral size can be inferred from the morphology of the rostral-most portion of the premaxillae, where the articulation facet for the bone is preserved (as in PIN 3142/299, Figure 3(n); *contra* Alifanov 2008).

The premaxilla is toothless, with a narrow ventral margin in the ventral view in PIN 3142/299 and ZPAL MgD-I/123. In contrast, two alveoli on the premaxilla are seen in *Br. kozlowskii* ZPAL MgD-I/116 (Figure 4(c,f)).

The accessory antorbital fenestra is elongated, similar in shape to the external nares, although slightly larger than the

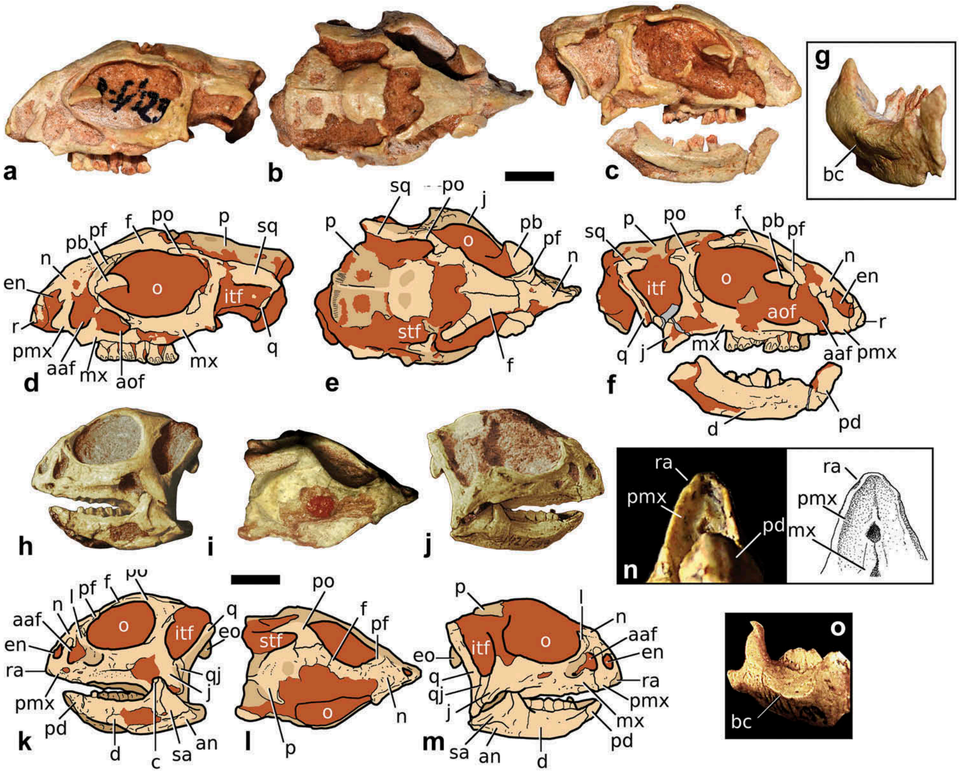

Figure 3. Very small protoceratopsid specimens from the Baruungoyot Formation. A–G, ZPAL MgD-I/123 referred to *Bagaceratops rozhdestvenskyi* Maryańska and Osmólska 1975 from Hermiin Tsav in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. G, right mandible in rostral view. H–O, PIN 3142/299, holotype of '*Gobiceratops minutus*' Alifanov 2003, junior synonym of *Bagaceratops rozhdestvenskyi*, from Hermiin Tsav in left lateral (h, k), dorsal (i, l) and right lateral (j, m) views; N, details of the anterior portion of snout in ventral view; O, right mandible in rostral view. Scale bar for A–F and H–M: 1 cm. Figure abbreviations: aaf – accessory antorbital fenestra, af – antorbital fossa, al – alveoli, an – angular, bc – buccal crest of dentary, c – coronoid, cv – cervical vertebrae, d – dentary, ej – epijugal, en – external nares, eo – exoccipital, f – frontal, fd – frontoparietal depression, itf – infratemporal fenestra, l – lacrimal, lb – limb bone, mx – maxilla, mxfo – anterior maxillary fossa, n – nasal, o – orbit. pa – parietal, pb – palpebral, pd – predentary, pf – prefrontal, pfe – parietal fenestration, pmx – premaxilla, pmt – premaxillary teeth, po – postorbital, q – quadrate, qj – quadratojugal, r – rostral, ra – rostral attachment site, sa – surangular, stf – supratemporal fenestra, sq – squamosal.

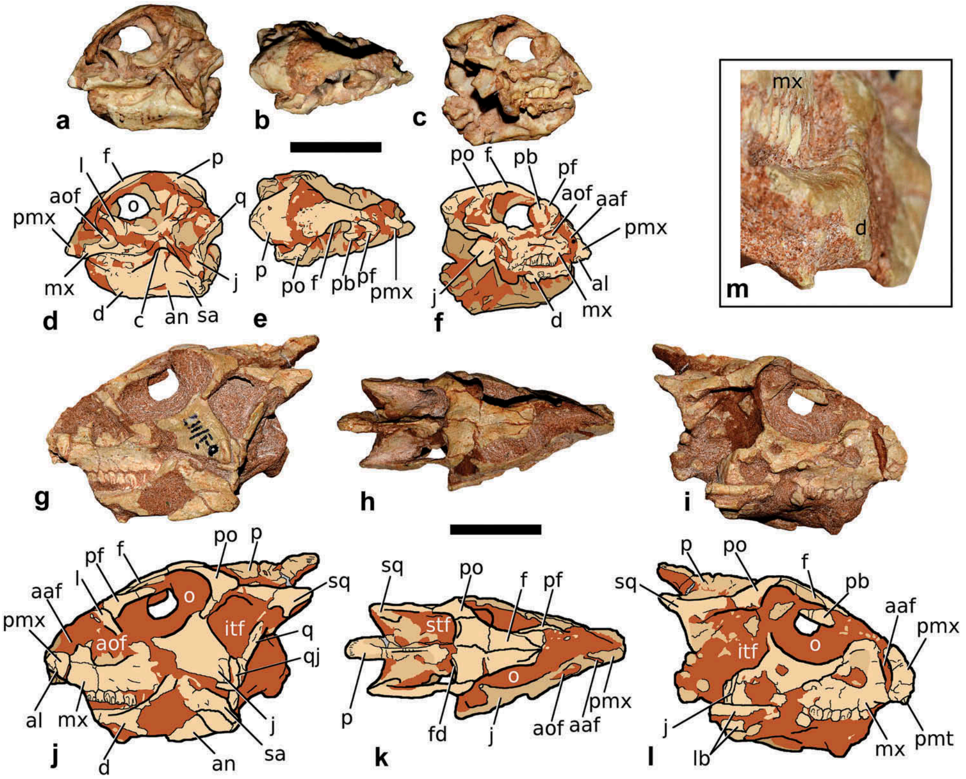

Figure 4. Protoceratopsid specimens from the Baruungoyot Formation with premaxillary dentition. A–F, ZPAL MgD-I/116, very small specimen referred to *Breviceratops kozlowskii* (Maryańska and Osmólska 1975) Kurzanov (1990) from Khulsan in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. G–M, ZPAL MgD-I/117, small specimen, holotype of *Breviceratops kozlowskii* (Maryańska and Osmólska 1975) Kurzanov (1990) from Khulsan in left lateral (g, j), dorsal (h, k) and right lateral (i, l) views. M, left mandible in rostral view showing no distinct buccal crest of the dentary. Scale bar for A–L: 2 cm.

latter in ZPAL MgD-I/123 and PIN 3142/299. The longer axis is parallel to that of the external nares. The antorbital fossa is located below the orbit, near the anteroventral corner. It is elongated, with the longer axis being nearly perpendicular to that of the external nares. The prefrontals are short and lack contact with the frontals in the smallest specimen (PIN 3142/299, ZPAL MgD-I/116), however, they are slightly longer, reaching the frontals in ZPAL MgD-I/123.

The nasals are fused medially, with a slight but distinct bump, approximately 1 mm in height. The morphology of the nasals in ZPAL MgD-I/116 (*Br. kozlowskii*) remains unknown due to the incompleteness of the material. The frontals are slightly arched dorsally in the lateral view, and gently concave ventrally along their interfrontal suture. The frontonasal and frontoparietal sutures are straight. No trace of the frontoparietal depression is observed.

The squamosals are slightly converging caudally in dorsal view (PIN 3142/299) or are nearly parallel to each other (ZPAL MgD-I/123), reaching the level of the caudal margin of the parietal. The parietosquamosal frill is preserved nearly complete only in ZPAL MgD-I/123. It is very thin (0.5 mm, measured at the midpoint of the caudal margin), with the caudal margin nearly straight in dorsal view and covered by longitudinal ripples. The low sagittal crest (1 mm in height) is developed at the level of the braincase, where the parietals are convex. Two gentle depressions are placed symmetrically in the rostral portion of parietals, near the frontoparietal suture. The frill is slightly weathered in ZPAL MgD-I/123 but there is no evidence for the presence of the frill fenestration. The supraoccipital is exposed only in PIN 3142/299. It is relatively large, wide, without the suture at the midline (Alifanov 2008).

All specimens with the lateral surface of the dentary bone preserved (PIN 3142/299, ZPAL MgD-I/123, and 134c) posses a subtle (1.0–1.5 mm in length) but distinct and sharp buccal crest (labial dentary ridge), V-shaped in cross section (Figure 3(g,o)). The only exception is a specimen of *Br. kozlowskii* (ZPAL MgD-I/116), where the surface is smooth (Figure 4(a,d)). In this specimen, also the height of dentary is relatively greater than in PIN 3142/299 and ZPAL MgD-I/123. There is no caudoventral (angular) process of the dentary bone in PIN 3142/299 and the rostral tip of the angular bone is not restricted from the contact with the ventral margin of the mandible, in contrast to ZPAL MgD-I/116.

There are six (ZPAL MgD-I/123, 116, PIN 3142/299) alveoli in the maxilla and six (PIN 3142/299, ZPAL MgD-I/120) or seven (ZPAL MgD-I/123) in the dentary.

Small individuals

All the small-sized specimens have an elongate skull, relatively narrow in dorsal view, with a short parietosquamosal frill (Figures 4(g–m); and 5). The lateral projection of the jugals in dorsal view is only slightly pronounced. The rostral bone is nearly complete only in one specimen (PIN 4487/26; Figure 5 (g–l)), being apparently higher than longer.

Although the ventral-most portion of premaxilla is not preserved in ZPAL MgD-I/124 and PIN 4487/26, the bone is extremely thin in this region, suggesting lack of the premaxillary dentition. In contrast, two premaxillary teeth are seen in the holotype of *Br. kozlowskii* (ZPAL MgD-I/117; Figure 4(g,j,i,l)).

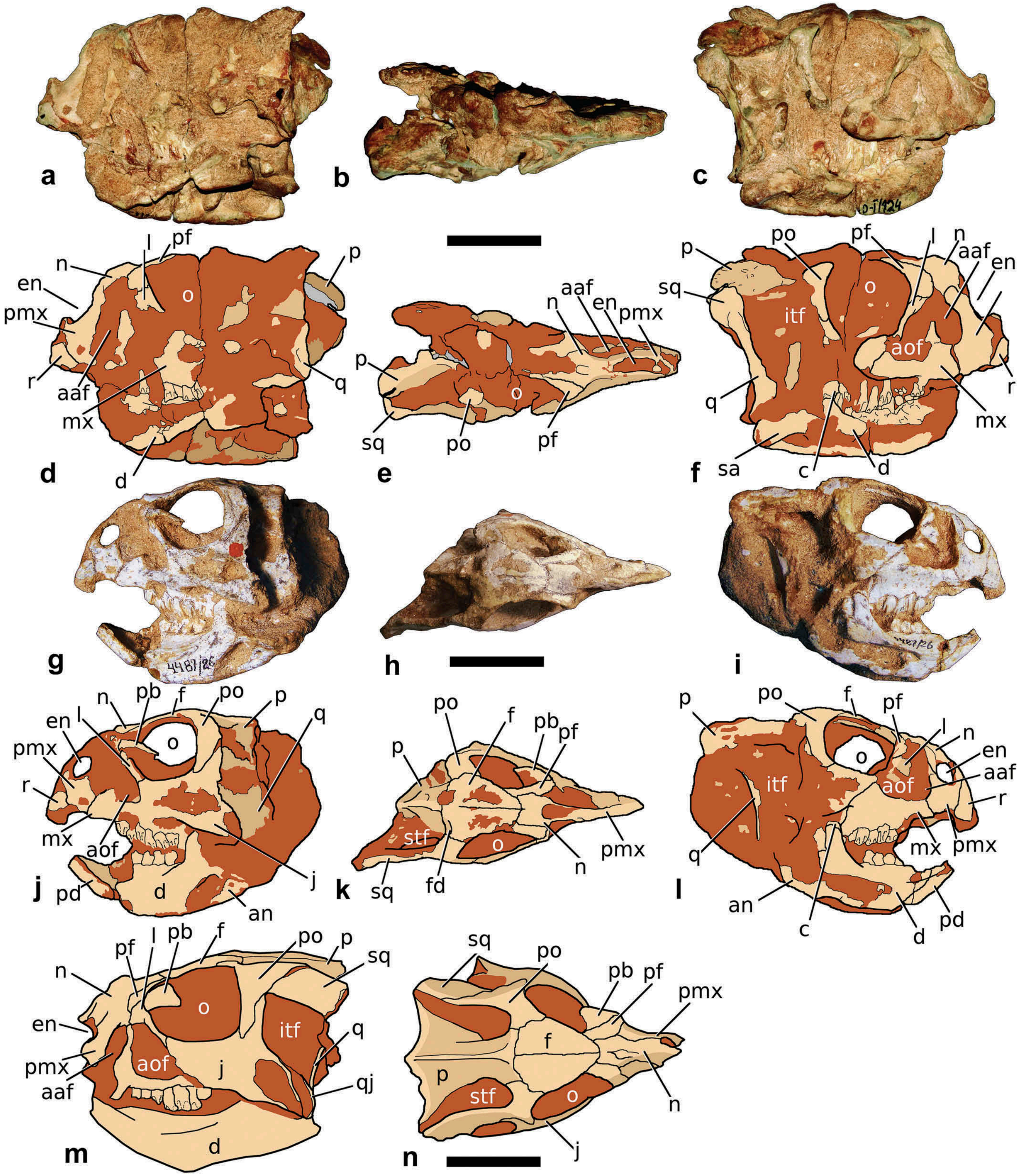

Figure 5. Small protoceratopsid specimens from the Baruungoyot Formation. A–F, ZPAL MgD-I/124 referred to *Bagaceratops rozhdestvenskyi* by Maryańska and Osmólska 1975 from Hermiin Tsav in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. G–L, PIN 4487/26, holotype of '*Lamaceratops tereschenkoi*' Alifanov 2003, junior synonym of *Bagaceratops rozhdestvenskyi*, from Khulsan in left lateral (g, j), dorsal (h, k) and right lateral (i, l) views; M–N, drawing of PIN 3142/1 from Hermiin Tsav (referred to *Breviceratops kozlowskii* by Kurzanov 1990, here referred to *Bag. rozhdestvenskyi*; after Kurzanov 1990) in left lateral (m) and dorsal (n) views. Scale bar 3 cm.

Margins of the accessory antorbital fenestra can be seen at the right side of ZPAL MgD-I/124 (Figure 5(c,f)), revealing that its size is slightly greater than that estimated for the external nares. Only the rostroventral margin of the fenestra is seen at the right side of PIN 4487/26 (Figure 5(i,l)). A wide separation of the premaxilla from the maxilla at the suture, reaching the ventral end, is seen in ZPAL MgD-I/117 (Figure 4(i,l)), suggesting the presence of a split-like fenestration.

The nasals are fused, with a small trapezoidal nasal horncore (ZPAL MgD-I/124, PIN 4487/26, PIN 3142/1). Morphology of the nasals in ZPAL MgD-I/117 (*Br. kozlowskii*) cannot be determined as this region of the skull is not preserved. The nasofrontal suture is U-shaped (PIN 4487/26, PIN 3142/1) or V-shaped (ZPAL MgD-I/117).

The prefrontals are relatively long, and the frontal depression is present in PIN 4487/26 and ZPAL MgD-I/117. The frontals are straight in the lateral view. The frill is very narrow in ZPAL MgD-I/117, with the sagittal crest extending far behind the caudal portion of the squamosals. The caudal margin is preserved only in the medial portion of the frill and there is no evidence for the fenestration. In ZPAL MgD-I/124, only the caudal portion of the right parietal is preserved, with the margin suggesting to represent the actual limit of the bone, that does not extend behind the caudal portion of the squamosal and does approach medially in the rostral direction. No sagittal crest is preserved. Only the right side of the frill is preserved in PIN 4487/26. The supraoccipital, as seen in ZPAL MgD-I/124, is fused and triangular in shape.

The buccal crest of the dentary is V-shaped in cross section in all specimens (ZPAL MgD-I/124, 134a, 134b, 140, PIN 4487/26) with the exception for the U-shaped crest in ZPAL MgD-I/117 (*Br. kozlowskii*; Figure 4(m)).

There are seven teeth in the maxilla (ZPAL MgD-I/117, 124, 134b, PIN 3142/1, 4487/26) and at least five in the dentary (five or more in PIN 4487/26 and seven in ZPAL MgD-I/134b).

Medium-sized individuals

All the medium-sized specimens have the lateral projections of the jugal bones, resulting in a triangular shape of the skull in dorsal view (Figures 6 and 7). The rostral bone is present completely only in MPC-D 100/535 and is triangular in the lateral view, with most of the ventral margin nearly straight and the tip curved anteroventrally (Figure 7(n)). The premaxilla is toothless, with no trace of the premaxillary alveoli.

The accessory antorbital fenestra has similar size and shape to the elongated external nares. The anteroventral process of the nasal is bifurcated and forms the dorsal margin of the external nares. The ventral process of the nasal is covered by the dorsocaudal projection of the premaxilla, resulting in the restricted, but present contact with the dorsal margin of the accessory antorbital fenestra (Figure 20(a)), contrary to the previous statements (Maryańska and Osmólska 1975; You and Dong 2003; Kirkland and DeBlieux 2010).

The nasals do not participate in the formation of the antorbital fossa (*contra* Maryańska and Osmólska 1975). The nasal boss is well developed into a trapezoidal horncore with the prominent caudal portion forming a spike of different size. In some specimens the spike contributes to the more than a half of the basal horncore length (ZPAL MgD-I/125, MPC-D 100/535; Figure 6(a–f); Figure 7(n); Figure 9(a); Figure 17(a,b)), while in others it is restricted to the caudalmost portion of the basal boss (ZPAL MgD-126, PIN 3142/3; Figure 6(m–r), Figure 7(a–f); Figure 17(c,d)). In some specimens, there are two symmetric rows of the tubercles present on both sides of the nasal horncore (ZPAL MgD-I/135, 301, IGM 100/1817; Figure 6(g–j); Figure 7(g–l); Figure 17(i,j)). The residual internasal suture is present in a few specimens (e.g., ZPAL MgD-I/125).

Maryańska and Osmólska (1975) claimed that the frontal bones are fused in the holotype specimen (ZPAL MgD-I/126), but the interfrontal suture can be traced at the mostly weathered dorsal surface of the bones (Figure 7(b,e)). The frontoparietal depression is rarely developed.

The postorbital process of the jugal extends dorsocaudally and contacts the squamosal. In contrast to the earlier statements (Maryańska and Osmólska 1975), the contact of the jugal and the squamosal is seen in the lateral view in some specimens (e.g., ZPAL MgD-I/126, 127; Figure 7(f)).

The parietosquamosal frill expands caudally and laterally. Frill fenestration can be observed in specimens with the preserved caudal-most portion of the parietal (MPC-D 100/506, 535, ZPAL MgD-I/310).

In all specimens with the preserved buccal crest of the dentary bone, it has a V-shaped cross section, with an exception for ZPAL MgD-I/139a – the incomplete left dentary with eight teeth and weakly developed and smooth (U-shaped) buccal crest.

There are eight (ZPAL MgD-I/125, 144) to ten (ZPAL MgD-I/126) maxillary teeth and more than seven (ZPAL MgD-I/126) to ten (ZPAL MgD-I/118) dentary teeth in the medium-sized skulls.

Large individuals

Large individuals have the jugals projecting laterally, a high snout and a long parietosquamosal frill (Figure 8).

Although the rostral bone is partially preserved only in one specimen (PIN 3142/4, Figure 8(g–l)), it can be inferred from the morphology of the premaxilla that the caudoventral projection of the rostral bone was well developed, covering most of the anteroventral margin of the premaxilla.

The accessory antorbital fenestrae have similar size and shape as the external nares. The maxilla forms a huge portion of the antorbital fossa. The maxillary diastema is relatively extended, in the largest specimen (ZPAL MgD-I/129) it is longer than 50% of the tooth row length (Figure 14). The teeth-bearing portion of the maxilla is deep and medially inclined in relation to the long axis of the skull.

The postorbital bears rugosities suggesting contact with the palpebral via connective tissue (Maidment and Porro 2010). The development of the frontoparietal depression varies among specimens, from the fossa being restricted to the caudal portion of the frontals (ZPAL MgD-I/129, Figure 8(b, e)) to the huge, shallow depression covering most of the caudal portion of the frontals (PIN 3142/4, Figure 8(h,k)). The parietosquamosal frill is long and wide, with the well-developed fenestration, and with a relatively strong dorsal inclination.

The dentary of PIN 3142/4 bears a sharp, pronounced buccal crest, V-shaped in the cross section. The angular bone seems to be not restricted by the caudal projection of the dentary.

At least nine maxillary teeth are present in ZPAL MgD-I/129. This condition in PIN 3142/4 cannot be determined because much of the jaw region is highly weathered.

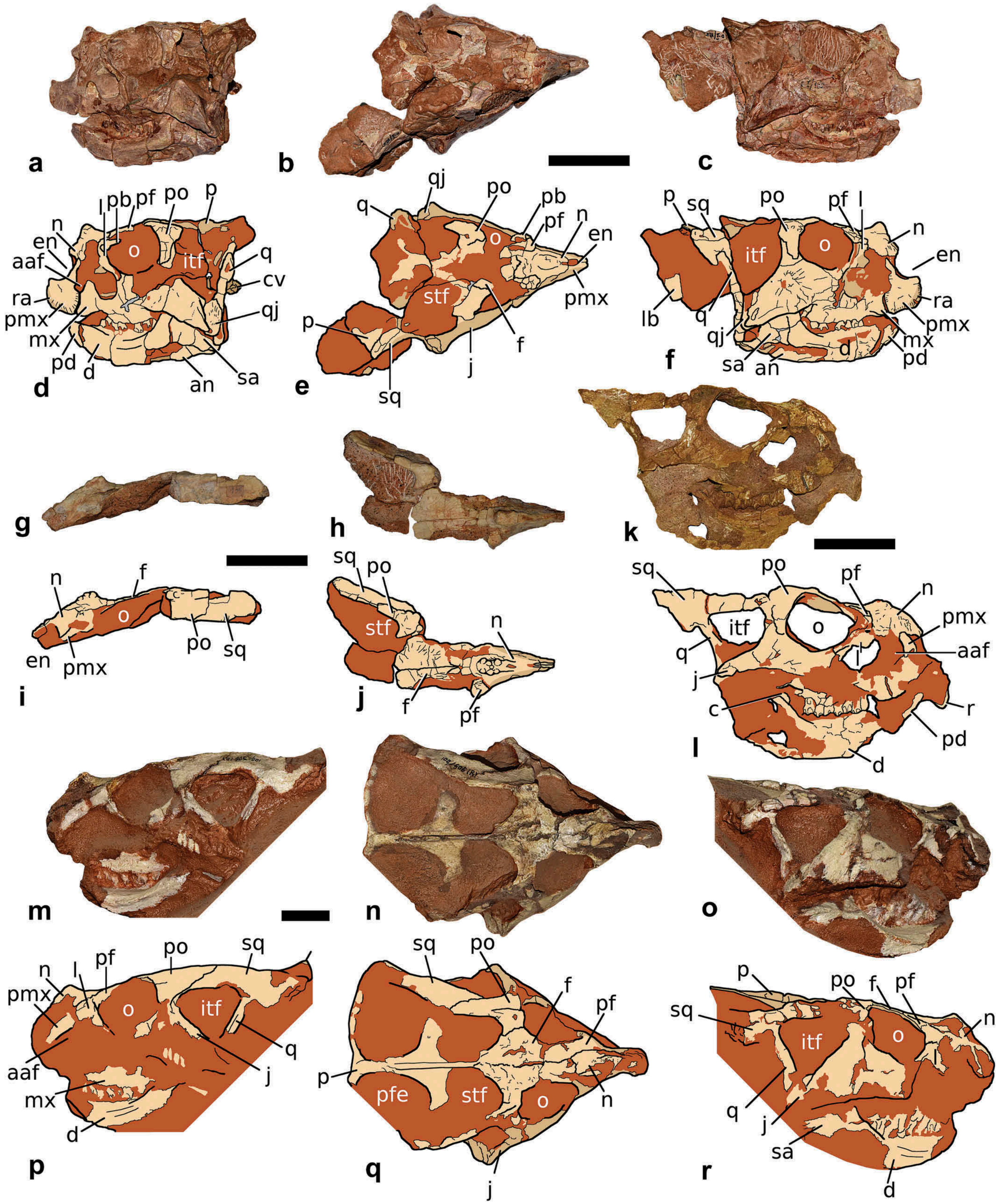

Figure 6. Medium-sized protoceratopsid specimens from the Baruungoyot Formation at Hermiin Tsav. A–F, ZPAL MgD-I/125 in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. G-J, ZPAL MgD-I/135 in left lateral (g, i) and dorsal (h, j) views. Both specimens were referred to *Bagaceratops rozhdestvenskyi* by Maryańska and Osmólska 1975. K–L, PIN 3142/3 (referred to *Breviceratops kozlowskii* by Kurzanov (1990)) in right lateral view. M–R, MPC-D 100/506 in left lateral (m, p), dorsal (n, q) and right lateral (o, r) views. Scale bar 5 cm.

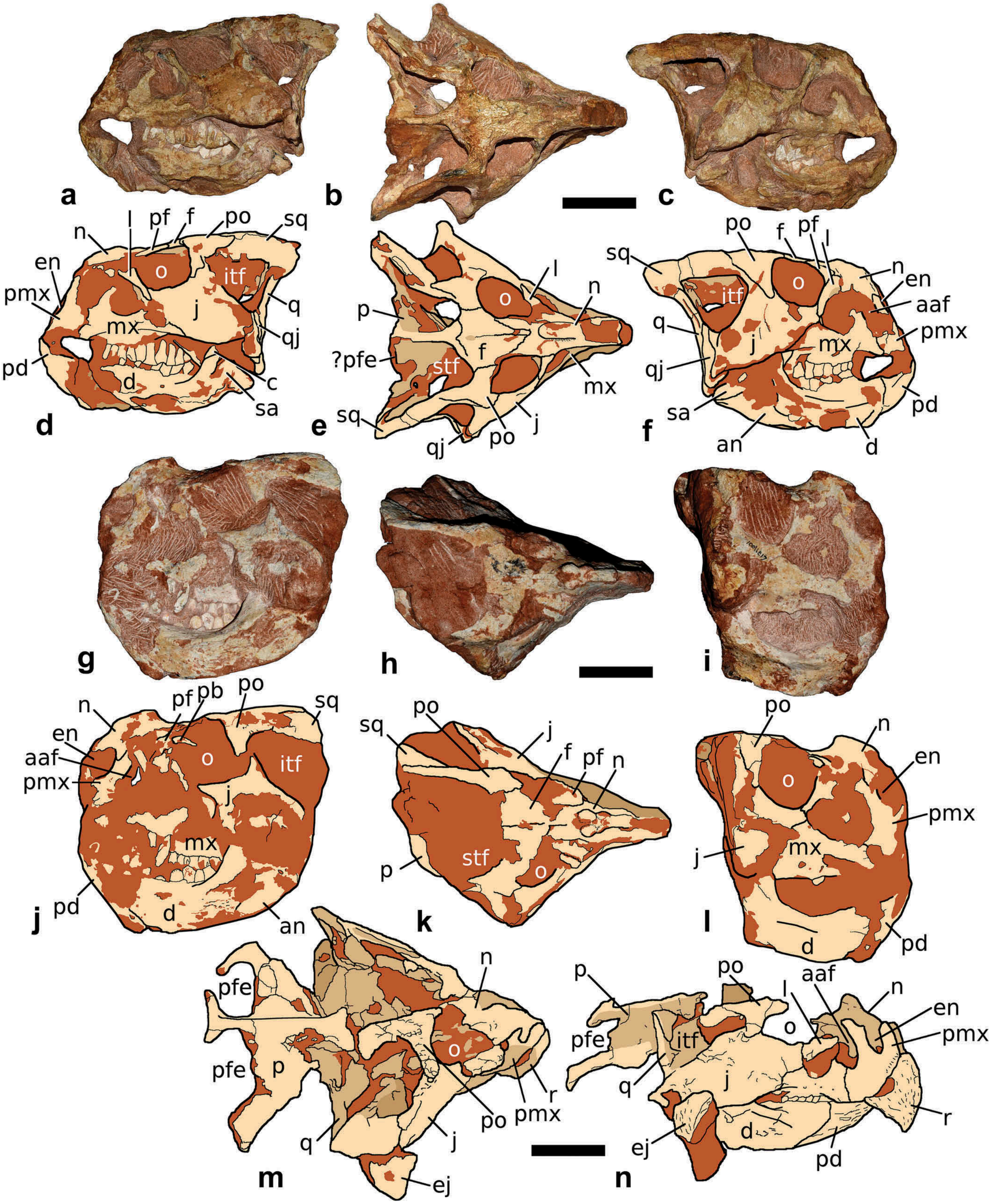

Figure 7. Medium-sized protoceratopsid specimens from the Baruungoyot Formation at Hermiin Tsav. A–F, ZPAL MgD-I/126, holotype of *Bagaceratops rozhdestvenskyi* in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. G–L, IGM 100/1817 in left lateral (g, j), dorsal (h, k) and right lateral (i, l) views. M–N, drawing of MPC-D 100/535 in dorsal (m) and right lateral (n) views. Scale bar: 5 cm.

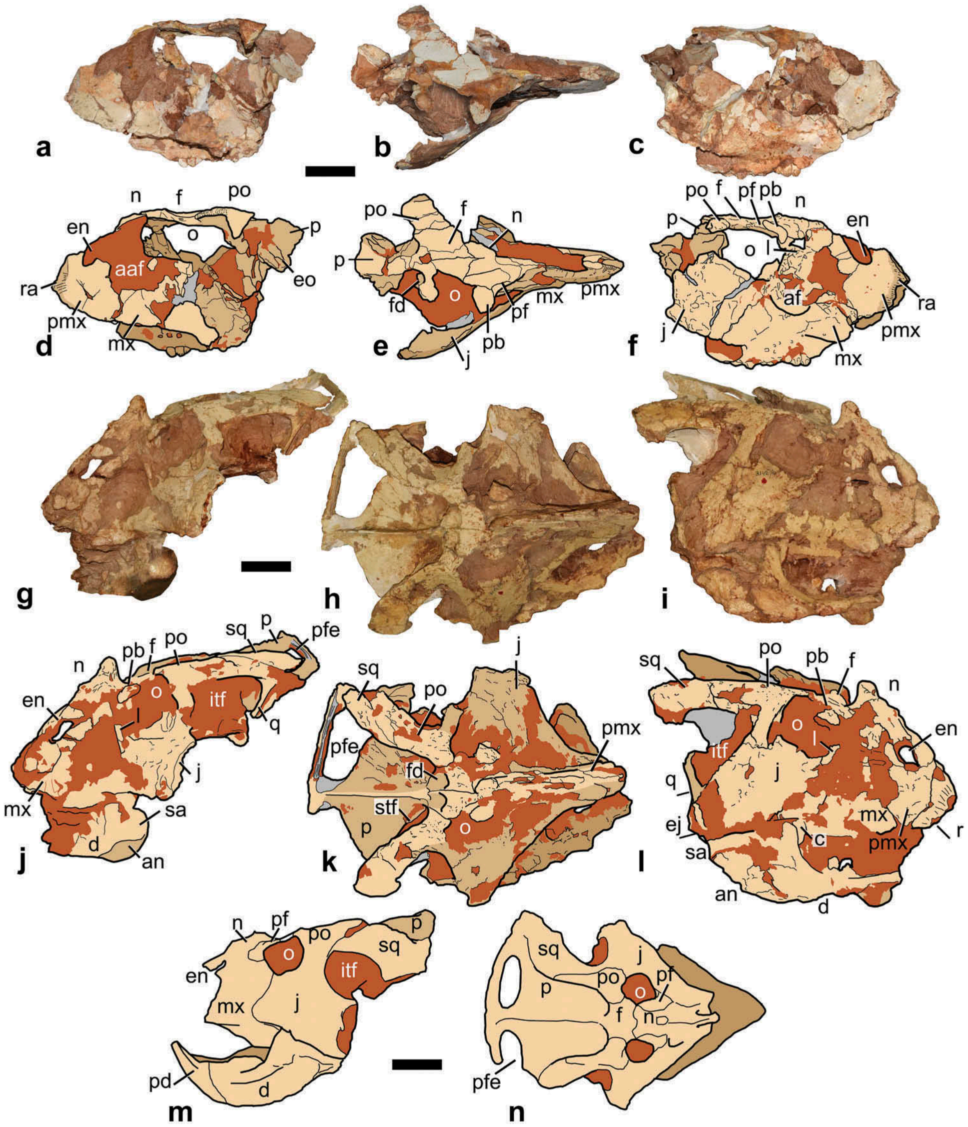

Figure 8. Large protoceratopsid specimens from the Baruungoyot Formation at Hermiin Tsav. (a–f), ZPAL MgD-I/129, referred to *Bagaceratops rozhdestvenskyi* by Maryańska and Osmólska 1975 in left lateral (a, d), dorsal (b, e) and right lateral (c, f) views. (g–l), PIN 3142/4, holotype of '*Platyceratops tatarinovi*' Alifanov 2003, junior synonym of *Bagaceratops rozhdestvenskyi*, in left lateral (g, j), dorsal (h, k) and right lateral (i, l) views. (m–n), drawing of PIN 3142/5, referred to *Breviceratops kozlowskii* by Kurzanov 1990 in left lateral (m) and dorsal (n) views, after Kurzanov (1990). Scale bar 5 cm.

Systematic paleontology

Dinosauria Owen 1842
Ornithischia Seeley 1887
Ceratopsia Marsh 1890
Neoceratopsia Sereno 1986
Coronosauria Sereno 1986
Protoceratopsidae Granger and Gregory 1923
Genus *Bagaceratops* Maryańska and Osmólska 1975

=*Gobiceratops* Alifanov 2008
=*Lamaceratops* Alifanov 2003
=*Magnirostris* You and Dong 2003
=*Platyceratops* Alifanov 2003

Type species

Bagaceratops rozhdestvenskyi

Diagnosis

As for the type species.

Bagaceratops rozhdestvenskyi Maryańska and Osmólska 1975
=*Gobiceratops minutus* Alifanov 2008
=*Lamaceratops tereschenkoi* Alifanov 2003
=*Magnirostris dodsoni* You and Dong 2003
=*Platyceratops tatarinovi* Alifanov 2003

Holotype

ZPAL MgD-I/126, a medium-sized skull lacking the tip of the snout and the caudal portion of the parietosquamosal frill.

Holotype locality and stratigraphy

Hermiin Tsav, Baruungoyot Formation, Ömnögov Province, Mongolia, Upper Cretaceous.

Referred material

ZPAL MgD-I/123, ZPAL MgD-I/124, ZPAL MgD-I/125, ZPAL MgD-I/127, ZPAL MgD-I/128, ZPAL MgD-I/129, ZPAL MgD-I/

130, ZPAL MgD-I/131, ZPAL MgD-I/132, ZPAL MgD-I/133a, ZPAL MgD-I/134a, ZPAL MgD-I/134b, ZPAL MgD-I/134c, ZPAL MgD-I/135, ZPAL MgD-I/137, ZPAL MgD-I/138, ZPAL MgD-I/140, ZPAL MgD-I/144, ZPAL MgD-I/145, ZPAL MgD-I/148, ZPAL MgD-I/149, ZPAL MgD-I/150, ZPAL MgD-I/152, ZPAL MgD-I/153, ZPAL MgD-I/301, ZPAL MgD-I/302, ZPAL MgD-I/306, ZPAL MgD-I/307, ZPAL MgD-I/310, IGM 100/1817, MPC-D 100/506, MPC-D 100/535, PIN 3142/1, PIN 3142/3, PIN 3142/4, PIN 3142/5, and PIN 3142/299 from Hermiin Tsav, Baruungoyot Formation, Ömnögov Province, Mongolia, Upper Cretaceous; ZPAL MgD-I/118, ZPAL MgD-I/120, IGM 100/3653, PIN 4487/26 from Khulsan, Baruungoyot Formation, Ömnögov Province, Mongolia, Upper Cretaceous; and IVPP V12513 from Bayan Mandahu, Bayan Mandahu Formation, Inner Mongolia, China, Upper Cretaceous.

Diagnosis

I confirm the following set of distinct features listed earlier (Maryańska and Osmólska 1975; Makovicky 2002) as diagnostic for *Bagaceratops rozhdestvenskyi*: well-developed accessory antorbital fenestra similar in size and shape to the external nares with restricted but present contact with the nasal (autapomorphy; Figure 20(a)), fused nasals with the prominent trapezoidal horncore present in even the smallest specimens (autapomorphy, Figure 9(a), Figure 17), sharp buccal crest of the dentary (autapomorphy; Figure 9(e)) and deeply bifurcated splenials (autapomorphy; Figure 9(g)).

All specimens of *Bag. rozhdestvenskyi* have an elongated maxillary diastema, longer than 30% of the teeth row (Figure 14), and lack of the angular process of the dentary at the caudoventral region of the bone, features seen only in a few specimens of *Protoceratops* spp. Among Protoceratopsidae, *Bag. rozhdestvenskyi* shares the edentulous premaxilla (Figure 9(c)) with *Protoceratops hellenikorhinus* and the presence of the accessory antorbital fenestra with *Breviceratops kozlowskii.*

Discussion

The distribution of the features among protoceratopsid material from the Baruungoyot Formation (Supplementary Material) suggests, that most of the taxonomically identifiable protoceratopsid specimens from Hermiin Tsav and Khulsan can be referred to *Bag. rozhdestvenskyi*. Only three specimens (ZPAL MgD-I/116, 117, 139a) are lacking any of those autapomorphies and they most probably represent the distinct sympatric species, *Breviceratops kozlowskii.*

Alifanov (2008) suggested that several specimens referred to *Bag. rozhdestvenskyi* by Maryańska and Osmólska (1975) are not conspecific with the remaining type series. He questioned the identification of the very small specimen ZPAL MgD-I/123 (Figure 3(a–g)) as a juvenile individual of *Bag. rozhdestvenskyi*. The distinguishing features listed by him (small overall size, large orbits, different proportions of the size of frontals and nasals, placement of the antorbital fossa entirely below the orbits, straight frontonasal suture, frontals excluded from the formation of the anterior margin of the supratemporal fenestra and 'number of other characters') are all juvenile traits, seen also in other ontogenetically young individuals of protoceratopsid dinosaurs.

ZPAL MgD-I/129 (Figure 8(a–f)) is not equal in size to the holotype (*contra* Alifanov 2008), in fact, the length of the maxilla (115 mm) is nearly two times larger than that in ZPAL MgD-I/126 (67 mm). Given the good correlation between the length of the maxilla and the partial basal length of skull (Supplementary Information), it can be concluded that skull ofZPAL MgD-I/129 was nearly twice as big as the holotype of *Bag. rozhdestvenskyi*. Comparison of the supraoccipital morphology in these two specimens is not possible, as this region in the holotype specimen is entirely covered by the sediment and was just schematically reconstructed by Maryańska and Osmólska (1975).

According to Alifanov (2008), the ventrocaudal (angular) process of the dentary is present in the isolated left mandible

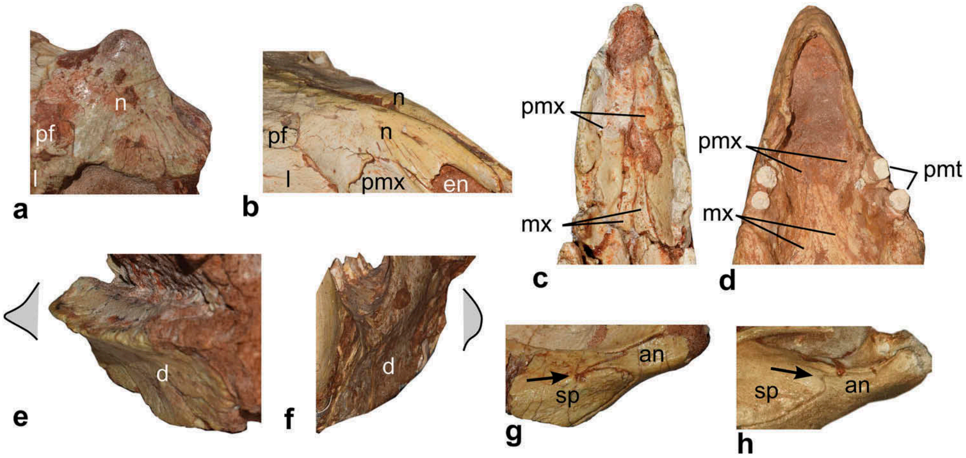

Figure 9. Differences in the anatomy of *Bagaceratops rozhdestvenskyi* and *Protoceratops andrewsi*. (a), fused nasal horncore in *Bag. rozhdestvenskyi* ZPAL MgD-I/125 from Hermiin Tsav. (b), paired nasals in *P. andrewsi* AMNH 6429 from Bayan Zag; both in right oblique view. (c), toothless premaxilla in *Bag. rozhdestvenskyi* ZPAL MgD-I/129 from Hermiin Tsav. (d), two teeth on the premaxilla of *P. andrewsi* AMNH 6433 from Bayan Zag; both in ventral view. (e), V-shaped buccal crest of the right dentary in *Bag. rozhdestvenskyi* ZPAL MgD-I/144 from Hermiin Tsav. (f), U-shaped buccal crest of the left dentary in *P. andrewsi* AMNH 6425 from Bayan Zag; both in anterior view. (g), deeply bifurcated splenial in *Bag. rozhdestvenskyi* ZPAL MgD-I/138 from Hermiin Tsav. (h), shallow bifurcation of the splenial in *P. andrewsi* PIN 3143/18 from Tögrögiin Shire; both in medal view. Features seen in *P. andrewsi* (b, d, f, h) are plesiomorphic among Neoceratopsia. Not to scale.

ZPAL MgD-I/137. This cannot be confirmed because the specimen is weathered at the region of the dento-angular and dento-surangular sutures. However, a very short trace of the suture at the caudoventral portion of the dentary bone suggests that there was no caudal projection of the dentary at all, like in other specimens of *Bag. rozhdestvenskyi*.

Although not every single specimen referred originally by Maryańska and Osmólska (1975) to *Bagaceratops rozhdestvenskyi* shows diagnostic characters, the presence of the autapomorphic features in ZPAL MgD-I/123, 129 and 137 allows their rather safe attribution to that taxon. However, some specimens lack any diagnostic traits and they are classified here as Protoceratopsidae indet. (ZPAL MgD-I/119, 121, 122, 133b, 136, 139b, 141, 142, 143, 147, 151, 154, 155, 303, 304, 305, 308, 309, 312, 316) or even Reptilia indet. (ZPAL MgD-I/146). A detailed list can be seen in Table 1 and in Supplementary Material.

Taxonomic identity of '*Gobiceratops minutus*'

Alifanov (2008) erected the new genus and species, *Gobiceratops minutus*, for a very small protoceratopsid specimen PIN 3142/299 (Figure 3(h–m)) collected in the 1970s at Hermiin Tsav. It was initially labelled as *Bagaceratops rozhdestvenskyi* by Kurzanov (1995, cited after Alifanov 2008).

Small size with the relatively large orbits and infratemporal fenestrae, short preorbital region and short and relatively wide, unfenestrated frill, placement of the entire antorbital fossa below the orbit, medially concave dorsal orbit margin in the dorsal view and relatively low number of the alveoli in jaws, were used to diagnose the new taxon by Alifanov (2008). Distinction of '*G. minutus*' has been recently questioned by Morschhauser (2012). In fact, the allegedly diagnostic features of this specimen are present in all other very small specimens of protoceratopsid dinosaurs (*Bagaceratops rozhdestvenskyi* ZPAL MgD-I/123, *Breviceratops kozlowskii* ZPAL MgD-I/116, *Protoceratops andrewsi* MPC-D 100/530).

Re-examination of the specimen has not confirmed the absence of the rostral bone. The marks at the lateral surface of the anteroventral margins of the premaxillae and the depression in this region suggest that the rostral bone was attached there (Figure 3(n)).

The shape of the accessory antorbital fenestrae cannot be precisely determined, as their posterior margins are not preserved. They were apparently large, but the size of the fenestra is slightly greater than that of the external nares also in ZPAL MgD-I/123.

A wide nasal with the small, but present nasal horn is also visible in ZPAL MgD-I/123. It is not possible to determine the shape of the nasofrontal suture in PIN 3142/299 as this region is damaged. The presence of the caudal process of the nasal is not sufficient to suggest U- or V-shaped suture, as such process is present also in ZPAL MgD-I/123, where the main (medial) portion of the nasofrontal suture is straight (Figure 3(b,e)).

No long caudal process of the maxilla is preserved in ZPAL MgD-I/123 but is visible in a very small *Br. kozlowskii* (ZPAL MgD-I/116). The crest on the jugal bone is typical for a number of protoceratopsid specimens of different size (ZPAL MgD-I/123, MPC-D 100/530, IGM 100/1021). No quadratojugal is preserved in ZPAL MgD-I/123, but the size of the bone in PIN 3142/299 is similar to that of the very small *Protoceratops* specimens from Tögrögiin Shiree locality of the Djadokhta Formation (IGM 100/1013) and Ukhaa Tolgod (IGM 100/1021), as well as in the very small *Br. kozlowskii* (ZPAL MgD-I/116).

The prefrontals of the holotype of '*G. minutus*' are shorter than in other protoceratopsid specimens, which may be related to the stage of ontogeny, as the left prefrontal in the slightly (30%) larger ZPAL MgD-I/123 is only a little longer than that of PIN 3142/299. The squamosal and jugal bones are in contact in many specimens of *Bag. rozhdestvenskyi*.

The close contact between the postorbitals and parietals, resulting in the exclusion of frontals from the anterior border of the supratemporal fenestra is visible also in the very small specimen of *Br. kozlowskii* (ZPAL MgD-I/116) as well as in *Protoceratops* from Tögrögiin Shiree (MPC-D 100/530) and Ukhaa Tolgod (IGM 100/1021). It cannot be seen in the very small *Bag. rozhdestvenskyi* (ZPAL MgD-I/123), because the caudal portion of the frontal process of the postorbital is damaged. Length of the frontal process of the postorbital is similar to that in the very small *Protoceratops* sp. (IGM 100/1013) from Tögrögiin Shiree. A relatively wide parietal with poorly developed sagittal crest is seen in ZPAL MgD-I/123 and in other protoceratopsids of similar size (*P. andrewsi* MPC-D 100/530).

The occipital region of the holotype of '*G. minutus*' cannot be compared with any other very small specimen of a protoceratopsid dinosaur, as this part is usually poorly preserved, as seen in the examined sample. However, the supraoccipital of the small *Bag. rozhdestvenskyi* ZPAL MgD-I/124 is similar in shape to that in PIN 3142/299. The foramen magnum is similar in size and shape in a very small *P. andrewsi* MPC-D 100/530 from Tögrögiin Shiree.

The dentary lacks the caudoventral process as in other *Bag. rozhdestvenskyi* specimens. The almost equal size of the angular and the surangular in the lateral view makes it similar to the other protoceratopsids (Morschhauser 2012). The short splenials are consistent with the overall short skull of the very small individual. Deep bifurcation of the splenial, the feature diagnostic for *Bag. rozhdestvenskyi*, cannot be determined because the caudalmost portion of the bone is not sufficiently preserved.

Alifanov (2008) claimed that PIN 3142/299 does not represent a juvenile individual, due to the worn teeth and the fusion of the skull bones. However, the sutures between many bones (between the premaxillae and between the nasal, prefrontal and lacrimal) can be recognised at least at the one side of the specimen. The worn teeth suggest a post-embryonic age of the individual (Erickson et al. 2017); however, they do not testify its maturity.

Given the lack of any autapomorphic characters and the presence of all features diagnostic for *Bag. rozhdestvenskyi* known from the same stratigraphic unit at the same locality, I propose to consider '*Gobiceratops minutus*' a junior synonym of *Bag. rozhdestvenskyi*. The only features making PIN 3142/299 different from the other specimens of *Bag. rozhdestvenskyi* are related to the early ontogenetic stage of the individual.

Taxonomic identity of '*Lamaceratops tereschenkoi*'

Alifanov (2003) erected a new species and genus for specimen PIN 4487/26 (Figure 5(g–l)), a nearly complete skull of a small individual collected at Khulsan (Baruungoyot Formation). Distinctness of the species was questioned by Makovicky and Norell (2006) and Morschhauser (2012) but some other authors continue to accept this taxon as valid (Alifanov 2008; Tereschenko 2008; Sissons 2009).

An elongated skull with relatively short squamosals nearly parallel to each other and the narrow supratemporal fenestrae, relatively large orbits, the size and the shape of the nasal horncore, are features changing during the ontogeny of the protoceratopsid dinosaurs, present in the individuals of size similar to that of PIN 4487/26 (e.g., *Bag. rozhdestvenskyi* ZPAL MgD-I/124, *Br. kozlowskii* ZPAL MgD-I/117, *P. andrewsi* AMNH 6421, ZPAL MgD-II/24).

Alifanov (2003) reconstructed the skull with the very high accessory antorbital fenestra of the longer axis twice as long as that of the external nares. However, only the anteroventral margin of the fenestra is preserved on the ascending caudal process of the right premaxilla, and there is no evidence for the shape and size different from the similar-sized specimens of *Bag. rozhdestvenskyi* (e.g., ZPAL MgD-I/124).

The nasofrontal suture is U-shaped, nearly straight at the medial portion, as in the very small specimen of *Bag. rozhdestvenskyi* (ZPAL MgD-I/123), which seems to be an intermediate condition in the protoceratopsid ontogeny. The dorsal surface of the frontals is weathered, many sutures are poorly preserved. The postorbital process of the frontal is clearly present at the right frontal. The caudally narrowing prefrontals are typical also for other protoceratopsids.

The development of the frontoparietal depression varies among specimens of *Bag. rozhdestvenskyi* (e.g. present in ZPAL MgD-I/129 and MPC-D 100/506) and is likely of little taxonomic value. The shape of the quadratojugal process of the jugal is not possible to be determined, as this portion is not preserved on either side of the specimen. The shape of the jugal process of the postorbital varies among specimens in both *Bag. rozhdestvenskyi* and *P. andrewsi*. Quadratojugals are not preserved in the specimen, their size and contribution to the formation of the lower temporal fenestra cannot be determined.

The M-shaped frontoparietal suture in PIN 4487/26 is like in other protoceratopsid specimens of similar size (e.g., *P. andrewsi* PIN 3143/6). The suture varies among *Bag. rozhdestvenskyi* and *Protoceratops* spp. and is usually related to the development of the frontoparietal depression and the sagittal crest of the frill.

All the diagnostic features of *Bag. rozhdestvenskyi* that are possible to detect, are present in PIN 4487/26: the fused nasals forming single, trapezoidal horncore, the huge accessory antorbital fenestra, the edentulous premaxilla, the sharp (V-shaped) buccal crest on the dentary. Morphology of the splenial bone cannot be determined because the natural margin of the bone is difficult to trace on the specimen.

Given the presence of all of the autapomorphies for *Bag. rozhdestvenskyi* in PIN 4487/26, lack of any distinguishable features, along with the confirmed presence of *Bag. rozhdestvenskyi* in Khulsan (specimens ZPAL MgD-I/118, IGM 100/3653; Makovicky 2002; Tables 1 and 2), I propose to consider PIN 4487/26 a small individual of *Bag. rozhdestvenskyi* and, consequently, '*Lamaceratops tereschenkoi*' as its junior synonym.

Taxonomic identity of 'Platyceratops tatarinovi'

Kurzanov (1990) referred the protoceratopsid cranial material collected at Hermiin Tsav to the new genus *Breviceratops kozlowskii*. For one large skull, PIN 3142/4 (described as PIN 3142/5 in Kurzanov 1990), the new genus and species *Platyceratops tatarinovi* was erected by Alifanov (2003). Distinctness of the species was later questioned (Makovicky and Norell 2006; Morschhauser 2012), however, no first-hand re-examination of the holotype specimen has been performed so far.

PIN 3142/4 (Figure 8(g–l), 17(e,f)) is a skull of a large size class, showing relatively late ontogenetic stage. Thus, many of the features described by Alifanov (2003) as diagnostic for '*Platyceratops tatarinovi*' are in fact observed in all protoceratopsid specimens of similar size, including: the wide lateral projection of the jugals in dorsal view, the size and the shape of the parietosquamosal frill, along with the fenestration and the medially leaned squamosal bar.

Table 2. Distribution of the ceratopsian dinosaurs in the Late Cretaceous localities of the Gobi Desert.

Formation	Locality	Protoceratopsidae	Leptoceratopsidae
Baruungoyot	Hermiin Tsav	*Bagaceratops rozhdestvenskyi* (Maryańska and Osmólska 1975)	
	Khulsan	*Bagaceratops rozhdestvenskyi* (this study) *Breviceratops kozlowskii* (Maryańska and Osmólska 1975)	
? Baruungoyot	Baga Tariach	indet. (Watabe and Tsogtbaatar 2004)	*Udanoceratops* sp. (Tereschenko 2008)
Bayan Mandahu	Bayan Mandahu	*Bagaceratops rozhdestvenskyi* (this study) *Protoceratops hellenikorhinus* (Lambert et al. 2001)	? *Udanoceratops* sp. (Jerzykiewicz et al. 1993)
? Djadokhta/ ? Baruungoyot	Üüden Sair	*Protoceratops andrewsi* (Handa et al. 2012)	*Udanoceratops tschizhovi* (Kurzanov 1992)
? Djadokhta	Alxa	*Protoceratops* sp. (Ji et al. 2017)	
	Bor Tolgoi	*Protoceratops* sp. (Saneyoshi et al. 2010)	
	Chimney Buttes	*Protoceratops* sp. (C. Mehling pers. comm.)	
	Gilbent Uul	indet. (Tereschenko 2008)	
	Shurg Uul	*Protoceratops* sp. (U. Sanjaadash pers. comm.)	
	Ukhaa Tolgod	*Protoceratops* sp. (P. Makovicky and M. Norell pers. comm.)	
	Zamyn Khond	*Protoceratops andrewsi* (U. Sanjaadash pers. comm.)	
Djadokhta	Bayan Zag	*Protoceratops andrewsi* (Granger and Gregory 1923)	*Bainoceratops efremovi* (Tereschenko and Alifanov 2003)
	Tögrögiin Shiree	*Protoceratops andrewsi* (Maryańska and Osmólska 1975)	

The shape and the size of the accessory antorbital fenestra cannot be determined, because no natural margins of the fenestra are preserved due to the intensive weathering of the skull in that region. The frontals are relatively small, mostly due to the good development of the nasal horncore anteriorly and the frontoparietal depression posteriorly. Both features vary within *Bag. rozhdestvenskyi* and *Protoceratops* spp. A small posterolateral process of the frontals and the orbital constriction are present. The frontonasal suture is V-shaped and relatively wide due to the overall increasement of the skull width and the caudal projection of the nasal horncore. A very narrow nasal of similar shape is observed also in the other specimens of *Bag. rozhdestvenskyi* (ZPAL MgD-I/125, MPC-D 100/535; Figure 6(a–f), 7(n), 17(a,b)). The morphology of the prefrontals is difficult to interpret due to their poor preservation in the specimen. The quadratojugal contributes to the formation of the lower margin of the infratemporal fenestration, as in other protoceratopsid specimens. The bifurcation of the squamosal process of the postorbital cannot be confirmed due to the incomplete preservation of that region.

All the diagnostic features of *Bag. rozhdestvenskyi* that are possible to detect in PIN 3142/4, are present: the fused nasals forming the single, trapezoidal horncore with prominent caudal portion, the edentulous premaxilla, and the sharp (V-shaped) buccal crest on the dentary.

Given the presence of the autapomorphies of *Bag. rozhdestvenskyi*, known from the number of specimens from Hermiin Tsav, in PIN 3142/4, and the lack of any distinguishable features, I propose to consider PIN 3142/4 a large individual of *Bag. rozhdestvenskyi* and, consequently, '*Platyceratops tatarinovi*' as its junior synonym.

Taxonomic identity of 'Magnirostris dodsoni'

You and Dong (2003) erected a new genus and species, *Magnirostris dodsoni*, for one large skull IVPP V12513 from Bayan Mandahu (Figure 10). Specimen lacking the left jugal, the left quadratojugal complex, and the parietosquamosal frill, was collected in 1988 by Sino-Canadian Paleontological Expedition from Bayan Mandahu. It was initially identified as

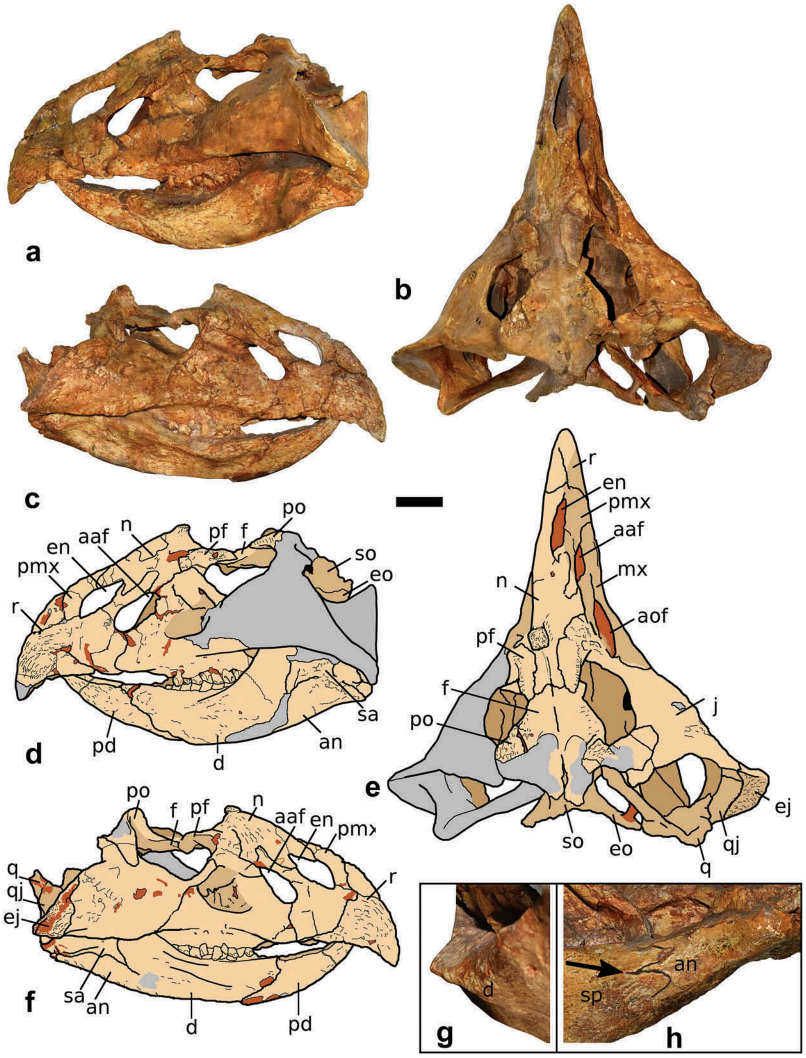

Figure 10. IVPP V12513, the large individual from Bayan Mandahu, Inner Mongolia, China, holotype of '*Magnirostris dodsoni*', junior synonym of *Bagaceratops rozhdestvenskyi*. Photographs and drawings in left lateral (a,d), dorsal (b,e) and right lateral (c,f) views. (g), right mandible in rostral view with distinct V-shaped buccal crest of dentary. (h), right mandible in medial view, with deeply bifurcated splenial bone. Both (g,h) are diagnostic features for *Bag. rozhdestvenskyi*. Scale bar for A–F: 5 cm.

Bagaceratops sp. (Jerzykiewicz et al. 1993). Its distinctness was questioned recently (Morschhauser 2012), but most studies consider it as a distinct taxon (Alifanov 2008; Kirkland and DeBlieux 2010; Sampson et al. 2013; Lund et al. 2016).

The rostral is covering nearly the whole ventral margin of the premaxilla, which is edentulous. The relatively low number of the maxillary teeth resembles that of *Bag. rozhdestvenskyi* (Figure 12). Against the previous description (You and Dong 2003), the maxilla is not contributing to the formation of the orbital margin (Figure 10(c,f)).

The purported horn at the right postorbital is a result of the bone deformation most likely caused by taphonomic process and is not observed at the left side (Figure 10, 16(c)). Similar deformation is seen at one specimen of *P. hellenikorhinus* from Bayan Mandahu (IMM 96BM1/7). The left, better-preserved postorbital is covered by rugosities and resembles those in large individuals of *Bag. rozhdestvenskyi* (ZPAL MgD-I/128, 129), *P. andrewsi* (e.g. AMNH 6438, PIN 614/63) and *P. hellenikorhinus* (e.g. IMM 96BM1/7).

You and Dong (2003) described the frontals of IVPP V12513 as fused, however, most of the caudal portion of the skull roof seems to be reconstructed by the preparator. The interfrontal suture can be traced at the rostral-most portion of the frontals, as the keel from the nasal horncore extends caudally (Figure 10(e)).

Splenials are deeply bifurcated (Figure 10(h)), however slightly shallower than in some specimens of *Bag. rozhdestvenskyi* (ZPAL MgD-I/138; Figure 9(g)). The buccal crest of the dentary is well developed and V-shaped in the cross section (Figure 10(g)).

The morphology of the rostral bone is the only one potentially distinct feature of IVPP V12513. Its elongation and development of the caudoventral process are greater than in any other protoceratopsid specimens (Figure 13). It may be, however, related to the advanced ontogenetic age of the individual (IVPP V12513 has partial basal skull length greater than that of any known specimen of *Bag. rozhdestvenskyi* from Baruungoyot Formation), and to the dorsoventral flattening of the specimen (post-mortem deformation).

Given the lack of any unquestionable distinct features, and the presence of all characteristics of *Bag. rozhdestvenskyi*, I propose to classify IVPP V12513 in this species. Thus, '*Magnirostris dodsoni*' is a junior synonym of *Bag. rozhdestvenskyi*.

Genus *Breviceratops* Kurzanov 1990

Type species

Breviceratops kozlowskii

Diagnosis

As for the type species.

Breviceratops kozlowskii (Maryańska and Osmólska 1975) Kurzanov (1990)
=?*Protoceratops kozlowskii* Maryańska and Osmólska 1975

Holotype

ZPAL MgD-I/117, small individual with skull lacking the tip of the snout, with articulated postcranial skeleton.

Holotype locality and stratigraphy

Khulsan, Baruungoyot Formation, Ömnögov Province, Mongolia, Upper Cretaceous.

Referred material

ZPAL MgD-I/116, very small skull from Khulsan, Baruungoyot Formation, Ömnögov Province, Mongolia, Upper Cretaceous.

Diagnosis

Protoceratopsid dinosaur with the premaxillary dentition and narrow accessory antorbital fenestration. Among Protoceratopsidae it shares the plesiomorphic condition of the presence of the premaxillary teeth with *P. andrewsi*, lack of the V-shaped buccal crest of the dentary with *Protoceratops* spp., and the presence of the accessory antorbital fenestration with *Bag. rozhdestvenskyi*. Morphology of the nasals remains unknown.

Discussion

Maryańska and Osmólska (1975) erected a new species, ? *Protoceratops kozlowskii*, for the material collected at Khulsan by the Polish-Mongolian Paleontological Expeditions in the 1970s. Later, Kurzanov (1990) attributed more material from Hermiin Tsav to that species and erected the new genus, *Breviceratops*. The Kurzanov's material was later referred to *Bag. rozhdestvenskyi* (Makovicky 2002; Morschhauser 2012) and to its junior synonyms '*Lamaceratops tereschenkoi*' and '*Platyceratops tatarinovi*' (Alifanov 2003). The medium-sized dentaries ZPAL MgD-I/118 described by Maryańska and Osmólska (1975) are indistinguishable from those of *Bag. rozhdestvenskyi* (Makovicky 2002), having a well-pronounced buccal crest, sharp and V-shaped in cross section.

Two skulls originally referred to *Br. kozlowskii* (the holotype ZPAL MgD-I//117 and ZPAL MgD-I/116, Figure 4) differ from *Bag. rozhdestvenskyi* in the presence of the premaxillary teeth and the lack of the sharp buccal crest of the dentary, both plesiomorphic features for Ceratopsia, among Protoceratopsidae shared with *P. andrewsi*. The well established accessory antorbital fenestration differs *Br. kozlowskii* from *P. andrewsi*. Based on these distinctions, I propose to consider *Br. kozlowskii* as a species distinct from the sympatric *Bag. rozhdestvenskyi* and sharing few plesiomorphic features with *P. andrewsi*.

One mandible from Hermiin Tsav (ZPAL MgD-I/139a), originally labelled as *Bag. rozhdestvenskyi* (Maryańska and Osmólska 1975) has a very weakly pronounced buccal crest and may instead belong to *Br. kozlowskii*, present in the same geological formation. Due to its fragmentary nature, it should be regarded as cf. *Breviceratops* sp. or Protoceratopsidae indet.

Attribution of the isolated postcranial remains

The postcranial skeleton in basal coronosaurs is rather conservative, however, displays a wide intraspecific variability (Makovicky and Norell 2006). In the PIN collection, there is at least one undescribed fairly complete skeleton with the cranial elements of *Bag. rozhdestvenskyi* (V. Alifanov and V. Tereschenko, pers. comm. 2015; probably it is the specimen from Hermiin Tsav referred to as PIN 3142/7 in Tereschenko 2007). Based on this specimen, Tereschenko (2007) listed the differences in the morphology of the vertebrae with respect to specimens of *P. andrewsi* and suggested the presence of *Bag. rozhdestvenskyi* postcranial material at Bayan Zag (PIN 614/29, 34 and 53) and Tögrögiin Shiree localities. He suggested the co-occurrence of these two species in the sediments of Djadokhta Formation (Tereschenko 2007, 2008; Tereschenko and Singer 2013).

However, examination of the more diagnostic, cranial material from the Bayan Zag and Tögrögiin Shiree localities of the Djadokhta Formation, convinced me that the only species identifiable there is *P. andrewsi*. This is consistent with the wide intraspecific variation within the postcranial skeleton of *Protoceratops andrewsi* (Makovicky and Norell 2006; Tereschenko 2018). I suggest that the similar range of variability might characterise the postcranial skeleton of *Bag. rozhdestvenskyi*, making the isolated postcranial material not diagnostic at the species and genus levels. The presence of *Bag. rozhdestvenskyi* in the Djadokhta Formation cannot be confirmed without diagnostic cranial material found there.

Bainoceratops efremovi Tereschenko and Alifanov 2003 was described on the base of few vertebrae from Bayan Zag. It may fall into the intraspecific variation of *P. andrewsi* (Makovicky and Norell 2006), however, similarities with leptoceratopsid dinosaurs were mentioned in its description (Tereschenko and Alifanov 2003; Tereschenko 2018). Its reinterpretation is reaching beyond the framework of this study.

Prior to the proper description of the intra- and interspecific variation in postcranial anatomy, made on a significant sample of specimens with preserved, articulated diagnostic cranial material of each of species, the protoceratopsid specimens lacking cranial material should be regarded as taxonomically undetermined.

Discussion

Ontogeny of *Bagaceratops rozhdestvenskyi*

During the ontogeny of *Bagaceratops rozhdestvenskyi*, the skull became taller at the occiput area due to the development of the frill, although relatively shorter in craniocaudal length when compared to the jugal or parietosquamosal frill width (Figure 11).

Development of the rostral bone cannot be traced in detail as only few specimens preserved this bone fairly completely. In *Protoceratops andrewsi*, growth of the rostral bone is rather isometric, with some degree of the intraspecific variation (Figure 13). The external nares are elongated and elliptical or tear-shaped, usually leaned dorsocaudally in relation to the long axis of the skull. They are similar in size and shape to the accessory antorbital fenestration, and the ratio remains constant during the whole growth. However, in the smallest specimens (ZPAL MgD-I/123, 124, PIN 3142/299) external nares are slightly smaller than the accessory antorbital fenestra.

The relative size of the orbits decreases, as noticed by Maryańska and Osmólska (1975). The antorbital fossa in the smallest specimens is located entirely below the orbits, with the longer axis parallel to that of the whole skull. During the ontogeny, it became more oval, deeper and placed more rostrally.

The premaxilla remained toothless during the whole development, and no traces of the premaxillary dentition can be observed, in contrast to the earlier suggestions (Sereno 2000). The jugals develop laterocaudally in the medium-sized and large individuals, sometimes reaching their position nearly perpendicular to the long axis of the skull in dorsal view (PIN 3142/4), similarly to *Protoceratops* spp. (Brown and Schlaikjer 1940; Lambert et al. 2001).

The co-ossification of the epijugal with the jugal might have occurred late in the ontogeny, as the many specimens of the very small and small *Bag. rozhdestvenskyi* have no traces of this bone. In the medium-sized specimens, fragments of the epijugal (in MPC-D 100/535, IGM 100/3653, ZPAL MgD-I/133a) and attachment scars on the jugal (ZPAL MgD-I/125) can be traced, suggesting that the epijugal ossification was present at least at this stage of the ontogeny. The best-preserved epijugal is seen in the largest specimen (IVPP V12513). A similar pattern is seen in *Protoceratops* spp., where the smallest specimens often have no traces of the epijugal (MPC-D 100/530, ZPAL MgD-II/6, IGM 100/1013, 1021). Comparably more frequent preservation of the epijugal in articulation with the jugal in larger specimens of *P. andrewsi* than in *Bag. rozhdestvenskyi* may be caused by the taphonomic factors (the different burial conditions in the Djadokhta and the Baruungoyot Formations) or may express the interspecific differences.

The nasal ornamentation in the form of the small, but distinct bump is present even in the smallest specimens (PIN 3142/

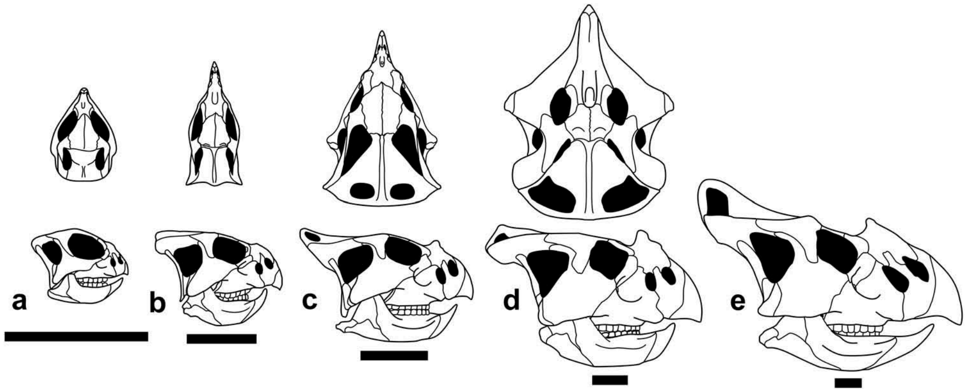

Figure 11. Ontogenetic changes in the cranial anatomy of *Bagaceratops rozhdestvenskyi*. Reconstructions based on: (a) very small PIN 3142/299, (b) small PIN 4487/26, (c) medium-sized ZPAL MgD-I/125, (d) large PIN 3142/4, (e) large IVPP V12513. Scale bar: 5 cm.

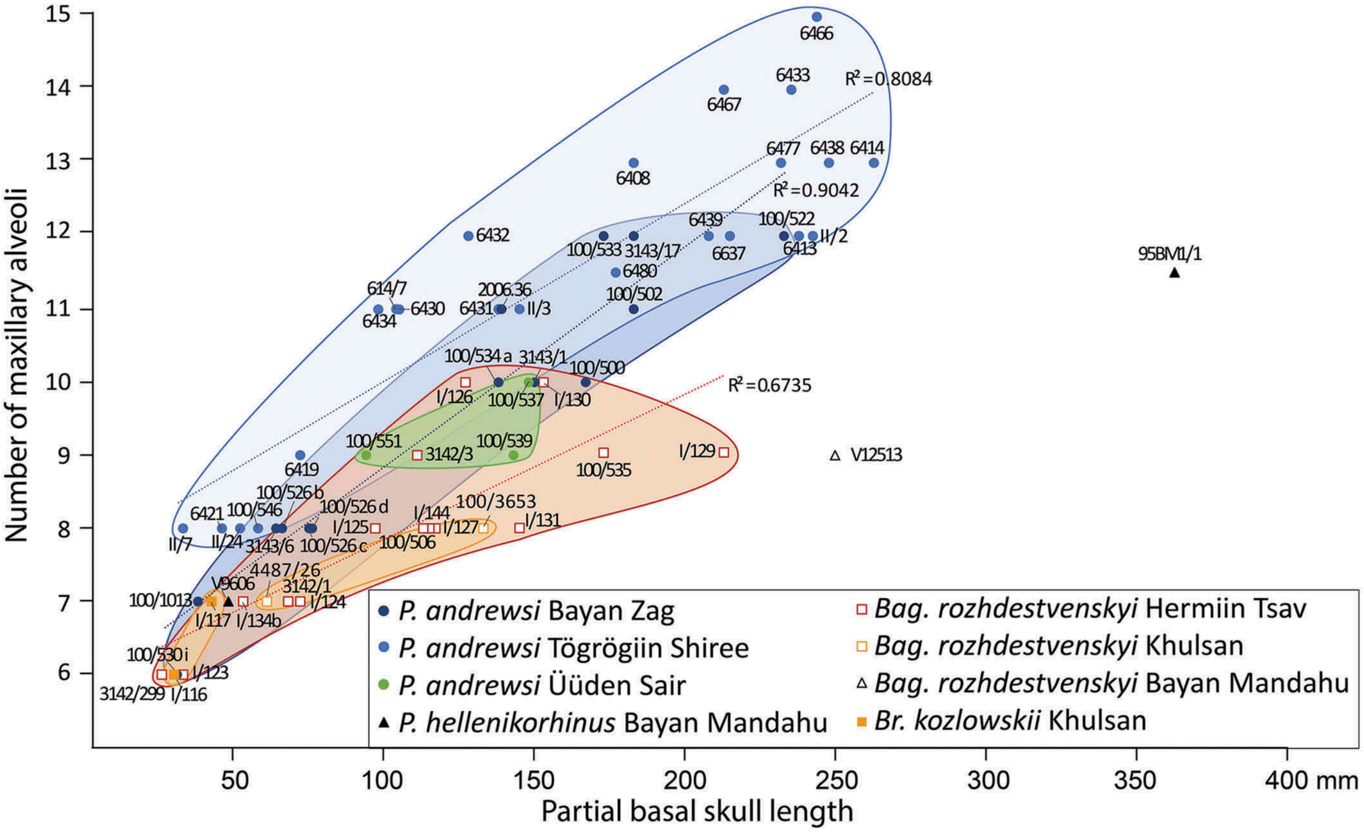

Figure 12. Relation of the number of maxillary teeth and the partial basal skull length of protoceratopsid dinosaurs from Hermiin Tsav (red) and Khulsan (orange) of Baruungoyot Formation, Bayan Zag (blue), Tögrögiin Shiree (dark blue) and Üüden Sair (green) of Djadokhta Formation and Bayan Mandahu (black). Unfilled marks are indicating *Bag. rozhdestvenskyi* specimens.

299, ZPAL MgD-I/123), in contrast to *P. andrewsi* (MPC-D 100/530). In all specimens of *Bag. rozhdestvenskyi* the nasals are fused medially. A horn developed and became more prominent and trapezoidal in shape during the growth of the animal, with the caudal portion forming a spike of various size.

The prefrontals, initially short and excluded from the contact with the frontals (PIN 3142/299) developed caudally. The frontals are nearly flat in the smallest specimens of *Bag. rozhdestvenskyi* (ZPAL MgD-I/123) but are inclined medially along the interfrontal suture in *Protoceratops* spp. (MPC-D 100/530, IGM 100/1013). The latter condition was observed in basal ceratopsian *Yinlong downsi* and suggested as its autapomorphy (Han et al. 2016).

The frontonasal suture is straight or U-shaped in the smallest *Bag. rozhdestvenskyi* (ZPAL MgD-I/123), while V-shaped in *Protoceratops* (MPC-D 100/530) and *Br. kozlowskii* (ZPAL MgD-I/117).

Small specimens (ZPAL MgD-I/124, PIN 4487/26) have elongated, very narrow in dorsal view skulls, similarly to some specimens of *P. andrewsi* of similar size (AMNH 6421, ZPAL MgD-II/24 from Bayan Zag). However, it seems that relatively larger specimens of *Bag. rozhdestvenskyi* still had narrow skulls, while in *P. andrewsi* it became wider (AMNH 6419 from Bayan Zag and MPC-D 100/526 from Tögrögiin Shiree are similar in partial basal length to ZPAL MgD-I/124 but have wider skulls in dorsal view).

The parietosquamosal frill developed caudally and laterally. In *P. andrewsi* its growth was positively allometric (Handa et al. 2012; Hone et al. 2016; Saneyoshi et al. 2017). In *Bag. rozhdestvenskyi* only few specimens preserved the frill, and it seems to have a quite wide range of variation. In the smallest specimens of *Bag. rozhdestvenskyi* its width is smaller (PIN 3142/299) or equal (ZPAL MgD-I/123) to the skull width along the postorbitals.

It seems plausible that in the protoceratopsid dinosaurs the sagittal crest was the first region of the parietosquamosal frill to develop caudodorsally (Figure 11(b)), as seen in a small (~40 mm of partial basal skull length) *Br. rozhdestvenskyi* (ZPAL MgD-I/117) and one very small (~30 mm of partial basal skull length) *Protoceratops* sp. (IGM 100/1008). However, there is no record of *Bag. rozhdestvenskyi* comparable in size to the holotype of *Br. kozlowskii* (ZPAL MgD-I/117). The latter is intermediate in size between the very small and small specimens of *Bag. rozhdestvenskyi*. ZPAL MgD-I/123, although similar in size to *Protoceratops* sp. IGM 100/1008, has a well-established caudal margin of the frill, with no caudal projection of the sagittal crest. The preserved part of the frill in ZPAL MgD-I/124 suggests a caudal expansion of the squamosal and the lateral portion of the parietal bone, but medially it is directed towards the rostrum. No sagittal crest is preserved in this specimen, but it might have been well developed, as in *Br. kozlowskii* ZPAL MgD-I/117.

Later in the ontogeny, the frill developed caudolaterally and the squamosal bars became more leaned dorsoventrally, 'lying' at the parietal frill at the caudal extremities. The frill is unfenestrated in the smallest individuals of *Bag. rozhdestvenskyi* (ZPAL MgD-I/

123). The smallest specimen of *Bag. rozhdestvenskyi* with preserved margins of parietosquamosal fenestration is a medium-sized MPC-D 100/506 (110 mm of the partial basal length), suggesting that the other individuals of that size class also possessed a fenestrated frill. In comparison, the largest specimen of a protoceratopsid with an unfenestrated frill is an undescribed specimen of *Protoceratops* sp. from Ukhaa Tolgod, of approximately 60 mm of the partial basal length (L. Panzarin, pers. comm.). However, such fenestration is rather well developed in a slightly (~65 mm of the partial basal length) larger *P. andrewsi* specimen from Tögrögiin Shiree (MPC-D 100/526) and that from Bayan Zag (AMNH 6419, 69 mm of the partial basal length).

During the ontogeny, dorsal inclination of the sagittal crest increase, however no specimen of *Bag. rozhdestvenskyi* reached the level of the inclination seen in some large specimens of *Protoceratops* spp.

The number of maxillary teeth is correlated with the skull length (Figure 12). The smallest specimens of *Bag. rozhdestvenskyi* have 6 alveoli (PIN 3142/299, ZPAL MgD-I/123), which is also true for the smallest *P. andrewsi* (MPC-D 100/530) and *Br. kozlowskii* (ZPAL MgD-I/116). However, during the ontogeny, specimens of *Bag. rozhdestvenskyi* and *P. andrewsi* of similar size have a different number of the maxillary alveoli. The number is greater in *P. andrewsi* (up to 14) than in *Bag. rozhdestvenskyi* (up to 10). That may be related with the elongation of the maxillary diastema. Data for *P. hellenikorhinus* is limited, however the very large holotype individual (IMM 95BM1/1) has at least 11 alveoli (Lambert et al. 2001).

The mandible became rostrocaudally longer and dorsoventrally taller during the ontogeny. In *Bag. rozhdestvenskyi* it is usually lower than in *P. andrewsi*. A prominent buccal crest of the dentary, V-shaped in the cross section, is seen even in the smallest specimens of *Bag. rozhdestvenskyi* (PIN 3142/299, ZPAL MgD-I/123). It became more pronounced during the ontogeny. In the smallest specimens of *P. andrewsi* (AMNH 6419, 6421, ZPAL MgD-II/24) and *Br. kozlowskii* (ZPAL MgD-I/116, 117), the buccal crest is not clearly developed. In larger individuals of *Protoceratops* spp., the crest is U-shaped at the cross section and usually weaker developed than in *Bag. rozhdestvenskyi* (Figure 9(e,f)).

Intraspecific variation

Only a few fairly complete specimens of *Bag. rozhdestvenskyi* have the rostral bone preserved (PIN 4487/26 from Khulsan, MPC-D 100/535 from Hermiin Tsav and IVPP V12513 from Bayan Mandahu). Its shape usually fits in the range of intraspecific variation of *P. andrewsi* (Figure 13), with the exception for IVPP V12513, that is fairly elongated (length to height ratio equal 1.16), much more than that of any of the specimens of *P. andrewsi* of similar size (AMNH 6429, 6438, PIN 614/63). However, the specimen is somewhat dorsoventrally flattened and this may have affected the observed elongation. Ontogenetic trajectory of the rostral development in *Bag. rozhdestvenskyi* remains unknown.

The ratio of the maxillary diastema length to the length of the teeth row is rather constant during the ontogeny of *Bag. rozhdestvenskyi* and *Protoceratops* spp. (Figure 14), however, there is some range of variation in both taxa. In all specimens of *Bag. rozhdestvenskyi* the length of the maxillary diastema is longer than 30% of the tooth row length, up to 54.17% (in ZPAL MgD-I/129), with mean value 0.405 specimens from Hermiin Tsav (N = 11), 0.444 for specimens from Khulsan (N = 2) and 0.476 for a specimen from Bayan Mandahu. *P. andrewsi* from Bayan Zag have the ratio 0.189 to 0.316 (mean 0.258, N = 26), from Tögrögiin Shiree 0.241 to 0.328 (mean 0.284, N = 11), from Üüden Sair 0.308 to 0.314 (mean 0.311, N = 2) and *P. hellenikorhinus* from Bayan Mandahu 0.211 to 0.286 (mean 0.248, N = 3). *Br. kozlowskii* from Khulsan have that ratio ranging from 0.222 to 0.250 (mean 0.236, N = 2), falling within the variation of *P. andrewsi*. Relative length of the diastema seems to be a distinctive feature of *Bag. rozhdestvenskyi*, with only a few specimens of *P. andrewsi* reaching similar values.

It was suggested that the morphology of the maxillary dentition can be used to distinguish species of protoceratopsid dinosaurs (Maryańska and Osmólska 1975; Alifanov 2003). It would suggest the ecological partitioning of the niches between sympatric species. Maryańska and Osmólska (1975) suggested that only the teeth in the central part of the maxilla have taxonomical value. These authorities observed differences in the depth of carinae and the shape of the indentations of the maxillary tooth crown, with *Bag. rozhdestvenskyi* having shallower carinae with low primary ridge and V-shaped 'pockets', while *P. andrewsi* having deeper carinae and U-shaped 'pockets' (Maryańska and Osmólska 1975; Tanoue et al. 2009).

However, these aspects change with the overall size of the skull and may vary even within a single specimen (e.g., in IVPP V12513; Figure 15(f)). Alifanov (2003) suggested that there are significant differences in the number of secondary ridges between allegedly sympatric taxa. He suggested that in *Bag. rozhdestvenskyi* there were only two secondary ridges at the mesial and one at the distal lobes. As seen in a few specimens (e.g., ZPAL MgD-I/129; Figure 15(e)), secondary ridges may be present variously even among the teeth within a single specimen, depending on the level of the wearing of the tooth and taphonomic factors. In PIN 4487/26 (holotype of '*Lamaceratops tereschenkoi*' by Alifanov 2003) the fourth tooth (the third preserved) of the right maxilla has only one secondary ridge at both the mesial and distal lobe; but the fifth tooth has two secondary ridges at the mesial lobe and one at the distal lobe (Figure 15(c)). In IVPP V12513 (holotype of '*Magnirostris dodsoni*' by You and Dong 2003) it is difficult to count the number of the secondary ridges due to the preservation aspects. At least four secondary ridges are present at the mesial lobe of the first maxillary tooth and three or four secondary ridges at the mesial lobes of the third and sixth tooth.

The palpebral is triangular in shape in dorsal view and dorsoventrally flattened, slightly arched in lateral view. It attaches to the anterodorsal corner of the orbit. It differs in size, being relatively small in some medium-sized specimens (ZPAL MgD-I/125, IGM 100/1813) and huge in the very small (ZPAL MgD-I/123), small (PIN 4487/26) and large (ZPAL MgD-I/129, PIN 3142/4) individuals.

The development of the frontoparietal depression can be determined only in a few specimens of *Bag. rozhdestvenskyi*, due to the frequently poor preservation of the caudal portion of frontals. It is variously developed in some individuals of the different size classes (PIN 4487/26, MPC-D 100/506, PIN 3142/

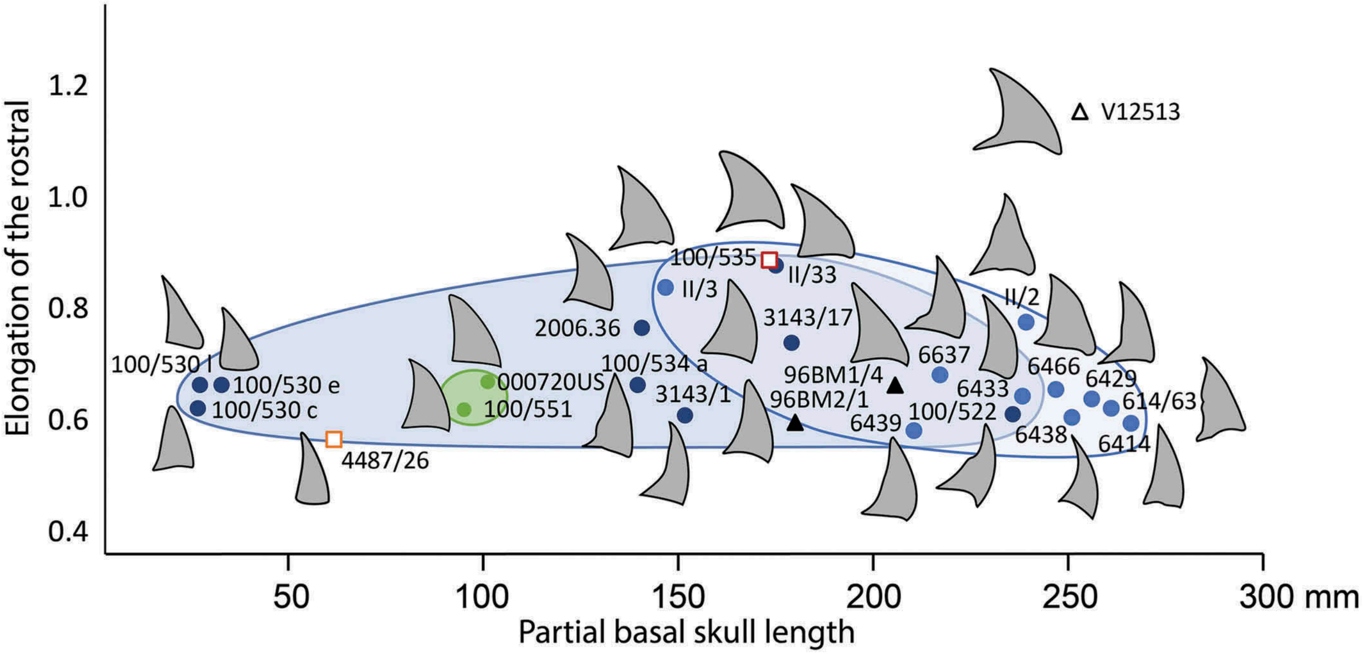

Figure 13. Elongation of the rostral bone (shown in lateral right view) in relation to the partial basal skull length in *P. andrewsi* and *Bag. rozhdestvenskyi.*

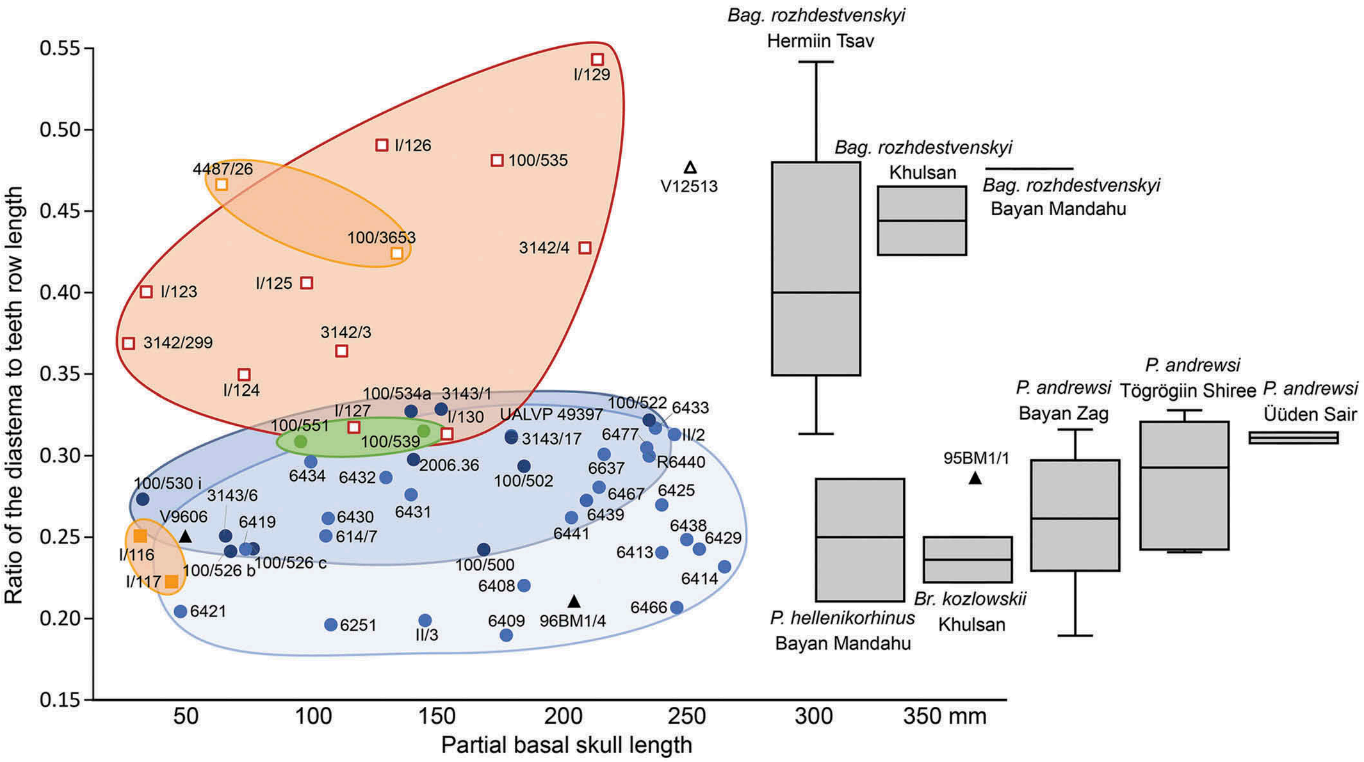

Figure 14. Elongation of the maxillary diastema (pictured as ratio of the maxillary diastema length to the length of the teeth row) in protoceratopsid specimen of different species and locality. Box-plots indicating range of variation of the diastema elongation within each of sample. *Bag. rozhdestvenskyi* have maxillary diastema always longer than 30% of the teeth row, while *P. andrewsi, P. hellenikorhinus* and *Br. kozlowskii* have maxillary diastema always shorter than 35% of the teeth row.

4, ZPAL MgD-I/129), while absent in other (PIN 3142/299, ZPAL MgD-I/126, 128 and ZPAL MgD-I/133a). In a few specimens of *Bag. rozhdestvenskyi* there is a shallow fossa placed medially at the caudal portion of the intrafrontal suture (e.g., ZPAL MgD-I/126).

The frontoparietal depression is developed in nearly all, even the smallest, individuals of *P. andrewsi* and *P. hellenikorhinus*, and its development and size are usually well correlated with the overall skull size. Some specimens of *P. andrewsi* seems to have very delicately pronounced depression (e.g., ZPAL MgD-II/3, MPC-D 100/503, AMNH 6413) and in the largest individuals both frontoparietal depressions are conjoined medially (e.g., MPC-D 100/500; Farke 2010).

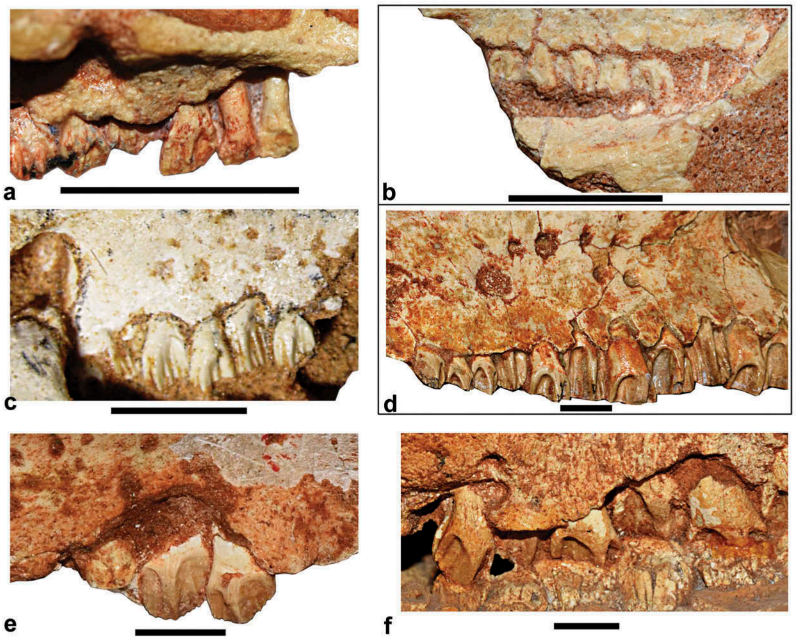

Figure 15. Comparison of the maxillary teeth in protoceratopsid dinosaurs. (a) right maxilla of the very small specimen of *Bag. rozhdestvenskyi* (ZPAL MgD-I/123). (b) left maxilla of the small specimen of *Br. kozlowskii* (ZPAL MgD-I/117). (c) right maxilla of the small specimen of *Bag. rozhdestvenskyi* (PIN 4487/26). (d) right maxilla of the medium-sized *P. andrewsi* (AMNH 6637), mirrored. (e) right maxilla of a large *Bag. rozhdestvenskyi* (ZPAL MgD-I/129). (f) left maxilla of the large *Bag. rozhdestvenskyi* (IVPP V12513). All in lateral view. Notice the presence of both U- and V-shaped indentations of the tooth crown within the single large specimen of *P. andrewsi* (d) and *Bag. rozhdestvenskyi* (f). Scale bar: 1 cm.

Only a few specimens of *Protoceratops* spp. lack visible frontoparietal depression (e.g., ZPAL MgD-II/404). A shallow frontoparietal depression is also seen in the type specimen of *Br. kozlowskii* (ZPAL MgD-I/117). The functional meaning of this structure remains unclear (Farke 2010).

The anterodorsal portions of the postorbital bones in large individuals of protoceratopsid dinosaurs (e.g., *Bag. rozhdestvenskyi* IVPP V12513, *P. andrewsi* MPC-D 100/522) are usually covered with wrinkles that were interpreted as cores for small horns (Brown and Schlaikjer 1940). Given the presence of similar pattern along the orbit margin on the prefrontal bones, more plausible is its interpretation as the marks of the attachment of the connective tissue extending from the palpebral, that roofed the orbit during the life of the animal, as in other ornithischian dinosaurs (Maidment and Porro 2010).

A few specimens of *Bag. rozhdestvenskyi* exhibit tubercles on the postorbital bone. In one *Bag. rozhdestvenskyi* specimen from Hermiin Tsav (ZPAL MgD-I/135), there is a row of at least two well-pronounced tubercles directing anterolaterally (Figure 16(b)). In many specimens of *Bag. rozhdestvenskyi* the small tubercle at the frontopostorbital suture can be observed (e.g., ZPAL MgD-I/125, 129, IVPP V12513; Figure 16(a,c)). There is no unambiguous postorbital horncore in any of the protoceratopsid specimens.

The thickened nasals forming the nasal horncore are known in all protoceratopsids with preserved nasal region (*P. andrewsi, P. hellenikorhinus, Bag. rozhdestvenskyi*). In some specimens of *Bag. rozhdestvenskyi* and *P. hellenikorhinus* there is a trapezoidal nasal horncore with the prominent caudal portion forming a spike. The length and the height of the caudal spike vary

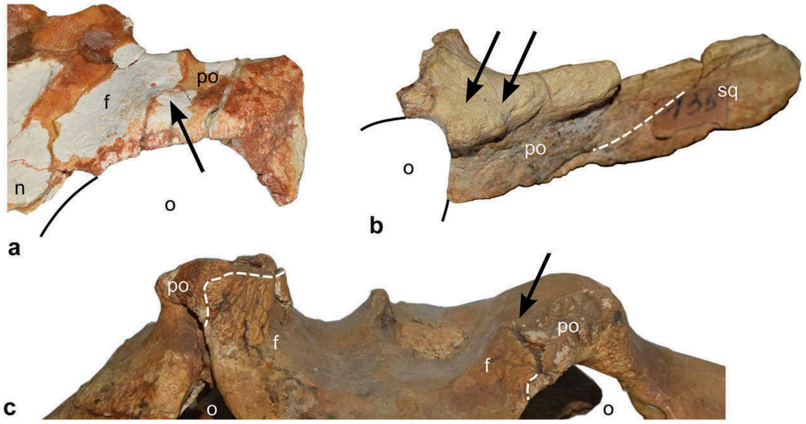

Figure 16. Variation of the postorbital in *Bagaceratops rozhdestvenskyi*. (a) ZPAL MgD-I/129 in anterodorsal view. (b) left postorbital of ZPAL MgD-I/135 in anterolateral view. (c) IVPP V12513 in anterior view. Arrows are indicating tubercles at the postorbital bone (b) and postorbitofrontal suture (a, c). Not to scale.

(Figure 17), in some individuals being barely seen (ZPAL MgD-I/124, 126), while in other contributing to most of the nasal horncore length (ZPAL MgD-I/125, PIN 3142/4, MPC-D 100/535). In the smallest specimens (PIN 3142/299, ZPAL MgD-I/123), the caudal spike is not observed.

Measurements of the nasal horncore suggests presence of two morphotypes in the medium-sized and large individuals: one with the caudal spike distinctly lower than 50% and shorter than 50% of the basal boss height and length, respectively, and the second one, narrow, with the caudal spike being longer and higher than 50% of the basal boss. No intermediate morphologies between these two can be observed in the sample, and the distribution of morphotypes is not related to the ontogeny, as both of them are present in the medium-sized and large individuals. Observed distribution of the nasal horncore morphotypes is similar to that of a sexually dimorphic feature.

The sexual dimorphism was suggested for *P. andrewsi* based on cranial (Brown and Schlaikjer 1940; Kurzanov 1972; Dodson 1976) and postcranial features (Tereschenko 2001). It was tested recently and rejected for most of the cranial aspects (Maiorino et al. 2015). However, the morphology of the nasal region of the skull has remained as potentially dimorphic. Quite similar pattern of the morphotypes distribution as in *Bag. rozhdestvenskyi* is seen in *P. andrewsi*, where some medium and large individuals have nasals only gently arched (condition present also in the smallest specimens), while the other display a more pronounced trapezoidal nasal horncore with a prominent caudal portion, although no distinct caudal spike can be observed in any *P. andrewsi* specimen. In the largest specimens of *P. hellenikorhinus* (IMM 95BM1/1 and one uncatalogued specimen housed at RBINS) the nasals form a trapezoidal horncore with a well-pronounced caudal spike. It should be noted, however, that the sample size of *Bag. rozhdestvenskyi* (N = 12) is too small to substantiate claims of the sexual dimorphism in this species, and the differences may as well reflect intraspecific variation or evolutionary changes.

Moreover, a few specimens exhibit a distinct nasal morphology. Three specimens of *Bag. rozhdestvenskyi* from the red beds of Hermiin Tsav have a trapezoidal horncore with two parallel rows of small bosses. There are two (IGM 100/1817) or three tubercles (ZPAL MgD-I/135, 301) placed along the lateral margins of nasals (Figure 17(i,j)). In ZPAL MgD-I/135 there is also a subtle central tubercle at the height of the second row of the lateral ones. There are fewer bosses in IGM 100/1817, but they are larger in size. Similarly as in IVPP V12513 from Bayan Mandahu, the nasal horncore is significantly wider at the top than at the base in rostral/caudal view of IGM 100/1817, ZPAL MgD-I/135 and 301 (Figure 17(g,i)). Although nasal morphology in these specimens is rather unique, the presence of all autapomorphic features able to detect in the most complete specimen, IGM 100/1817, reveals that it does belong to *Bag. rozhdestvenskyi*.

ZPAL MgD-I/310, the fragmentary specimen of *Bagaceratops* sp. from Hermiin Tsav contains the proximal portion of the nasal bones with the dorsal margin of the external nares preserved. Nasals are fused dorsally with no distinguishable suture. The suture can be traced, however, at

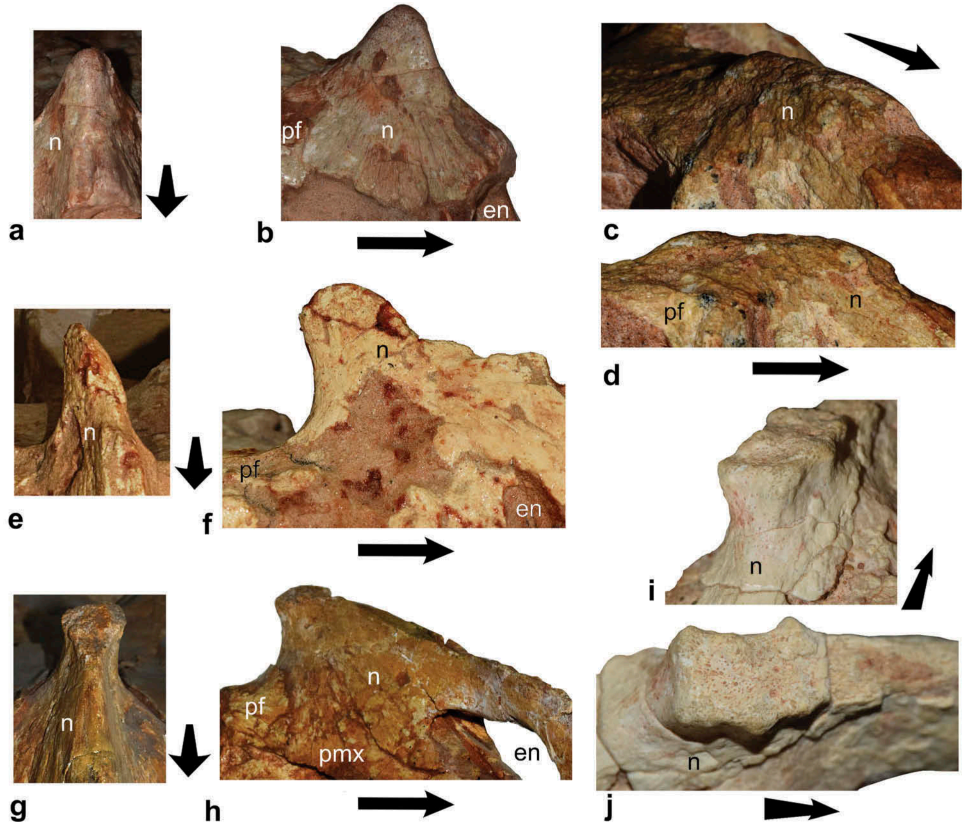

Figure 17. Nasal horncore morphology in *Bagaceratops rozhdestvenskyi*. ZPAL MgD-I/125 in rostral (a) and right lateral (b) views. ZPAL MgD-I/126 in right anterodorsal (c) and right lateral (d) views. PIN 3142/4 in rostral (e) and right lateral (f) views. IVPP V12513 in rostral (g) and right lateral (h) views. ZPAL MgD-I/135 in right caudolateral (i) and dorsal (j) views. Arrows are indicating rostral direction. Not to scale.

the cross section of the anterior portion of nasals. Dorsal portion of the nasal forms a narrow elevation and two small tubercles are present at both sides of the dorsocaudal premaxillae processes. Dorsal surface of the nasal cavity is folded, lowering ventrally along the intranasal suture, same is seen in ZPAL MgD-I/125.

The parietosquamosal frill and the parietal fenestration are known to vary within *P. andrewsi* (Handa et al. 2012). Although the examined specimens have no well-preserved frill region, their variation is similar to that observed in *Bag. rozhdestvenskyi*, i.e. with relatively greater fenestration in a medium-sized MPC-D 100/506 than in larger MPC-D 100/535 and PIN 3142/5.

Distribution of Protoceratopsidae in Central Asia

Two localities, Hermiin Tsav and Khulsan yielded reach protoceratopsid material from the Campanian Baruungoyot Formation (Jerzykiewicz 2000). Among the 57 specimens collected from Hermiin Tsav, 33 exhibit diagnostic aspects and can be assigned to *Bagaceratops rozhdestvenskyi* (Table 1). Only one specimen, ZPAL MgD-I/139a, has a plesiomorphic anatomy and should be regarded as Protoceratopsidae indet. or cf. *Breviceratops* sp. Ten protoceratopsid specimens were reported from Khulsan, six of them are determinable at the species level, including four specimens of *Bag. rozhdestvenskyi* and two specimens of *Br. kozlowskii* (Table 1).

Protoceratopsid remains are extremely abundant in the rocks of the Djadokhta Formation, also Campanian in age, but probably older than Baruungoyot (Gradziński et al. 1977; Jerzykiewicz et al. 1993; Dashzeveg et al. 2005). More than 130 specimens were collected from Bayan Zag and at least 60 from Tögrögiin Shiree. *Protoceratops andrewsi* is the only recognisable species there. A few postcranial specimens coming from these localities (PIN 614/29, 34, 53 and PIN 3143/11) were referred to *Bagaceratops* sp. (Tereschenko 2007, 2008; Tereschenko and Singer 2013). However, due to the incompleteness of the specimens, which are represented mostly by vertebrae, and due to the huge intraspecific variation in the postcranial anatomy of *P. andrewsi* (Makovicky and Norell 2006), the material cannot be precisely identified and should be considered as Protoceratopsidae indet. Similar is the case of the isolated vertebrae PIN 4550/3 from Gilbent Uul (Gilbentu), assigned to *Bagaceratops* sp. (Tereschenko 2007).

Nine protoceratopsid specimens were collected from the rocks in Üüden Sair (Handa et al. 2012), that may be younger than the Djadokhta Formation (Jerzykiewicz and Russell 1991; Rougier et al. 2016). Three of them can be undoubtedly assigned to *P. andrewsi* (MPC-D 100/537, 538, 551). One specimen (MPC-D 100/539) lacks a premaxillary dentition. The fairly complete skull and skeleton MPC-D 100/551 was erroneously referred to *Bag. rozhdestvenskyi* (as GI SPS 100/588 in Varriale 2011 and 100/528 in Nabavizadeh and Weishampel 2016), although the presence of the premaxillary dentition and the paired nasals clearly reveal its identity as *P. andrewsi*. One uncatalogued medium-sized skull and skeleton with the field number 000720 US was preliminarily described as *Bag. rozhdestvenskyi* (Watabe and Tsogtbaatar 2004). Although the specimen is fairly complete, most of the diagnostic features are ambiguous. The condition of the nasals is unknown, although the field report states that it had a horn-like projection reaching frontals (Watabe and Tsogtbaatar 2004). Unfortunately, the projection was no longer present in the specimen during my visit to MPC (Ulaanbaatar) in October 2016 and it is recorded only at several photographs taken until the damage was done (L. Panzarin, pers. comm.). It has a well-developed frontoparietal depression. The buccal crest of the dentary is nearly V-shaped in the cross section. Despite some similarities to *Bag. rozhdestvenskyi*, this may be in fact a specimen of *Protoceratops* sp. It requires, however, further study.

Protoceratopsid remains are very abundant in Ukhaa Tolgod (Dashzeveg et al. 1995; Gao and Norell 2000). The strata there were correlated with the Djadokhta Formation but may be slightly younger (Makovicky 2008). The rich material belongs possibly to a new, not yet described taxon (P. Makovicky & M. Norell pers. comm).

Bayan Mandahu locality strata were considered equivalents of the Djadokhta Formation (Jerzykiewicz et al. 1993), although sometimes are assigned to the distinct unit, Bayan Mandahu Formation (Longrich et al. 2010). Sixteen specimens of the protoceratopsid dinosaurs were described from there so far (Dong and Currie 1993; Lambert et al. 2001; You and Dong 2003; Sissons 2009; Hone et al. 2010). At least 12 other, uncatalogued protoceratopsid specimens were collected there and are housed at RBINS, IMM and IVPP (P. Currie & D. Hone, pers. comm.). Most of the diagnostic material belongs to *P. hellenikorhinus* and only one (IVPP V12513) can be referred to *Bag. rozhdestvenskyi*.

One embryonic specimen from Bayan Mandahu, IVPP V10604 was referred to *Bagaceratops* (Dong and Currie 1993). It, possesses a premaxillary dentition and a fairly well-developed accessory antorbital fenestra, similarly to *Br. kozlowskii* and some specimens of *P. andrewsi*. IVPP V16281, referred to *Bag. rozhdestvenskyi* (Sissons 2009), has paired nasals and plausibly belongs to *P. hellenikorhinus*. The material was not found in IVPP collection during my visit in November 2016. No undoubted specimens of *P. andrewsi* were collected from Bayan Mandahu (Supplementary Information).

A protoceratopsid material from Alxa, Inner Mongolia belonging to *Protoceratops* sp. was reported recently (Ji et al. 2017). It has no premaxillary dentition (Ji Shu'an pers. comm.) that suggests some similarities to *P. hellenikorhinus* from Bayan Mandahu.

Evolution of the Protoceratopsidae

Bagaceratops rozhdestvenskyi exhibits many derived features and is known from the Baruungoyot and Bayan Mandahu Formations, where it co-occurs with, respectively, *Breviceratops kozlowskii* and *Protoceratops hellenikorhinus*. Plesiomorphic in anatomy, *P. andrewsi* occurs only in the Djadokhta Formation, where it is the only protoceratopsid taxon (Table 2). It seems very plausible, and congruent with the earlier stratigraphic implications (based on faunistic comparisons), that sediments with *P. andrewsi* are older than those with the other members of the Protoceratopsidae.

Distribution of the apomorphic features is mosaic in protoceratopsids (presence of the accessory antorbital fenestration in *Bag. rozhdestvenskyi* and *Br. kozlowskii*, lack of the premaxillary dentition in *Bag. rozhdestvenskyi* and *P. hellenikorhinus*). Some of the derived features are also occasionally seen in *P. andrewsi* (lack of premaxillary teeth in AMNH 6431, loosening at the premaxillo-maxillary suture in AMNH 6408). Shift in the intraspecific variation of *P. andrewsi* collected from different localities is observed in the number of maxillary teeth (Figure 12). It is the highest in the specimens coming from Bayan Zag (up to 15 maxillary alveoli in AMNH 6466), and relatively lower in individuals from Tögrögiin Shiree (up to 12) and Üüden Sair (up to 10, although no specimens of the 'large size class' were collected from there). A similar pattern is seen in the elongation of the maxillary diastema (mean ratio of the maxilla diastema to the teeth row length; Figure 14). It is lowest in the individuals from Bayan Zag (0.25) and higher in Tögrögiin Shiree (0.28) and Üüden Sair (0.30).

In all recent phylogenetic analyses, *Protoceratops* and *Bagaceratops* are sister taxa (Morschhauser 2012; Sampson et al. 2013; Farke et al. 2014; Zheng et al. 2015). Given that. I suggest that the most parsimonious evolutionary scenario is the ancestry of *P. andrewsi* in relation to the other protoceratopsid species (Figure 18). It is possible that specimens of *P. andrewsi* from different localities represent successive episodes in the phyletic evolution (anagenesis) within one lineage or even population. Localities with *P. andrewsi* record in the Ömnögovi area are placed very close to each other (Figure 1) and are unlikely to be isolated by any topographic barriers in the desert environment that would prevent hybridisation of the co-occurring populations.

The derived feature of the edentulous premaxilla is seen in *Bag. rozhdestvenskyi* and *P. hellenikorhinus*. It is possible, that the reduction of the premaxillary teeth took place independently in *Bag. rozhdestvenskyi* and *P. hellenikorhinus*, as it convergently evolved also in other ceratopsian lineages. *Bag. rozhdestvenskyi* and *Br. kozlowskii* share the derived feature of the accessory antorbital fenestration, that is present also in some ceratopsoid dinosaurs (Figure 20). In *P. andrewsi*, there is some variation in the loosening of the premaxillo-maxillary suture, however no single specimen from the Djadokhta Formation has fully developed accessory antorbital fenestra.

A recent study on cranial musculature in Ornithischia (Nabavizadeh 2018) suggests lack of the 'cheek' muscles and enhances the meaning of the buccal crest of the dentary as the attachment site for the *M. adductor mandibulae externus superficialis*. If true, it may suggest that the various development of the buccal crest in Protoceratopsidae is related with the increase in size of the attachment site for that muscle (and would suggest relatively greater jaw strength in *Bag. rozhdestvenskyi*).

Convergences between Protoceratopsidae and Ceratopsoidea

Although the Protoceratopsidae and Ceratopsoidea differ in the overall morphology, with the latter group reaching greater

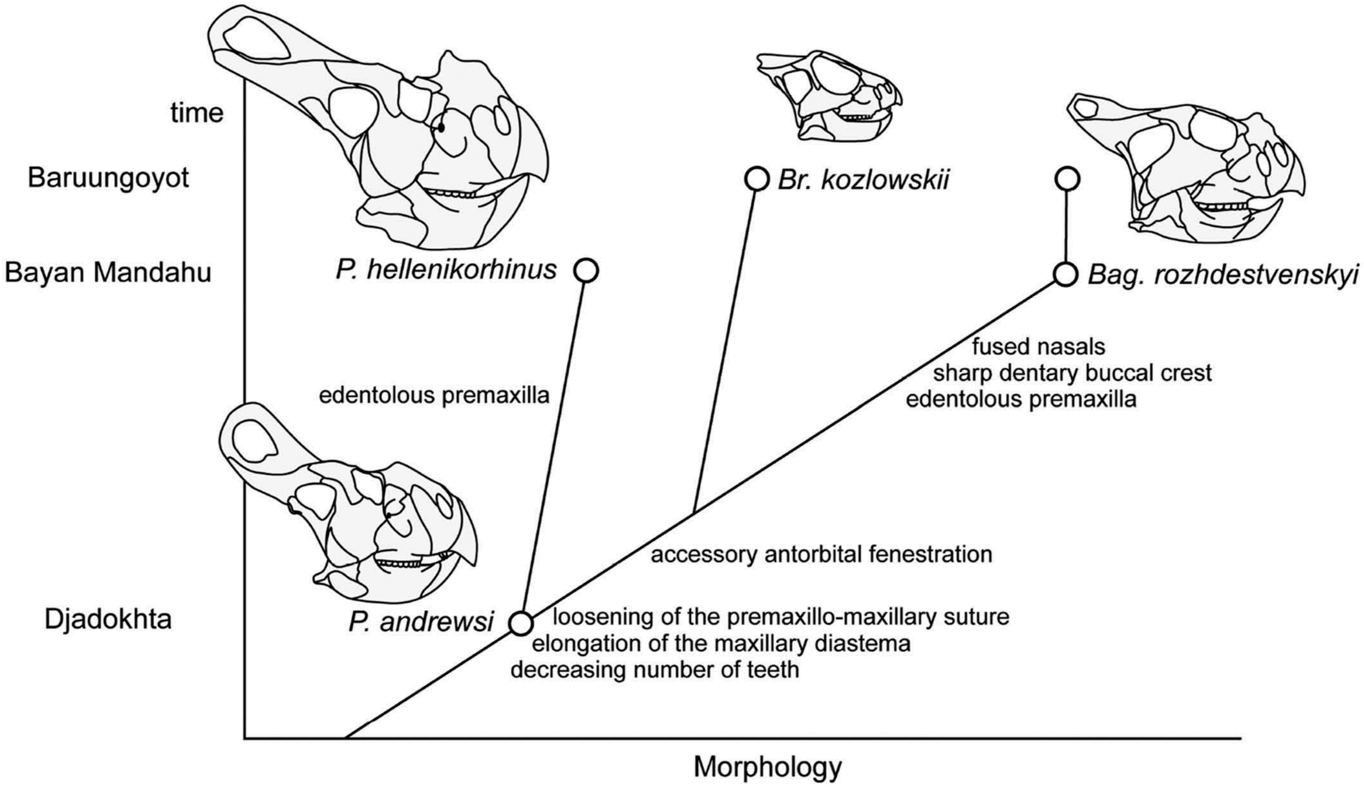

Figure 18. Hypothetical phylogenetic relationships among members of Protoceratopsidae basing on the mosaic distribution of the apomorphic features and distribution of each of species within the geological formations.

size of the skull and increasing number of teeth, some anatomical aspects of these two lineages seem to be convergent (Figure 19). Features discussed below may be tested in future with new material and additional analyses. It, however, reaches beyond the framework of this study.

The nasal horncore is present in both Protoceratopsidae and Ceratopsidae, but not in the basal ceratopsoid *Zuniceratops christopheri* that has a plesiomorphic condition of unfused and unadorned nasals (Wolfe et al. 2010). Among the protoceratopsid dinosaurs, only *Bag. rozhdestvenskyi* has fused nasals, even in the earliest stages of its ontogeny. Among the Ceratopsidae, nasals are known to fuse rather late in the ontogeny of Centrosaurinae (McDonald 2011) and Chasmosaurinae (Horner and Goodwin 2008), however, the smallest specimen of *Chasmosaurus belli* have already entirely fused nasals (Currie et al. 2016). Additionally, in chasmosaurines a novel ossification, the epinasal, developed that fused to the nasal later in ontogeny (Horner and Goodwin 2008).

The presence of the three canine-like premaxillary teeth is a primitive condition for the Marginocephalia, present in basal ceratopsian *Yinlong downsi* (Xu et al. 2006) and some basal Neoceratopsia (*Liaoceratops yanzigouensis, Archaeoceratops* spp., *Aquilops americanus, Auroraceratops rugosus*; Tanoue et al. 2009; Morschhauser 2012; Farke et al. 2014). There are two premaxillary teeth in *Chaoyangsaurus youngi* (Zhao et al. 1999) and at least one in *Xuanhuaceratops niei* (Zhao et al. 2006). Basal leptoceratopsid *Cerasinops hodgskissi* and protoceratopsids *Protoceratops andrewsi* and *Breviceratops kozlowskii* clearly have two teeth on the premaxilla (Brown and Schlaikjer 1940; Maryańska and Osmólska 1975; Chinnery and Horner 2007). All the Psittacosauridae, the neoceratopsian *Mosaiceratops azumai*, more derived Leptoceratopsidae (*Prenoceratops pieganensis, Montanoceratops cerorhynchos, Leptoceratops gracilis, Udanoceratops tschizhovi*), derived Protoceratopsidae (*Bagaceratops rozhdestvenskyi, Protoceratops hellenikorhinus*), and all the Ceratopsoidea (including *Zuniceratops christopheri*) have edentulous premaxillae (Sternberg 1951; Maryańska and Osmólska 1975; Kurzanov 1992; Lambert et al. 2001; Chinnery 2004; Makovicky 2010; Sereno 2010; Wolfe et al. 2010; Zheng et al. 2015).

However, in a few specimens of *Protoceratops andrewsi*, premaxillary dentition cannot be traced, i.e. AMNH 6431, 6434 from Bayan Zag and MPC-D 100/539 from Üüden Sair (Handa et al. 2012). It may not be a cause of the poor preservation of the fossils, as both in AMNH 6431 and 6434 the ventral margin of at least one premaxilla seems to be preserved, with no bulges for alveoli able to trace at their lateroventral surface. Among the Protoceratopsidae,

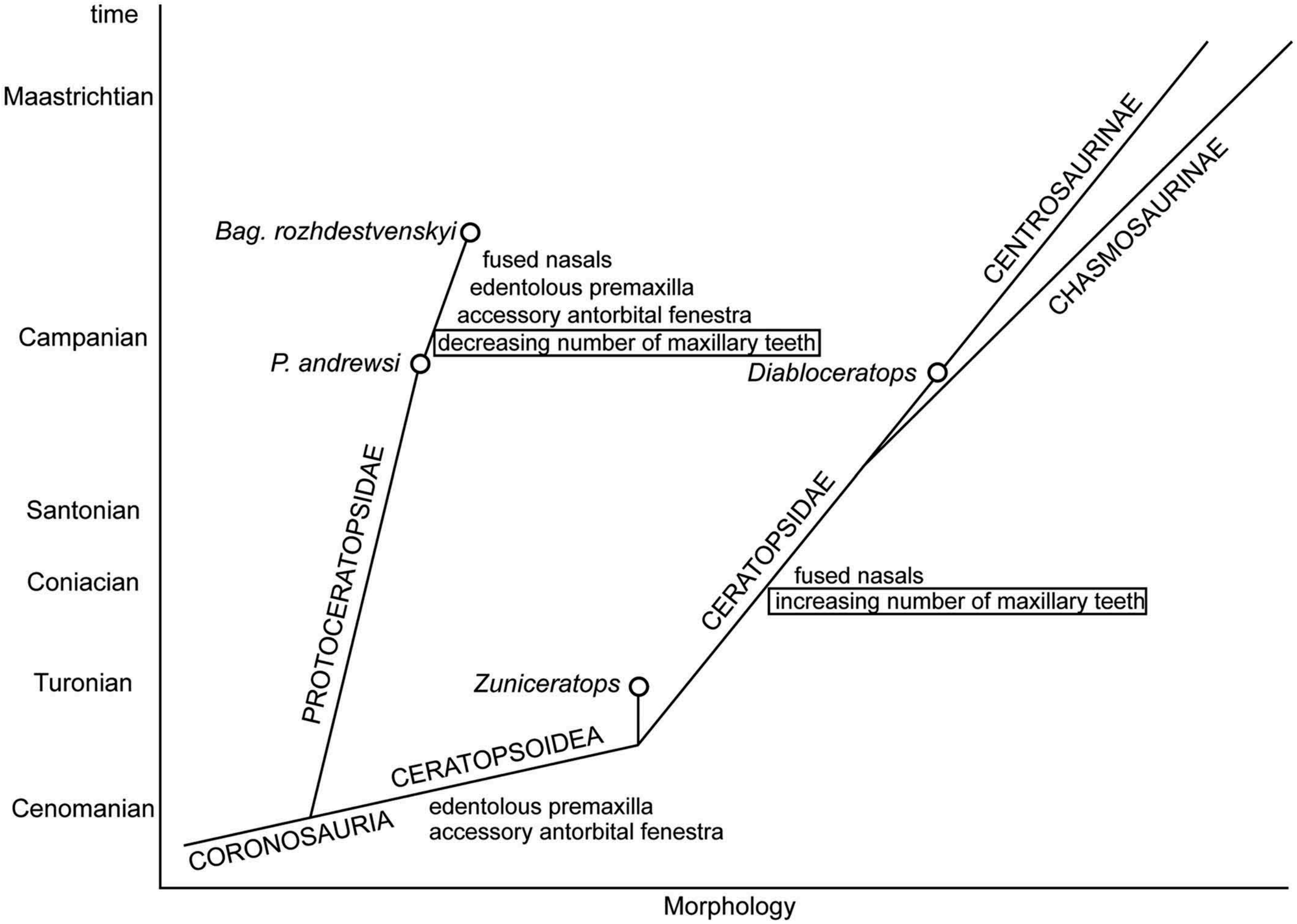

Figure 19. Distribution of the derived features among Coronosauria. Listed are convergences occurring in evolution of protoceratopsid and ceratopsoid dinosaurs, as well different trends in count of maxillary teeth (decreasing in protoceratopsid lineage and increasing in ceratopsid lineage).

loss of the premaxillary dentition may be connected with the elongation of the diastema. All species without premaxillary teeth (*Bag. rozhdestvenskyi, P. hellenikorhinus*) have the teeth row relatively shorter and the number of the maxillary teeth lower than *P. andrewsi* (Fig. 12, 14). A plausible explanation for the reduction of the premaxillary teeth is that the caudally projecting rostral bone has covered nearly whole ventral margin of the premaxilla, as seen in some *Bagaceratops* specimens (e.g., IVPP V12513).

The accessory antorbital fenestra (='additional antorbital fenestra' *sensu* Maryańska and Osmólska 1975; ='subnarial fenestra' *sensu* Alifanov 2003) is an opening perforating the premaxillo-maxillary suture at the dorsal portion, in the area of the contact with the ventral portion of the nasal (Figure 20). Such fenestra opens to the nasal cavity and is visible in the lateral view. It should be noted that it is not a structure homologous to the accessory/additional antorbital fenestra (maxillary fenestra) of theropod dinosaurs (Holtz and Brett-Surman 2012). Judging from its placement, the perforation might be related to biomechanical aspects of the feeding apparatus or might have provided the space for a soft tissue of unknown nature.

Loosening of the premaxillo-maxillary suture developed in a few lineages of the neoceratopsian dinosaurs. It is present in nearly all members of the Protoceratopsidae, and in some Ceratopsoidea. Among protoceratopsids, a well-pronounced accessory antorbital fenestra is seen only in *Bag. rozhdestvenskyi* with a dorsal contribution of the nasals (Figure 20A), and in *Br. kozlowskii*.

In many specimens of *Protoceratops andrewsi,* the area of the contact between the premaxilla and maxilla is difficult to trace because bones are very thin in this region and easily break. Some traces of the loosening of the premaxillo-maxillary suture can be seen in a number of specimens, even in the holotype (AMNH 6251). It may take the form of a gap between the caudodorsal rami of premaxilla and the anterior rami of maxilla, especially in the dorsal portion of the suture, near the contact with the nasal bone, however without the contact with the latter one (AMNH 6251, 6408). Sometimes it is only visible at the one side of the skull (AMNH 6431). Loosening at the suture may also be further developed and reach the nasals, but without any impact on the shape of the premaxilla and maxilla (e.g., MPC-D 100/519, Figure 20(b)). Even though, most of the specimens have no trace of the loosening. In some specimens lacking the additional fenestration, the shallow vertical depression is present along the premaxillo-maxillary suture (AMNH 6414, 6429, 6439).

P. hellenikorhinus seems to lack any fenestration or loosening at the premaxillo-maxillary suture; however, determination of the condition is difficult due to the weathered surface of the bone in most specimens. In *Br. kozlowskii* (ZPAL MgD-I/116, 117) there is a wide separation between the premaxilla and maxilla along the premaxillomaxillary suture. It is narrower than the fenestration seen in the specimens of *Bag. rozhdestvenskyi* similar in size. The caudal margin is not pronounced, being relatively straight (resembling natural, unfenestrated suture), however, the rostral margin conforms to the arched shape of the premaxilla (Figure 4(i,l)). Contribution of the nasal bones to this fenestra remains unknown.

In the basal ceratopsoid *Zuniceratops christopheri* the fenestra was two to three times smaller than the external nares. The nasal contributes extensively to the dorsal margin (Figure 20(c)). Among the Centrosaurinae, the accessory antorbital fenestration is well developed only in the basal centrosaurines *Diabloceratops eatoni* (Figure 20(d)) and *Sinoceratops zhuchengensis* (Xu et al. 2010). In the Chasmosaurinae the accessory antorbital fenestra is variably present among each of species. In the smallest described specimen of *Chasmosaurus* cf. *belli* (UALVP 52613, Currie

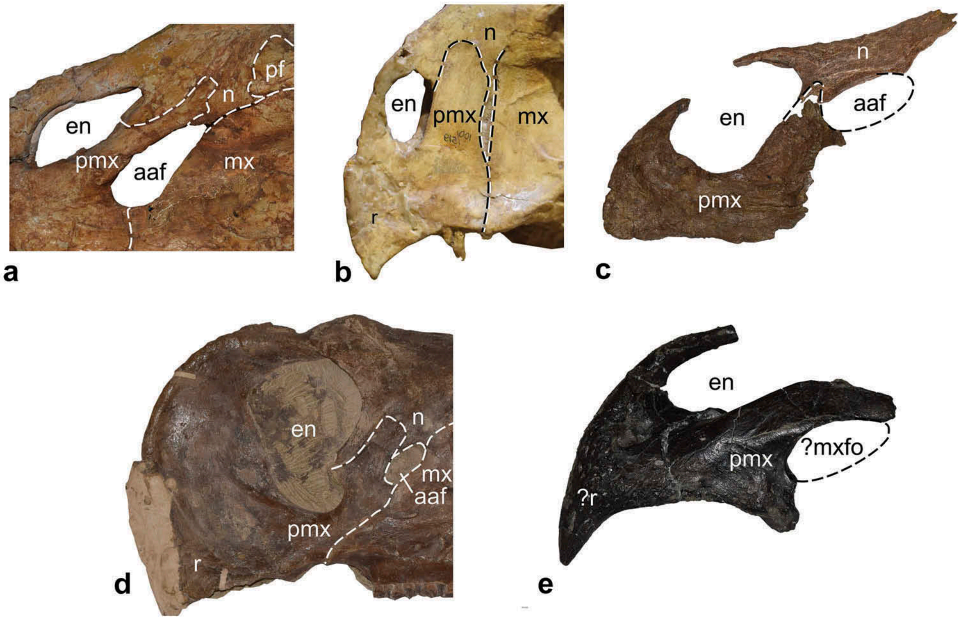

Figure 20. Premaxillo-maxillary suture in ceratopsian dinosaurs in lateral left view. (a) *Bagaceratops rozhdestvenskyi* IVPP V12513. (b) Premaxillo-maxillary loosening in *Protoceratops andrewsi* MPC-D 100/519 (mirrored). (c) *Zuniceratops christopheri* MSM P2225 (left premaxilla) and MSM P3197 (left nasal). (d) *Diabloceratops eatoni* UMNH 16699. (E) Premaxillo-maxillary fenestra (?anterior maxillary fossa) in *Ajkaceratops kozmai* MTM V2009.192.1. Not to scale.

et al. 2016), it forms a comma-shaped split between the dorsal-most portion of the dorsal projection of the premaxilla and maxilla. Fenestration is seen only in several larger specimens of the genus (*Chasmosaurus* sp. AMNH 5401, *Ch. russelli* CMN 8800; Campbell 2014), in *Pentaceratops sternbergii* (AMNH 1624, Lehman 1993; AMNH, p. 6325), *Agujaceratops mariscalensis* and in the holotype specimens of *Kosmoceratops richardsoni* and *Utahceratops gettyi* (Sampson et al. 2010; Lehman et al. 2017). Dorsal margin of the accessory antorbital fenestra is formed by the ventral projection of the nasal bone.

The enigmatic *Ajkaceratops kozmai* from the Late Cretaceous of Hungary, originally described as a ceratopsian (Ősi et al. 2010), has a fenestra at the suture between the premaxilla and the maxilla (Figure 20(e)). This fenestra was originally thought to be homologous with the accessory antorbital fenestration of *Bag. rozhdestvenskyi*. Unlike the ceratopsians, the nasal in *Ajkaceratops* seems to be completely excluded from the margin of the fenestration. The ascending process of the premaxilla expands laterally, causing the dorsal margin of the fenestration to lie significantly further laterally from the longitudinal axis of the skull than the external nares.

Similar condition characterises the basal neornithischian dinosaur *Thescelosaurus neglectus* NCSM 15738, where the ascending process of the premaxilla is bounding the anterior maxillary fossa (Boyd 2014). Thus, the presence of the opening seen in *Ajkaceratops* may not prejudge its close affinities with *Bagaceratops*, seen in some recent phylogenetic analyses (Farke et al. 2014). Ceratopsian affinities of *Ajkaceratops* were questioned (Makovicky 2012), although recent reports suggest the presence of the ceratopsian material in the Csehbánya Formation, where *Ajkaceratops* material was found (Virág and Ősi 2017).

Conclusions

Ceratopsian material collected from the Gobi Desert enables determination of the intraspecific and ontogenetic variation in the morphology of the skull of *Bagaceratops rozhdestvenskyi*. The recently erected taxa, *Lamaceratops tereschenkoi, Platyceratops tatarinovi, Gobiceratops minutus* from the Baruungoyot Formation and *Magnirostris dodsoni* from the Bayan Mandahu Formation have all the autapomorphic features seen in *Bag. rozhdestvenskyi*. Given the lack of any distinct characters for each of these purportedly distinct species, I propose to regard them as junior synonyms of *Bag. rozhdestvenskyi*. This expands the geographic and stratigraphic distribution of *Bagaceratops* to the Bayan Mandahu Formation, Inner Mongolia. Morphology of the nasal horncore in *Bag. rozhdestvenskyi* may be an expression of the sexual dimorphism, however its intraspecific variation further complicates the picture.

The plesiomorphic anatomy and the stratigraphic distribution of *Protoceratops andrewsi* suggest that it was more primitive than *Bag. rozhdestvenskyi*. Given its position in the recent phylogenetic studies, it may be ancestral for *Bag. rozhdestvenskyi* and, plausibly, other protoceratopsid dinosaurs. The main changes in the evolution of Protoceratopsidae was connected with the transformation of the feeding apparatus. The evolution of the protoceratopsid dinosaurs was mosaic, and the undoubted recognition of each of their species requires a diagnostic, well-preserved cranial material. Determination of the taxonomic identity of the isolated postcranial material of early neoceratopsians at the specific and generic levels is difficult and should be avoided prior to proper osteological description and recognition of the postcranial intraspecific variation.

Several anatomic features evolved independently in Protoceratopsidae and Ceratopsoidea, including the reduction of the premaxillary dentition, the fusion of the nasals and the development of the accessory antorbital fenestra. Such fenestration has a wider distribution within the Coronosauria than it was originally thought. Its function, however, remains unknown.

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