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Bainoceratops efremovi, a New Protoceratopid Dinosaur (Protoceratopidae, Neoceratopsia) from the Bain-Dzak Locality (South Mongolia)

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Abstract—A new horned dinosaur, *Bainoceratops efremovi* gen. et sp. nov., is described on the basis of vertebral series from the well-known Bain-Dzak locality (Mongolia). The new form is distinguished from *Protoceratops andrewsi* Granger et Gregory, 1923, which is typical of Djadokhta deposits, by vertebral morphology and shows close relationships to *Udanoceratops tschizhovi* Kurzanov, 1992 and *Leptoceratops gracilis* Brown, 1914 in the following characters. The cranial surfaces of the centra of the presacral vertebrae are concave, while the caudal surfaces are flat. The diapophyses of the ninth dorsal vertebra are round in cross section, and the interprezygapophyseal spaces in this and the next vertebra are narrow. The synapophyseal facets of the posteriormost dorsal vertebra are sculptured.

Key words: New Protoceratopid, Neoceratopsia, South Mongolia, Upper Cretaceous.

INTRODUCTION

During the revision of collections of the Mongolian Paleontological Expedition of the Academy of Sciences of the USSR from the well-known Bain-Dzak locality (South Gobi, Mongolia) dated to the Upper Cretaceous (Djadokhta), a vertebral series from one and the same vertebral column (PIN, no. 614-33) attracted our attention. These vertebrae have been tentatively attributed to *Protoceratops andrewsi* Granger et Gregory, 1923, the only known abundant species of horned dinosaurs from Central Asia. However, a cursory inspection revealed some peculiar features and stimulated verification of the previous attribution. With this aim in view, all the available specimens of the mentioned species from the collections of the Mongolian Paleontological Expedition of the Academy of Sciences of the USSR (1946–1949) and the Joint Soviet–Mongolian Paleontological Expedition (from 1969 till now) were studied.

MATERIALS AND METHODS

The following abbreviations of institutions are used in the present study: (NMC) National Museum of Canada and (PIN) Paleontological Institute of the Russian Academy of Sciences.

The following specimens were involved in the study: (PIN, no. 614-30) anterior part of the vertebral column, (PIN, no. 614-31) middle dorsal and sacral vertebrae, (PIN, no. 614-32) caudal region, (PIN, no. 614-35) posterior cervical and dorsal vertebrae, and (PIN, no. 614-61) anterior dorsal vertebrae from the Bain-Dzak locality. In addition, PIN, nos. 3143-4, 3143-5, 3143-7, 3143-9 (skeletons), 3143-12 (posterior dorsal, sacral, and anterior caudal vertebrae), and 3143-16 (dorsal, sacral, and anterior caudal vertebrae) from the Tugrikiin-Shire locality were examined. The following material on cf. *Bagaceratops* sp. was used for comparison: (PIN, no. 3143-11) caudal vertebrae 5-20; (PIN, no. 614-29) vertebrae column without cervical vertebrae 1–4, sacral 3–6, and caudal vertebrae 2-?10, ?15, and subsequent posterior vertebrae; (PIN, no. 614-34) neural arch of cervical vertebra 5, dorsal vertebrae 1 and 3–7, centra of sacral 1-7 and caudal 1 vertebrae, and caudal vertebrae 2, 3, and ?10; (PIN, no. 614-53) sacral region of the vertebral column and caudal vertebrae 1-7 (or 8) and several from the middle caudal region; (PIN, no. 614-62) two posterior dorsal vertebrae; and (PIN, no. 4550-3) from the first cervical to the ninth dorsal vertebrae; all specimens come from Gilbentu-2 located 7 km southeast of the Gilbentu locality (Efremov, 1962); (PIN, no. 3907-11) *Udanoceratops tschizhovi*, skeleton, Udan-Sair locality (Kurzanov, 1992); and *Leptoceratops gracilis*, cast of skeleton NMC, no. 8887 (Brown, 1914) housed at the PIN. Published data were analyzed as well (Brown, 1914; Brown and Schlaikjer, 1940, 1942; Sternberg, 1951; Chinnery and Weishampel, 1998; etc.).

During the study of specimen PIN, no. 614-33, we considered the possibility of displaying the intraspecific variability characteristic of protoceratopsids (Brown and Schlaikjer, 1940; Rozhdestvenskii, 1965; Kurzanov, 1972; Maryanska and Osmólska, 1975;

Dodson, 1976), including age-related variations (Brown and Schlaikjer, 1940; Sternberg, 1951; Chinnery and Weishampel, 1998; Tereschenko, 2001) and sexual dimorphism, well-known for the axial skeleton of terrestrial tetrapods (Barbadillo and Sanz, 1983; Porkert and Grosseova, 1984; Tereschenko, 1991a, 1997, 2001). Because the discussed specimen differs appreciably from *Protoceratops andrewsi* and other protoceratopids with known postcranial morphology, it is described as a new genus and species, *Bainoceratops efremovi* gen. et sp. nov.

For morphological description of vertebrae we adopted the nomenclature used by Osborn and Mook (1921), Hoffstetter and Gasc (1969), Baumel and Witmer (1993), and Wilson (1999). The identification of vertebral serial numbers was made using a guide compiled on the basis of the entire studied material. The numbers in the text and figures denote serial numbers of vertebrae in the following regions of the vertebral column: (cv) cervical, (th) thoracic or dorsal, (sc) sacral, and (cd) caudal vertebrae.

SYSTEMATIC PALEONTOLOGY

Family Protoceratopidae Granger et Gregory, 1923

Genus *Bainoceratops* Tereschenko et Alifanov, gen. nov.

E t y m o l o g y. After the Bain-Dzak locality and the generic name *Ceratops*.

T y p e s p e c i e s. *Bainoceratops efremovi* sp. nov.

D i a g n o s i s. Medium-sized protoceratopid. Body up to 2.5 m. long. Centra of presacral vertebrae short, of medium depth. Their cranial surface moderately concave and caudal surface flat. Ventral crest of cv 6 and 7 well-pronounced, thick, oval in cross section, extending beyond cranial edge of centrum. Parapophyseal facet of these vertebrae oriented dorsolaterally. Diapophyses of cv 7 with narrow bases and oriented dorsolaterally at an angle of 40° to horizontal plane. Prezygapophyseal facet of this vertebra projecting for approximately one-third of its length and extending laterocranially at 80° to longitudinal axis of vertebra. Ventral crest on corpus of cv 9 absent.

Prezygapophyses of th 9 and 10 drawn together, two infraparapophyseal crests present. In th 9, lateral edge of prezygapophyseal facet curved inward, short and round in cross section diapophyses inclining caudolaterally at about 35° to longitudinal vertebral axis. Posteriormost th (?13) with centrum extended dorsoventrally, short prezygapophyses with facets oriented in transverse plane at angle less than 20° to horizontal, and small process on spinopostzygapophyseal crest above postzygapophyseal facet; synapophyses relatively short and projecting laterally; their facetclearly outlined, extended, and inclined at about 45°; crest extending across middle of long axis of synapophyseal present facet; postzygapophyseal crest poorly pronounced; caudosynapophyseal crest short; and neurapophysis positioned at more than 90° to vertebral centrum.

In posteriormost sacral vertebra, transverse processes projecting laterally, their bases round in cross section; zygapophyses widely spaced and postprezygapophyseal crest weakly pronounced; prezygapophyseal facet concave; and prespinal crest passing onto neural arch an level with dorsal surface of postzygapophyses and midlength of vertebral centrum.

In first two or three caudal vertebrae, base of spinous process approximately half as long as vertebral centrum; cranial vertebral incisure smaller than caudal incirsure; and postzygapophyses not contacting each other ventrally. In cd 1, transverse processes projecting laterocaudally, and prespinal crest wedging in between relatively poorly pronounced spinoprezygapophyseal crests. In cd 2, spinous process inclined caudally at angle less than 60° to horizontal and transverse processes projecting caudolaterally at about 70°. In cd ?10–11 and cd ?18–19, facets for connection with haemapophyses (chevron bones) notably concave. Cranial and caudal surfaces of cd ?18–19 centra flat, their prezygapophyses positioned at angle about 20° to horizontal.

C o m p o s i t i o n. Type species.

C o m p a r i s o n. The genus *Bainoceratops* differs from all other representatives of the family Protoceratopidae by the extension of the ventral crest beyond the anterior profile of the centrum of cv 6 and 7; the absence of ventral crest in cv 9; the inward curvature of the lateral edge of the prezygapophyses of th 9; the presence of two well-developed infraparapophyseal crests on th 9 and 10; the strongly inclined long axis of the facet of the synapophysis of the posteriormost dorsal vertebra, the presence of a small process on the spinopostzygapophyseal crests close to the facet of the postzygapophysis, of this vertebra the presence of the caudosynapophyseal crest, and the inclination of its neurapophysis to the centrum at the greatest angle; weakly developed postprezygapophyseal crest; a more caudal position of the transition of the prespinal crest onto the neural arch and lateral orientation of transverse processes of the posterior sacral vertebra; the weakly developed spinoprezygapophyseal crest and laterocaudally oriented transverse processes of cd 1; the greatest caudal inclination of the spinous process and the caudolateral orientation of the transverse processes at an angle of approximately 70° on cd2; and the least dorsocranial orientation of the prezygapophyses of cd ?18–19.

In addition, the new genus differs from *Leptoceratops* by the shorter diapophyses and the same dimensions of their facet as those of the parapophysis on th 9; the vertically elongated caudal surface of the centrum and the ventrocaudal orientation of the long axis of the synapophyseal facet of the posterior dorsal vertebra; and the deep fossae for connection with the haemapophyses of the centra of cd ?10–11 and cd ?18–19.

Unlike *Udanoceratops*, the presacral vertebrae of the new genus have longer and deeper centra with less concave cranial and caudal surfaces. The centra of cv 6 and 7 have wide ventral crests. The prezygapophyseal facet of cv 7 is inclined laterocranially. In th 9, the lateral edge of the prezygapophyseal facet is more strongly curved, and the laterocaudal orientation of the diapophyses relative to the longitudinal vertebral axis is less pronounced. In the posteriormost dorsal vertebra, the centrum is extended dorsoventrally, the prezygapophyses are turned to a greater extent, the synapophyses project laterally, the postsynapophyseal crest is developed, the synapophyseal facet is more elongated and has a median crest and a weakly indented edge. In the posteriormost sacral vertebra, the postprezygapophyseal crest is poorly pronounced. The base of the spinous process of cd 1–2 (3) is craniocaudally shorter. The spinoprezygapophyseal crest in cd 1 is weakly developed; and the transverse processes of cd 2 are more inclined caudally.

The new genus differs from *Protoceratops* by the short centra of the presacral vertebrae with a flat caudal surface; the parapophyseal facet of cv 6 and 7 is oriented more caudally; the diapophyses of cv 7 have narrower bases and a different angle of inclination; and the prezygapophyseal facet of cv 7 is elongated and only slightly projects. In th 9, the interprezygapophyseal distance is small, the lateral edge of the prezygapophyseal facet is curved, and the round diapophyses are less inclined caudolaterally. In th 9 and 10, the prezygapophyses are drawn together. The posteriormost dorsal vertebra has a centrum dorsoventrally elongated, the articular surfaces of the prezygapophyses are short and oriented almost horizontally, the postsynapophyseal crest is poorly pronounced and short, and the synapophyses only slightly project and their facets are elongated, rough, and have the median crest. In the posteriormost sacral vertebra, the zygapophyses are widely spaced, the spinoprezygapophyseal crest is absent, and the prezygapophyseal facet is with more concave and rounded. In cd 1, the spinoprezygapophyseal crests are weaker and the prespinal crest wedges in between them. The base of the spinous process in cd 1-2 (3) is shorter craniocaudally. In the anterior caudal vertebrae, the caudal vertebral incisure is larger than the cranial incisure, and the facets of the postzygapophyses are disjunct. The transverse processes of cd 2 are more inclined caudally. The articular surfaces for the chevrons are concave in cd ?10–11 and cd ?18–19.

The new genus differs from cf. *Bagaceratops* sp. found in the Gilbentu-2 locality by the short and comparatively low centra of the presacral vertebrae with flat caudal surfaces. The parapophyseal facet in cv 6 is turned more caudally. In cv 7, the bases of the diapophyses are narrower, and the prezygapophyseal facets are elongated and only weakly projects. In th 9, the lateral edge of the prezygapophyseal facet is curved, and the diapophyses are more rounded and stronger inclined caudolaterally. In th 9 and 10, the interprezygapophyseal distance is small. In the posteriormost dorsal vertebra, the articular surfaces of the prezygapophyses are short and almost horizontal, the postsynapophyseal crest is shorter, and the facet of the weakly projecting synapophyses is extended, rough, and has a median crest. In the posteriormost sacral vertebra, the zygapophyses are widely spaced, the spinoprezygapophyseal crest is absent, and the facet of the prezygapophyses is more rounded. The prespinal crest is weakly developed in cd 1 but wedges deeper in between the prezygapophyses of the preceding vertebra. The postzygapophyseal facets of cd 2 and several subsequent vertebrae are more strongly separated from each other; the transverse processes of cd 2 are less inclined caudally. The articular surfaces for the haemapophyses are strongly concave in cd ?10–11 and cd ?18–19.

R e m a r k s. The vertebral morphology of *Bainoceratops* shows that it is more similar to *Leptoceratops* and *Udanoceratops* than to *Protoceratops* and cf. *Bagaceratops*. Unlike the latter two genera, it has short centra of the presacral vertebrae with concave cranial and flat caudal surfaces (in *Udanoceratops*, the cranial surface of the vertebral centra is concaved stronger than the caudal surface); the diapophyses of th 9 are almost circular in cross section; the interprezygapophyseal space in th 9–10 is narrow; and the synapophyseal facet of the posteriormost dorsal vertebra is sculptured.

In addition, the new genus displays similarity to *Leptoceratops* in the length, width, and depth of the presacral vertebral centra, having concave cranial and flat caudal surfaces, as well as in the less indented edge of the elongate synapophyseal facet, which has a median crest, and in a small angle of inclination of the prezygapophyseal facet to the horizontal in the posteriormost dorsal vertebra.

The new genus is similar to *Udanoceratops* in the weakly projecting prezygapophyses with transversally elongated facets in cv 7, the dorsal curvature of the lateral edge of the prezygapophyseal facets of th 9, only slightly projecting synapophyses of the posteriormost dorsal vertebra, widely spaced zygapophyses, inclination and transverse expansion of the prezygapophyseal facet in the posteriormost dorsal vertebra, extension of the prespinal crest between the spinoprezygapophyseal crests almost to the edge of the interzygapophyseal incisure in cd 1, wider disconnection of the inferior edges of the postzygapophyseal facets in the anterior caudal vertebrae, and deep concave articular surfaces for chevrons on the centra of cd ?10–11 and cd ?18–19.

Variations in relative length and depth of presacral vertebral centra are presented in Table 1.

Bainoceratops efremovi **Tereschenko et Alifanov, sp. nov.**

E t y m o l o g y. Named in honor of the paleontologist I.A. Efremov.

H o l o t y p e. PIN, no. 614-33; vertebrae: cv 6, 7, and 9; th ?1, ?5–7, and 9–13; sc 8; and cd 1–3, ?10–11, and ?18–19; Mongolia, southern Gobi, Bain-Dzak locality; Upper Cretaceous, Djadokhta Formation.

Table 1. Variation in relative length (*L*') and relative depth (*H*') of the vertebral centra within the presacral region of the vertebral column in some members of the family Protoceratopidae*

Species	*L*'	*H*'	Body length, m
Bainoceratops efremovi	0.6–0.9	0.9–1.2	2.5
Udanoceratops tschizhovi	0.5–0.7	0.7–1.1	4.0
Leptoceratops gracilis	0.6–0.9(?)	0.9–?	2.2
Protoceratops andrewsi	0.7–1.1	0.8–1.2	1.5–2.5
cf. *Bagaceratops* sp.	0.8–1.3	1.0–1.6	1.5–2.5

Notes: * The relative length (and depth) of the vertebral centrum are considered to be the ratio of absolute length (depth) to the cranial width of the same vertebra. If the ventral and dorsal surfaces of a vertebral centrum differ in length, the mean value is taken for the absolute length. The absolute depth is calculated as the mean between the cranial and caudal depths of the centrum.

Parameters *L*' and *H*' for ?cv 7 of *L. gracilis* are determined using a figure (Brown, 1914, text-fig. 8). The total length of animals was reconstructed on the basis of our materials and the data published by Sternberg (1951), taking into account the technique proposed earlier by Tereschenko (1990, 1991b).

Description (Figs. 1, 2). The majority of the vertebrae examined are satisfactorily preserved. Judging from the inconspicuous suture between the neural arch and the centrum of all presacral vertebrae, except for the posteriormost cervical and the first dorsal vertebrae, the vertebral column belongs to a mature individual.

Cervical region (Figs. 1a–1g)

The cervical vertebrae are distinguished by the positions of the parapophyses on the vertebral centrum and the diapophyses on the neural arch and the greater ventral length of the centra than the dorsal length, which is connected with the cervical ventral curvature (lordosis).

The sixth vertebra of the holotype is partially damaged. The ventral crest projects beyond the lower surface of the centrum for about one-quarter of its depth. The postparapophyseal depression is well developed and the postparapophyseal crest (syn. margo ventralis) is weak and disappears caudal to the midlength of the centrum. The supradiapophyseal crest merges with the lateral surface of the prezygapophyses approximately in the midlength of the facets. The infradiapophyseal crest extends ventrocaudally from the ventral surface of

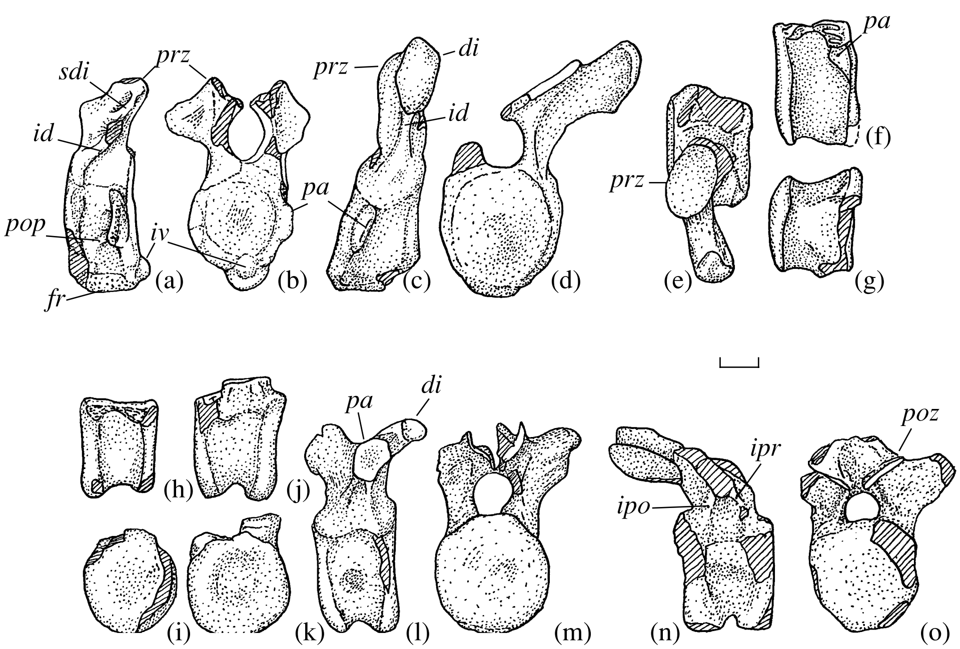

Fig. 1. *Bainoceratops efremovi* gen. et sp. nov., holotype PIN, no. 614-33; (a, b) cv 6, (c–e) cv 7, (f, g) cv 9, (h, i) th ?5, (j, k) th ?7, (l, m) th 9, and (n, o) th 10; (a, c, f, h, j, l, n) lateral view, (b, d, i, k, m) anterior view, (e) dorsal view, (g) ventral view, (o) rear view, (a, f, h, n) right lateral view, and (c, l) left lateral view. Designations: (*di*) diapophyses, (*fr*) ventral crest of vertebral centrum, (*id*) infradiapophyseal crest, (*ipo*) infrapostparapophyseal crest, (*ipr*) infrapreparapophyseal crest, (*iv*) internal extraarticular ankylosis, (*pa*) parapophysis, (*pop*) postparapophyseal crest, (*poz*) postzygapophysis, (*prz*) prezygapophysis, and (*sdi*) supradiapophyseal crest. Scale bar, 1 cm.

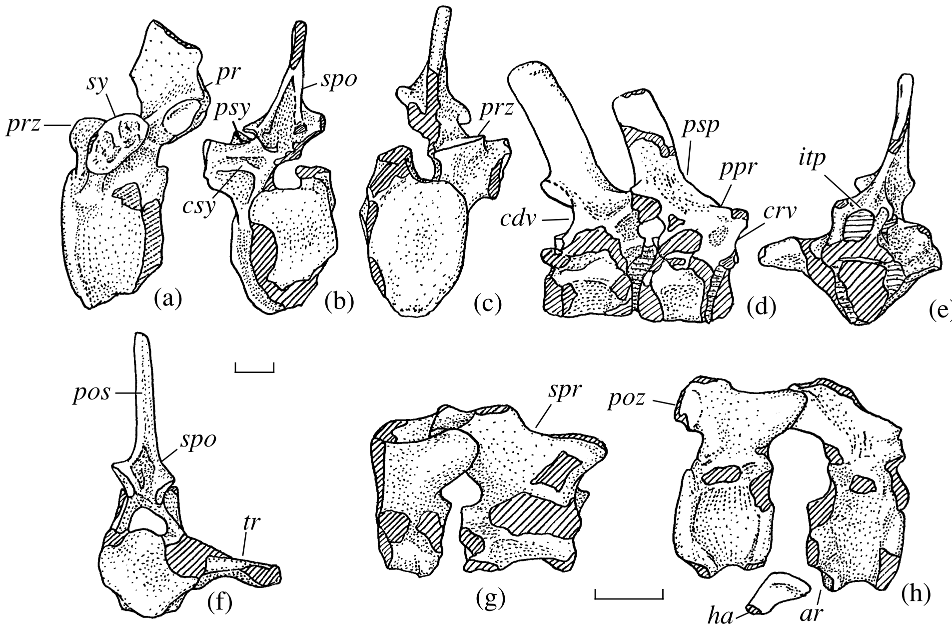

Fig. 2. *Bainoceratops efremovi* gen. et sp. nov., holotype PIN, no. 614-33; (a, b, c) th 13, (d) sc 8–cd 1, (e) sc 8, (f) cd 1, (g) cd ?10–11, and (h) cd ?18–19; (a, d, g, h) lateral view, (c, e) anterior view, (b, f) rear view, (a) left lateral view, and (d, g, h) right lateral view. Designations: (*ar*) articular fossa for haemapophysis, (*cdv*) caudal vertebral incisure, (*crv*) cranial vertebral incisure, (*csy*) caudosynapophyseal crest, (*ha*) fragment of haemapophysis, (*itp*) interprezygapophyseal incisure, (*pos*) postspinal crest, (*ppr*) postprezygapophyseal crest, (*pr*) process of the spinopostzygapophyseal crest, (*psp*) prespinal crest, (*psy*) postsynapophyseal crest, (*spo*) spinopostzygapophyseal crest, (*spr*) spinoprezygapophyseal crest, (*tr*) transverse process, and (*sy*) synapophyses. Scale bar, 1 cm.

the diapophyses to the bases of the pedicles of the neural arch. The cranial surface of the centrum bears a well-pronounced tubercle above the ventral crest; apparently, this is an element of intervertebral ankylosis.

The seventh vertebra of the holotype lacks the right half of the neural arch. The ventral crest is wider and more weakly projects beyond the cranial surface of the centrum than those of cv 6. The postparapophyseal depression and the postparapophyseal crest are absent. The facet of the parapophysis is dorsoventrally elongated, its anterior edge terminates short of reaching the cranial surface of the vertebra; dorsally, it contacts with the suture but does not pass onto the neural arch. Caudally and dorsally, the diapophyses are inclined to the transverse axis of the vertebra at the angle of 20°–25° and 35°–40° (in *P. andrewsi* and cf. *Bagaceratops* sp., these angles are approximately 10° smaller). The prezygapophyses and postzygapophyses are connected by the interzygapophyseal crest (syn. margo lateralis). The prezygapophyseal facet, which is extended transversally, is oriented laterocranially (in *U. tschizhovi*, laterocaudally; in *P. andrewsi* and cf. *Bagaceratops* sp., almost cranially; see Fig. 3). The prezygapophyses are short and project beyond the edge of the cranial incisure for approximately one-third of the facet length.

The ninth vertebra of the holotype is represented by the centrum with a damaged cranioventral region. The cranial half of the ventral surface is slightly convex and cavernous. The parapophysis holds the extreme craniodorsal position and should extend slightly onto the neural arch.

Thoracic region (Figs. 1h–1o, 2a–2c)

It is difficult to determine the serial numbers of nine vertebrae at our disposal, because they are disconnected and poorly preserved, except for the posteriormost vertebra. Notice that *P. andrewsi* has 21 presacral vertebrae; *L. gracilis, U. tschizhovi*, and cf. *Bagaceratops* sp. have 22 each, and nine of them belong to the cervical region. Since the new species shows morphological similarity to *L. gracilis* and *U. tschizhovi* (see above), which have 13 dorsal vertebrae, it is reasonable to identify our five posterior presacral vertebrae as vertebrae 9-13. As four anterior (?1, ?5–7) and other vertebrae near the posteriormost dorsal vertebrae are represented by differently preserved centra, only rough identification is possible using their dimensions and surface sculpturing. Therefore, ?1, ?5–7, and ?12 dorsal vertebrae are considered but not described here.

In each dorsal vertebra, except for the posteriormost, the corpus lacks, ventral crest, the parapophyses are located close to the diapophyses and positioned on the neural arch. The propositions of the centra change along the vertebral column. In the first vertebra, the ventral length of the centrum slightly exceeds the dor-

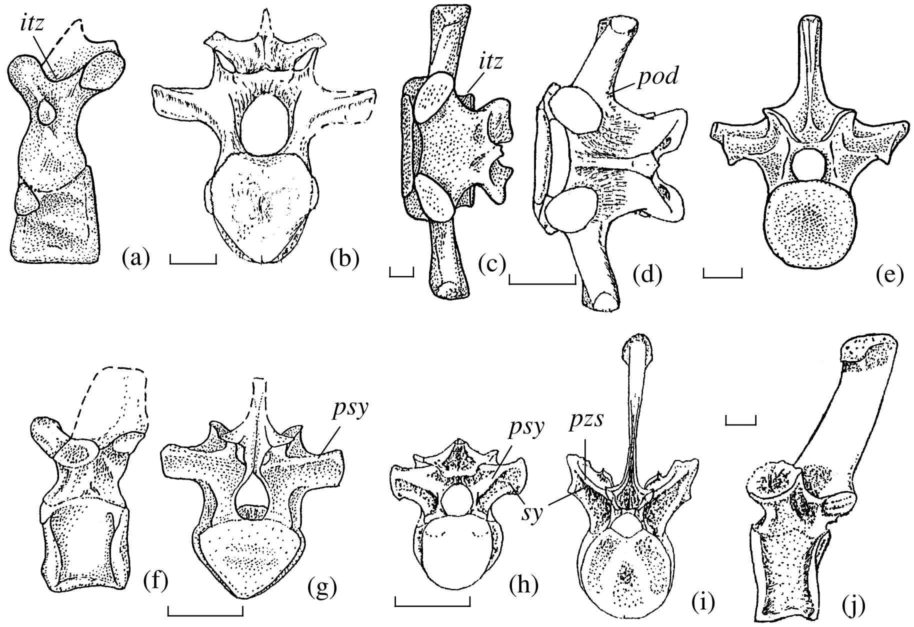

Fig. 3. Presacral vertebrae: (a, b, e–g) *Protoceratops andrewsi* Granger et Gregory: (a, b) PIN, no. 614-35, (e–g) PIN, no. 3143-7, (c, i, j) *Udanoceratops tschizhovi* Kurzanov, PIN, no. 3907-11, (d, h) cf. *Bagaceratops* sp.: (d) PIN, no. 614-29 (reconstruction), (h) PIN, no. 614-62, (a, b) cv 6, (c) cv 7, (d) cv 8, (e) th 9, (f–j) posteriormost dorsal vertebra; (a, f, j) lateral view, (b, e) anterior view, (c, d) dorsal view, and (g, h, i) rear view. Designations: (*itz*) interzygapophyseal crest, (*pod*) postdiapophyseal crest, and (*pzs*) postzygasynapophyseal crest; for other designations, see Fig. 2. Scale bar: (a–c, e) 1 cm, (d) 1.7 cm, and (f–j) 2 cm.

sal length; further caudally, the two lengths become equal; from the fifth (sixth?) dorsal vertebra, the dorsal length becomes greater than the ventral length. This is connected with the development of the arcuate curvature of the vertebral column. In addition, up to the ninth vertebra, the width and depth of the cranial and caudal surfaces of the centra are almost identical. Further caudally, the depth prevails over the width; in *U. tschizhovi*, these parameters are stable over the entire region; in *P. andrewsi*, the width becomes substantialy greater than the depth; in *L. gracilis*, the cranial surface of the centra becomes oval in shape and oriented vertically and the caudal surface is slightly compressed dorsoventrally; and in cf. *Bagaceratops*, the depth is much greater than the width in the anterior dorsal vertebrae, and this difference decreases caudally (Fig. 3).

The ninth vertebra of the holotype lacks postzygapophyses and a transverse process. The diameter of the parapophyseal facet is almost twice as large as the facet of the short and round in cross section diapophysis. The infrapreparapophyseal and infrapostparapophyseal crests are distinct (in other protoceratopids, only the infrapreparapophyseal crest is clearly developed). The diapophyses are oriented caudolaterally at 30°–35° to the longitudinal axis of the vertebra. The articular surfaces of the prezygapophyses closely approach each other medially. The prezygapophyses are long and project anteriorly for three-fourth of the length of their facets, which are oriented in a transverse plane at an angle of 50° to the horizontal. The spinal canal is relatively large, approximately half as deep as the vertebral centrum. The lateral edge of the prezygapophyseal facet, being curved inward, forms a locking mechanism similar to that described in the lumbar vertebrae of certain Recent bovids (Klimov, 1950). This mechanism increases the rigidity of this region of the vertebral column against the vertical curvature (Halpert *et al.*, 1987). This character is weakly expressed in *U. tschizovi* and absent in *P. andrewsi* and cf. *Bagaceratops* sp.

The tenth vertebra of the holotype is strongly damaged. The lateral projection of the cranial articular surface of the centrum is flat, and that of the caudal surface is slightly concave. The infrapreparapophyseal crest is developed better than the infrapostparapophyseal crest. The lower edges of the prezygapophyseal facets are spaced wider than those of th 9 and retain a small space containing the prespinal crest.

The eleventh vertebra of the holotype is represented by the centrum a with damaged cranial surface and right pedicle of the neural arch, retaining the base of the parapophysis under which only the infrapreparapophyseal crest is observed.

The posteriormost (13th) dorsal vertebra has a slightly convex profile of the cranial surface of the centrum and a concave profile of the caudal surface. The centrum is oval, vertically elongated, and tapers ventrally to form a crest. The synapophyses projects laterally for 30–35% of the longitudinal axis of the centrum (in *P. andrewsi* and cf. *Bagaceratops* sp., it projects laterally for 40–45%). The sculptured articular surface of the synapophyses is weakly concave peripherally and the median crest divides it into the diapophyseal and parapophyseal fossae. The extended synapophyseal facet is inclined dorsally and posteriorly at an angle of 45°–50° to the horizontal. The spinopostzygapophyseal crest extends on the caudal surface of the base of the spinous process and the postzygapophyses and terminates in a small process short of the facet edge. The weakly developed postsynapophyseal crest fuse with the neural arch cranial to the postzygapophyseal facet and forms a short branch (the caudosynapophyseal crest), which abruptly descends ventrally and extends to the caudoventral segment of the neural arch pedicles (in *P. andrewsi*, a narrow postsynapophyseal crest extends relatively gently sloping throughout the whole caudal surface of the synapophysis and fuses with the neural arch under the cranial edge of the postzygapophyseal facet; in cf. *Bagaceratops* sp., a similar crest expands medially, its dorsal half fuses with the neural arch cranial to the postzygapophyseal facet, and the ventral half extends to the caudodorsal part of the neural arch pedicles). The postzygapophyseal facet is S-shaped, the prezygapophyseal facet is flat and positioned in transverse plane at 10°–15° to the horizontal. The short prezygapophyses extend for a half of the facet length (in *P. andrewsi* and cf. *Bagaceratops* sp., they project anteriorly for almost the whole facet length). The neurapophysis is positioned at an angle of 100° to the vertebral centrum (this is determined by the angle between the straight line between the centers of the prezygapophyses and postzygapophyses and a perpendicular to the longitudinal axis of the centrum). The latter is caused by the fact that the prezygapophyses are located lower than the postzygapophyses (in other protoceratopids, this angle is at most 90°, because the pre- and postzygapophyses are usually on the same level).

Sacral region (Figs. 2d, 2e)

The sacral region is represented in the holotype by the posteriormost sacral vertebra in its natural articulation with three anterior caudal vertebrae. A weak backward curvature of the spinous process is a characteristic feature of this vertebra in all protoceratopids, the point of curvature is below the midlength of the process. The serial number of this vertebra is not known with certainty because *P. andrewsi* (Brown and Schlaikjer, 1940), cf. *Bagaceratops* sp., and *U. tschizhovi* have eight sacral vertebrae, while *L. gracilis* has seven (Sternberg, 1951). Notice that, in *L. gracilis*, the number of sacral vertebrae was determined in young animals, while the seventh and sixth sucral vertebrae should become fused in adults (Russell, 1970), like in *U. tschizhovi* (Tereschenko, 2001), which is closely related to *L. gracilis* (Kurzanov, 1992). Since the prezygapophyseal facet of the eighth sacral vertebra of *U. tschizovi* is rough, which is evidence of the immobility of this articulation, one may expect the fusion between the zygapophyses of the seventh and eighth vertebrae in aged animals; this has not been registered in *L. gracilis.* At the same time, in specimen NMC no. 8887, the transverse processes of the vertebra next to sc 7 project craniolaterally and expand distally, like in sc 8 of the majority of protoceratopids. On this basis, one may assume that *L. gracilis* has eight vertebrae in the sacral region, and, consequently, the new species should also have eight sacral vertebrae.

In the eighth vertebra, the cranial and caudal surfaces are concave in lateral view and subpentagonal in front view (two upper sides are connected to the pedicles of the neural arch; two middle sides, to the transverse processes; and the lower side, to the ventral crest of the vertebral centrum). The bases of the transverse processes are round in cross section. The distance between the prezygapophyses is less than the interpostzygapophyseal distance. The distance between the ventral edges of the contralateral facets of the pre- and postzygapophyses is large and almost equal to the facet width, like in *U. tschizovi* (in *P. andrewsi* and cf. *Bagaceratops* sp., this distance is very short and the postzygapophyseal facets contact each other ventrally). The prespinal crest extends between the hardly visible postprezygapophyseal crests and disappears on a level with the caudal edge of the round prezygapophyseal facets. The prezygapophyseal facet is concave and inclined in the transverse plane at about 60° to the horizontal. The cranial edge of the spinous process passes onto the neural arch above the prezygapophyseal facet near the midlength of the vertebral centrum and forms a large incisure (other protoceratopids lack such incisure, because this edge usually passes onto the neural arch cranial to the midlength of the vertebral center, on a level with the caudal quarter of the prezygapophyseal facets, or caudal to these facets, as in cf. *Bagaceratops* sp.).

Caudal region (Figs. 2d, 2f–2h)

The caudal region is represented by seven vertebrae of the holotype, three anterior vertebrae cd ?10–11 and cd ?18–19 are preserved in natural articulation. A trauma of the tail base, which occurred during the animal's lifetime, is seen in this specimen: a crack extends along the postzygapophysis of the first and the prezygapophysis of the second caudal vertebra. The zygapophyseal articulations of these vertebrae display maximal lateral flection and torsion. Both cranial and as caudal to this articulation, similar positional relationships between adjacent vertebrae are less pronounced. Probably, the calcification of intervertebral discs between the posteriormost sacral and three first caudal vertebrae and its presence anterior to the cv ?18 is associated with a long hypodynamia of the tail.

Similar to *U. tschizhovi* and *L. gracilis*, the new species displays a change of angle of inclination of the prezygapophyses to the horizontal in sagittal plane from cd 1 to cd ?18–19. In cd 1 of *B. efremovi* sp. nov., this angle is 45°–50°; caudally, it becomes half as great. In the same sequent of the vertebral column of

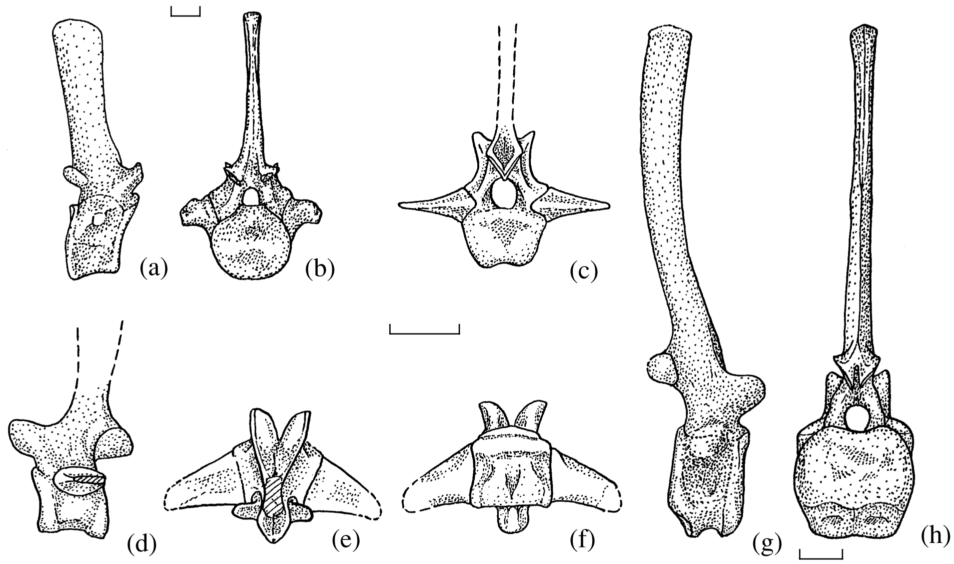

Fig. 4. Caudal vertebrae: (a, b, g, h) *Udanoceratops tschizhovi* Kurzanov, PIN, no. 3907-11, (c–f) *Protoceratops andrewsi* Granger et Gregory, PIN, no. 3143-7 (a, b) cd 1, (c–f) cd 3, and (g, h) cd 13 (?14); (a, d, g) lateral view, (b, c, h) rear view, (e) dorsal view, (f) ventral view, (a, g) right lateral view, and (d) left lateral view. Scale bar, 2 cm.

U. tschizhovi and *L. gracilis*, this angle decreases to a much lesser extent, i.e., from 40°–45° to 30°–35° in *U. tschizhovi* (Fig. 4) and from 50°–55° to 40°–45° in *L. gracilis*. In *P. andrewsi* and cf. *Bagaceratops* sp., on the contrary, this angle increases from 20°–25° to 40°–45° in the former and from 35°–40° to 55°–60° in the latter.

The anterior caudal vertebrae of *B. efremovi* sp. nov. are heterocoelous, like those of other representatives of the same family. These vertebrae differ in the of centra from the presacral vertebrae of birds where the cranial and caudal surfaces of centra are anteriorly concave in ventral view and posteriorly concave in lateral view (Gurtovoi and Dzerzhinsky, 1992). The observation of these vertebrae in the same sequence in available protoceratopids shows the opposite relation. Applying to dinosaurs the definition proposed by Borkhvardt (1982, p. 82) for birds, one may say that the heterocoelous centra of these vertebrae are characterized as procoelous in the vertical plane and as opisthocoelous in the horizontal plane.

The predominance of the dorsal length of the vertebral center over the ventral length is a common character of three anterior caudal vertebrae of protoceratopids. In the new species, the dorsal sectors of the cranial and caudal sides of the centra project in these vertebrae peaks, visors similar to those of *U. tschizovi* and cf. *Bagaceratops* sp. On the one hand, this is connected with the formation of the descending section of the spinal curvation in the region of the fail base, and, on the other hand, with a decrease in mobility between adjacent vertebrae relative to the horizontal rotation axis. The three vertebrae have well-pronounced ventral crests; their presence in the third vertebra is evidence of the absence of chevron between this and the next vertebral centrum. In the first two (or three) caudal vertebrae, the cranial vertebral incisure is smaller than the caudal incisure. Like in cf. *Bagaceratops* sp., the ratio of the centrum length to the length of the spinous process base in the first two vertebrae is 1.8–2.0 (in *P. andrewsi* and *U. tschizhovi*, this ratio is at most 1.6). In these and succeeding vertebrae of the new species, the postzygapophyseal facets do not contact ventrally, while in *P. andrewsi* and in cd 1 of cf. *Bagaceratops* sp. the lower edges of these facets are fused to form a crest, which enters the narrow interprezygapophyseal space of the next vertebra.

The first caudal vertebra of the holotype is fairly well preserved. A weakly developed crest extends along the lateral surface of the prezygapophyses (like in *U. tschizhovi*) and is fused with the dorsocranial part of the transverse process. The base of the transverse process is slightly extended craniocaudally. The prespinal crest extends between weakly pronounced spinoprezygapophyseal crests nearly to the anterior edge of the interprezygapophyseal incisure. The vertebral width between the prezygapophyses is less than the width between the postzygapophyses, the same is true with reference to the next vertebra. The spinous and transverse processes are inclined at about 60° dorsocaudally and laterocaudally, respectively.

The second vertebra is worse preserved than the first one. The transverse processes extend caudally at 65°–70° (in cf. *Bagaceratops* sp., at 45°–50°; in *P. andrewsi*, at about 80°; and in *U. tschizhovi*, at 90°). The spinoprezygapophyseal crest is better developed than in the preceding vertebra. The facet of the prezygapophysis is located above the postzygapophyseal facet. The spinous process is inclined dorsocaudally at approximately 50°.

The left side of the third vertebra of the holotype is damaged. The point of fusion of the spinoprezygapophyseal crests with the cranial edge of the spinous process is relatively narrow and reminds one of the *P. andrewsi* and cf. *Bagaceratops* sp. The prezygapophyses curve outwards and are oriented dorsocranially; their facets are slightly curved upward in the transverse plane. The transverse processes project caudolaterally at about 80° (in cf. *Bagaceratops* sp., at 55°; in *P. andrewsi*, at about 65°).

The centra of cd ?10–11 of the holotype are deformed, without spinous and transverse processes. Two crests, which form the edges of fossal for the attachment of chevron bones caudal to the midlength of the centra, extend along the ventral surfaces of the centra of these and succeeding vertebrae. The prezygapophyses of cd ?11 are slightly curved upward and project craniodorsally at about 30°, their facets are inclined in the transverse plane at about 80° to the horizontal.

Cd ?18–19 are similar in preservation and morphology, they lack spinous processes. The platycoelous vertebrae are almost square in lateral view and subtrapezoid in anterior view (two dorsal sides are connected to the transverse processes and two ventral sides are connected to the haemapophyses). The prezygapophyses project cranially in the sagittal plane at 15°–20° to the horizon. The prezygapophyseal facet is inclined in the transverse plane at 85°–90° to the horizontal. The transverse processes are very short (in *U. tschizhovi*, they are knoblike; and in *L. gracilis*, they are absent).

M a t e r i a l. Holotype.

CONCLUSIONS

To date, 11 forms of the Protoceratopidae have been described from the Cretaceous of Asia: *Protoceratops andrewsi* (Granger and Gregory, 1923), *Microceratops gobiensis* (Bohlin, 1953), *Bagaceratops rozhdestvenskyi* (Maryanska and Osmólska, 1975), *Breviceratops kozlowskii* (Maryanska and Osmólska, 1975), *Asiaceratops salsopaludalis* (Nessov *et al.*, 1989), *Udanoceratops tschizhovi* (Kurzanov, 1992), *Bagaceratops* sp. (Dong and Currie, 1993), *Kulceratops kulensis* (Nessov, 1995), *Archaeoceratops oshimai* (Dong and Azuma, 1997), *Graciliceratops mongoliensis* (Sereno, 2000), and *Bainoceratops efremovi* gen. et sp. nov. Four forms of this list occur in Djadokhta deposits: *U. tschizhovi*, *Bagaceratops* sp., *P. andrewsi*, and *B. efremovi* gen. et sp. nov., of which the latter two were found in the same locality Bain-Dzak. It is reasonable to suppose that the Djadokhta Time was the golden age in the evolution of Asian protoceratopids. The presence of several species in Bain-Dzak calls for the revision of taxonomic diversity of the Protoceratopidae from the Djadokhta localities of Mongolia.

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