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# Sexual Dimorphism in the Postcranial Skeleton of Protoceratopsids (Neoceratopsia, Protoceratopsidae) from Mongolia

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Received February 17, 2000

**Abstract**—The study of horned dinosaurs housed at the Paleontological Institute of the Russian Academy of Sciences revealed 19 structural parameters of the postcranial skeleton that distinguish males from females. Based on comparisons of age and sexual variation and the analysis of the functional significance of sexual differences, a morphobiological interpretation of sexual dimorphism in protoceratopsids is given.

## INTRODUCTION

The presence of presumable sexual dimorphism in skeletons of *Protoceratops andrewsi* was first mentioned by Gregory and Mook (1925). Subsequently, Brown and Schlaikjer (1940) indicated sexual differences in *Protoceratops* skulls and indicated that variability in the length of the hindlimb segments can be associated with individual or sexual variation. At the same time, Rozhdestvensky (1965) proceeded *a priori* from the assumption that sexual characteristics in skeletons of extant and extinct reptiles are difficult to determine and poorly pronounced. Kurzanov (1972) and Dodson (1976) indicated that sexual dimorphism was probably absent in the postcranial skeleton of protoceratopsids.

In parallel, the concept of the set of secondary sexual characteristics in the skull of *P. andrewsi* changed. As Brown and Schlaikjer (1940) indicated, a well-pronounced character of this kind is the presence of a rudimentary nasal horn in males and the absence of such elements in females. When comparing the skulls from the Bain-Dzak and Tugrikiin-Shire localities, Kurzanov marked "a deviation from the general trend of age variation of the protoceratopsid horn" and concluded that "such differences in the development of the nasal horn cannot be attributed to individual variation" (Kurzanov, 1972, p. 110). In *Bagaceratops*, either sex may possess a well-pronounced nasal horn; therefore, sexual differences distinguished in protoceratopsid skulls are inapplicable to this form (Maryanska and Osmolska, 1975). When analyzing the growth and formation of sexual differences in the ontogenetic development of *Protoceratops*, Dodson (1976) put in doubt the use of the above parameters for sex identification and proposed to critically revise the genera and species of advanced Ceratopsia. Subsequently, Chapman (1990) failed to reveal the patterns of the formation of sexual dimorphism in Protoceratopsidae and indicated that certain

other sexual characteristics were of little significance. When studying these problems, I realized that to resolve the question of the presence or absence of sexual differences in ceratopsians required examination of the postcranial skeletons.

The main questions considered in this study, the results of which were published earlier (Tereshchenko, 1997), are as follows: (1) analysis of sexual dimorphism in certain members of Protoceratopsidae combined with data on sexual differences in living tetrapods; (2) comparisons of the development of sexual differences with age changes in the structure of the postcranial skeleton; and (3) functional estimation of certain sexual characteristics.

The following abbreviations are used in this paper: American Museum of National History (AMNH), National Museum of Canada (NMC), and Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

## MATERIALS AND METHODS

The material for this study includes the relatively complete and fragmentary skeletons of 18 individuals (mainly adults) of *Protoceratops*, *Udanoceratops*, and *Bagaceratops* (Table 1). The main subjects of the study were members of the genus *Protoceratops*, since their skeletons form a large part of the sample examined. A cast of a *Leptoceratops gracilis* skeleton (NMC 8887) stored at PIN was used for comparisons. Published data on *Montanoceratops cerorhynchus* (Brown and Schlaikjer, 1942; Chinnery and Weishampel, 1998) and *L. gracilis* (Stemberg, 1951; Russel, 1970) were also used.

The vertebrae are described on the basis of the terminology proposed by Osborn and Mook (1921) and Wilson (1999).

Table 1. Age and species structure of the horned dinosaurs examined\*

Age stage	Number, sex, and length of specimen**	Species
Immature young	3142/7 (F – 480)	<i>Bagaceratops</i> sp.
	4046/11 (“M” – 935)	<i>Udanoceratops</i> sp.
Mature young	614–61 (“M” – 830?)	<i>Protoceratops andrewsi</i>
	614–35 (F – 830)	<i>Protoceratops andrewsi</i>
	614–31 (“M” – 880?)	<i>Protoceratops andrewsi</i>
	3143/7 (F – 1020)	<i>Protoceratops andrewsi</i>
	3143/5 (M – 1050?)	<i>Protoceratops andrewsi</i>
Mature adult	614–30 (“F” – 1140)	<i>Protoceratops andrewsi</i>
	3143/12 (M – 1180)	<i>Protoceratops andrewsi</i>
	3143/16 (“M” – 1170)	<i>Protoceratops andrewsi</i>
	3907/11 (M – 2170)	<i>Udanoceratops tschizhovi</i>
	4550–3 (F – 790)	<i>Bagaceratops</i> sp.
	614–62 (“F” – 890?)	<i>Bagaceratops</i> sp.
	614–34 (M – 1040?)	<i>Bagaceratops</i> sp.
Old	3143/9 (F – 1190)	<i>Protoceratops andrewsi</i>
	3143/4 (F – 1290?)	<i>Protoceratops andrewsi</i>
	614–53 (F – 770?)	<i>Bagaceratops</i> sp.
	614–29 (M – 760)	<i>Bagaceratops</i> sp.

\* Collection numbers from PIN designate the following Mongolian localities: (614) Bain-Dzak, (3143) Tugrikiin-Shire, (4550) Gilbentu, (3142) Khermin-Tsav, (3907) Udan-Sair, and (4046) Baga-Tariach (Baga-Tarachi).

\*\* Animal body length in mm, is given in the parentheses following sex index, (M) male and (F) female; sex identified by supplementary sexual characters is shown in quotation marks.

Sexual differences were revealed by the method proposed by Nopcsa (1929), who studied sexual variation in extinct reptiles “by the establishment of correlation between a set of parameters, at least one of which is undoubtedly a primary or secondary sexual character that allows the determination of the secondary sexual nature of the others” (Davitashvili, 1961, p. 482). The initial prerequisites for the present study are data on sexual differences in living tetrapods (Sokolov, 1971; Tereshchenko, 1980; Barbadillo and Sanz, 1983; etc.) and their functional interpretation (Dement’ev, 1940; Tereshchenko, 1991a; Slijper, 1946; Bauwens *et al.*, 1997). These differences are observed in functional modifications (Schmalhausen, 1968), in our case, mainly in the structural details of the postcranial skeleton determined by the different functions of males and females in reproduction. According to the theory for the correlation (Severtsov, 1939, 1945; Schmalhausen, 1939, 1968, 1982, 1983), such sexual features probably first appeared as a result of ergontic correlation. In the course of subsequent autonomization of ontogeny, the latter can be substituted by morphogenetic dependence. This approach provides theoretical substantiation for the method for the reconstruction of the pattern of sexual differences applied by Nopcsa (1929).

As sexual dimorphism is examined, the measurements of specimens are taken into account, since the

growth rates of horned dinosaurs are unknown. An attempt to solve this question in *Protoceratops* was unsuccessful; however, it did not confirm the hypothesis that the growth rate of nonavian dinosaurs was close to the growth rate of birds and substantially higher than those of nondinosaurian reptiles (Norell 1995). In addition, it is known that sexual maturity in most vertebrates is accompanied by an abrupt decrease in the growth rate (Schmalhausen, 1984). In reptiles, this occurs in the mature adult stage (Sergeev, 1939). It is commonly accepted that dinosaurs may have grown for their entire lifetime (Carroll, 1988). Male protoceratopsids were probably larger and bulkier than females of the same age, as in certain living reptiles (Brown and Schlaikjer, 1940).

Functional specialization of sexual characters in female amniotes is mainly associated with adaptation for bearing and laying eggs (procreation), whereas in males, it is associated with the perfection of the locomotor apparatus. In living animals, males and females are distinguishable with certainty on the basis of three key parameters: (1) the spinous processes of the thoracic vertebrae are higher in males than in females (Stromer, 1915; Slijper, 1946; Bogert, 1964; Sokolov, 1971; Tereshchenko, 1980, 1991a; Barbadillo and Sanz, 1983); (2) the abdominal cavity is larger in volume in females than in males (Vorob’ev, 1932;

**Table 2.** The age stages of *Protoceratops* and their manifestation in the morphology of the vertebral column

Age stage	Structural vertebral features
Immature young	Three anterior cervical and all sacral vertebrae are isolated; the neural arches on all vertebrae are isolated from the centers; and the transverse processes (pleurapophyses) are isolated from the centers of the sacral vertebrae.
Mature young	Three anterior cervical and three anterior sacral vertebrae fused (sincervicum and sinsacrum); the neural arches begin to merge with the vertebral centers (from 3c and 1s to 5–7t). Initially, in the sacral region (3s to 7s), the zygapophyses merge with each other and the pleurapophyses merge with the centers. Subsequently, the vertebral centers merge with each other. At the end of the stage, 7s merges with 8s and the distal parts of the pleurapophyses merge with each other.
Mature adult	The suture between the center and the neural arch is faintly discernible in all vertebrae, except for the sincervicum and 1–4s, where it is indistinguishable. In 5–8s, the suture between the center and the pleurapophysis is visible. At the end of the stage, the sinsacrum consists of eight vertebrae.
Old	The sutures between the centers and neural arches of all vertebrae are invisible; the posterior thoracic vertebra becomes fused with the anterior sacral vertebra to form the sinsacrum consisting of nine vertebrae.

Darevskii, 1967, 1979; Tereshchenko, 1980, 1991a; Porkert and Grosseova, 1984; Bauwens 1997); and (3) the pelvis is narrower in males than in females (Vorob'ev, 1932; Shell, 1933; Dement'ev, 1940; Klimov, 1950; Sokolov, 1971; Tereshchenko, 1980, 1991a). In addition, extant and extinct male reptiles are characterized by a more gracile postcranial skeleton than females of the same age (Raath, 1990; Carpenter, 1990; Tereshchenko, 1991a; Farlow 1995).

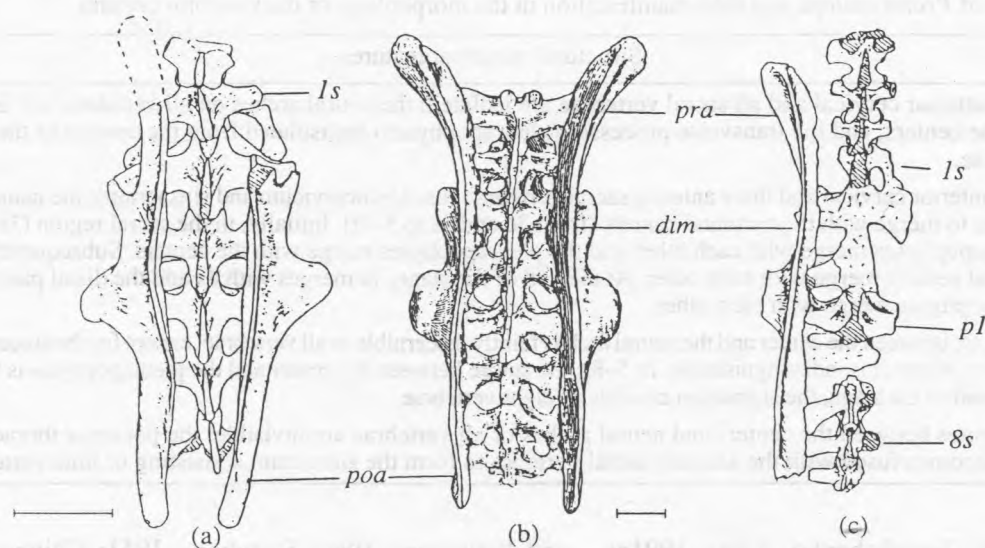
Since available ceratopsians were divided into males and females on the basis of these main parameters, additional sexual differences (supplementary parameters) in the postcranial skeleton were discovered. In living reptiles, a set of sexual characters is rather stable within a family (Tereshchenko, 1991a). Therefore, for the specimens in which the main parameters of sexual differentiation were not estimated due to incomplete preservation, sex was identified on the basis of supplementary parameters (Table 1). The supplementary parameters include (1) the curvature of the vertebral column; (2) the inclination of the vertebral–costal articulation; (3) the structure of the diapophyses and the spinous processes of the thoracic vertebrae; (4) the orientation of the spinous process of the axis; (5) the relief on the dorsal surface of the postzygapophyses of 4–6c;<sup>1</sup> (6) the inclination of the facets on the zygapophyses of 8c and inclination of the neurapophysis between the prezygapophyses and postzygapophyses of 9c; (7) the shape of the ilium; and (8) the curvature of the ischium.

The determination of age stages of protoceratopsids was performed by two methods based on morphological changes and on the extent to which sexual dimorphism in the vertebral column and pelvic girdle developed. In the first case (Table 2), original data and previously published data on the age variation in protoceratopsid postcranial skeletons were used (Brown

and Schlaikjer, 1940; Sternberg, 1951; Chinnery and Weishampel, 1998). The main difficulties encountered in distinguishing age stages were associated with the absence of data on the axial skeleton of juveniles. Therefore, the stages in Protoceratopsidae were determined by analogy with living reptiles. The vertebrae of juveniles (at the stage of intensive growth) contain a thick periosteal layer and are rich in cartilaginous tissue at the articulations between the vertebral centers of the zygapophyses. Therefore, juvenile vertebrae should be slightly rounded, and the facets of the zygapophyses should be clearly visible only in the central part of the articular surface and worn at the periphery. The spinous processes should have a rough cranial side and indented distal edges, with a fossa for the apical cartilages (cartilaginous site at the distal ending of the process). Since the vertebrae of young protoceratopsids consist of two segments, the sutural surfaces on the neural arches and vertebral centers should be poorly pronounced and these elements should be only weakly differentiated in different regions of the vertebral column. Specimens characterized by such structural features are not available, i.e., the juveniles are not present.

Young immature individuals are distinguished conventionally, since the structure of the vertebral column meets the description given in Table 2 only in specimen PIN, no. 4046/11. The other specimen (PIN, no. 3142/7) lacks five anterior cervical vertebrae, the first three of which should be unfused at this stage (Sternberg, 1951). Hence, it may be a very young mature individual. In this case, it is taken into account that in the postcranial skeletons of living reptiles, the formation of sexual differences is clearly visible in ontogenetic development. Therefore, irrespective of individual size, it is possible to determine the age stage of a specimen by the extent to which the sexual differences have developed (Tereshchenko, 1991a). This allowed the estimation of the age structure in available specimens, taking into account the fact that, in living reptiles, the secondary sexual characters first appear in young immature individuals. In young mature animals,

<sup>1</sup> Hereinafter, numbers in the text and figures designate the ordinals of vertebrae in (c) cervical, (t) thoracic, (s) sacral, and (cd) caudal regions.



**Fig. 1.** Pelvic girdle of Protoceratopsidae, dorsal view: (a) *Bagaceratops* sp., female, PIN, no. 3142/7; Mongolia, Khermin-Tsav locality; Upper Cretaceous, Barungoiot Formation; (b) *Montanoceratops cerorhynchus*, male, AMNH, no. 5464; USA, Montana; Upper Cretaceous, Edmonton Formation (Brown and Schlaikjer, 1942); and (c) *Protoceratops andrewsi*, female, PIN, no. 3143/9; Mongolia, Tugrikiin-Shire locality; Upper Cretaceous, Dzhadokhtskaya Formation. Designations: (*dim*) dorsal margin of ilium, (*pl*) pleurapophysis, (*pra*) preacetabular process, and (*poa*) postacetabular process. Scale bar, 2 cm.

they become more strongly developed and reach their maximum manifestation in adults; in old animals, sexual differences decrease.

## RESULTS AND DISCUSSION

### *Age and Sexual Variation*

The small sample size does not allow a detailed examination of the formation of sexual differences in the ontogeny of protoceratopsids. However, based on the above characteristics, one can reconstruct the main features of this process. Below, the main focus is on morphological changes of the pelvic girdle, since the changes of the axial skeleton are presented in Table 2.

**Young immature individuals.** In females, the ilium is weakly S-shaped in dorsal view; the preacetabular process curves laterally, the postacetabular process curves medially, and the dorsal edge of the ilium at 2–4s turns externally (Fig. 1a). This is observed in female *Bagaceratops* sp. at this age stage. In males, the postacetabular process is relatively straight and the edge of the ilium is oriented dorsally for almost its entire length, which is observed at later ontogenetic stages in all male specimens (Fig. 1b). In male *Udanoceratops* sp., the available spinous processes of the thoracic vertebrae are approximately 1.5 times higher than in female *Bagaceratops* sp., although the arcs of the dorsal curvature are approximately equal in these forms (50–60°). However, because of the absence of young immature *P. andrewsi* and the presence of animals of only one sex in both *Bagaceratops* and *Udanoceratops*, these parameters are questionable.

**Young mature individuals.** Medium-sized young animals show an intensive formation of sexual differences. Thus, at the end of the early half of this ontogenetic stage, the arcs of the cervical curvature in females and males are, on the average, 30° and 50°, respectively; and the arcs of the dorsum in females and males are approximately 40° and 60°, respectively (Figs. 2a–2d). The spinous processes of the thoracic vertebrae of the males become more than 1.5 times higher than those of females (Figs. 3a, 3b, 3d, and 3e). In males and females, the ilium curves more strongly in the horizontal plane, mainly at the expense of the preacetabular process. In large young mature females, the dorsal part of the laterally flattened ilium curves externally at the 5–6s level. This is not observed in males.

**Adult mature individuals.** Medium-sized adults retain sexual differences in the axial skeleton characteristic of the previous stage. In contrast, the lateral curvature of the dorsal part of the postacetabular process becomes stronger in females; this increases the conventional width of the pelvis (the distance between the dorsal edges of the rami of these processes), particularly posterior to 6s. In large females, a weak and externally arched curvature develops in the central part of the ischium; in males, this bone is straight in the transverse plane.

**Old individuals.** In females, the arc of natural curvature of the vertebral column decreases and the relative height of the spinous process (the ratio of the vertebral length at the prezygapophyses and postzygapophyses to the vertebral height) of the thoracic vertebrae approaches those of males. For example, in female PIN, no. 3143/9, the neurapophysis on 5t is 450 mm

long (the vertebral length at the prezygapophyses and postzygapophyses), the spinous process is 420 mm high; the arc of the cervical curvature is approximately  $15^\circ$ ; and the dorsal arc is  $35^\circ$ . In addition, the external curvature of the postacetabular processes of old females increases; therefore, sexual differences in this character increase. The distance between the dorsal edges of the processes is smaller in males than in females, particularly at 7–8s (Figs. 1b and 1c).

### Sexual Dimorphism

Since the available material on *P. andrewsi* is abundant and diverse, the variation of sexual characters in this species is examined in detail. The list of sexual characters in mature adults consists of 19 parameters. Based on these data, one can estimate the variability of sexual dimorphism in *Bagaceratops* sp. and *Udanoceratops tschizhovi*.

*Protoceratops andrewsi* (Figs. 1c, 2a, 2b, 3a–3f, and 4a–4f).

(1) The arcs of the cervical curvature in females and males are  $25^\circ$ – $35^\circ$  and  $40^\circ$ – $45^\circ$ , respectively. The arc of the dorsal curvature in females is  $40^\circ$ – $45^\circ$ ; in males,  $55^\circ$ – $60^\circ$ . The thoracic region of females is approximately 10% longer than those of males. The neck is approximately the same length in either sex, since the vertebrae of females are somewhat shorter, but the different length of the cervical arc results in similar values of the neck length.

(2) In males, the spinous processes of the thoracic and, probably, sacral vertebrae are 45–50% higher than those of females.

(3) In females, the relative height of the spinous process of the thoracic vertebrae ranges from 1.3 to 1.8; in males, from 0.8 to 1.2. The neurapophyses of these vertebrae are approximately the same length in either sex.

(4) In males, the spinous process of 3t is inclined dorsocaudally at an angle of approximately  $45^\circ$  to the horizontal; in females, the angle is  $55^\circ$ .

(5) From the first to the penultimate thoracic vertebrae in males, the angle between the axis of the vertebral–costal articulation and the longitudinal axis of the body decreases from  $60^\circ$ – $65^\circ$  to  $25^\circ$ – $30^\circ$ ; in females, from  $45^\circ$ – $50^\circ$  to  $10^\circ$ – $20^\circ$ .

(6) In females, the distal part of the diapophysis on 4–8t (in particular, on 5–7t) curves slightly ventrally, in contrast to those of males.

(7) In males, the diapophyses on 1–10t (11t) deviate dorsally to a greater extent than in females, i.e., the angle between the diapophyses and the horizontal decreases (especially posterior to 5t) in the transverse plane from  $60^\circ$ – $65^\circ$  to  $10^\circ$ – $15^\circ$  (in the penultimate vertebra). In females, the angle decreases from  $45^\circ$ – $50^\circ$  to  $0^\circ$ – $5^\circ$ .

(8) In females, the diapophysis base on 4–8t is wider than in males; therefore, in dorsal view, female vertebrae appear shorter than male vertebrae.

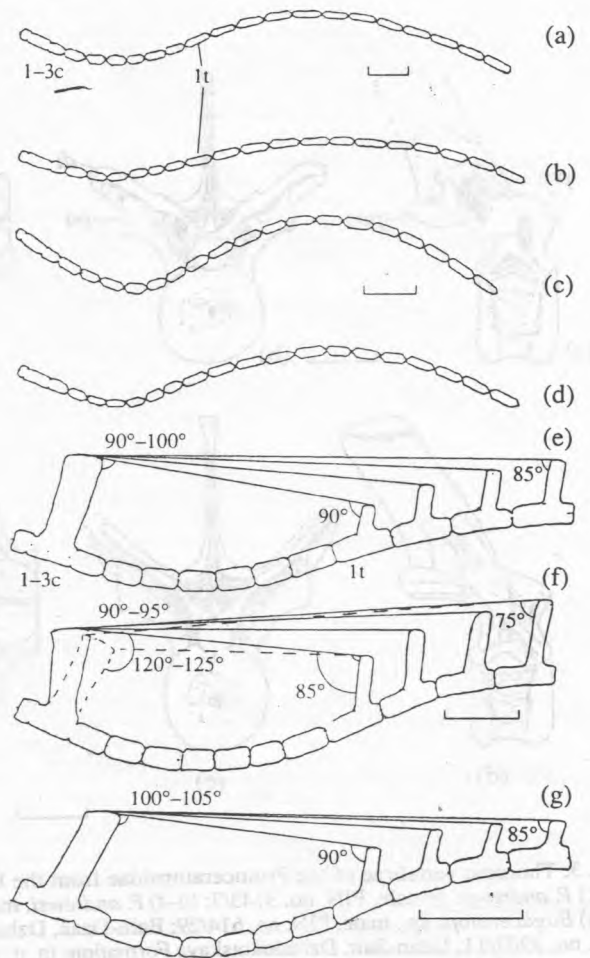


Fig. 2. Diagram of the cervical and thoracic regions of the vertebral column in Protoceratopsidae from the Upper Cretaceous of Mongolia: (a, f) *P. andrewsi*, male, PIN, no. 3143/5; (b, e) *P. andrewsi*, female, PIN, no. 3143/7; Tugrikiin-Shire, Dzhadokhtskaya Formation; (c) *Bagaceratops* sp., male, PIN, no. 614/29; Bain-Dzak, Dzhadokhtskaya Formation; and (d, g) *Bagaceratops* sp., female, PIN, no. 4550/3; Gilbertu, Barungoiot Formation; (a–d) sexual differences in cervical and dorsal curvature and (e–g) dependence of the inclination of the axial spinous process on the cervical curvature, the height of the spinous processes of the anterior thoracic vertebrae, and the effect of the forces of the spinalis cervicis muscle of the neck on the thoracic spinous processes. Scale bar, 4 cm.

(9) In males, the spinous processes on 5–11t (12t) are transversely expanded at the ending, in contrast to those of females.

(10) The spinous process of the axis in females is directed dorsally or slightly caudally; in males, slightly cranially.

(11) The supradiapophysial crest in females at the base of the prezygapophysis on 4c curves cranially and slightly projects anteriorly; in males, the crest is almost straight and occupies a laterocranial position.



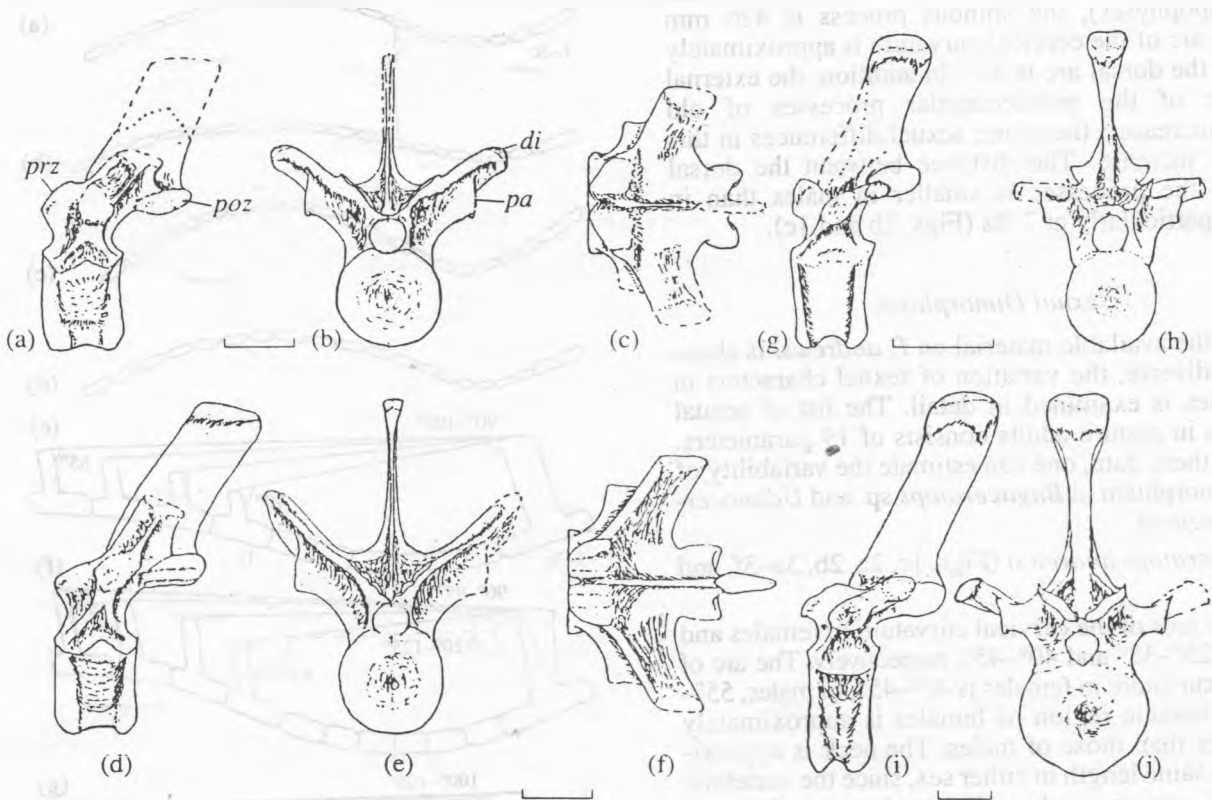


Fig. 3. Thoracic vertebrae of the Protoceratopsidae from the Upper Cretaceous of Mongolia: (a–f) 5t, (g, h) 9t, and (i, j) 10t; (a–c) *P. andrewsi*, female, PIN, no. 3143/7; (d–f) *P. andrewsi*, male, PIN no. 3143/5; Tugrikiin-Shire, Dzhadokhtskaya Formation; (g, h) *Bagaceratops* sp., male, PIN, no. 614/29; Bain-Dzak, Dzhadokhtskaya Formation; and (i, j) *Udanoceratops tschizhovi*, male, PIN, no. 3907/11; Udan-Sair, Dzhadokhtskaya Formation; (a, d, g, i) lateral view; (b, e, h, j) front view; and (c, f) dorsal view. Designations: (*di*) diapophysis, (*pa*) parapophysis, (*prz*) prezygapophysis, (*poz*) postzygapophysis. Scale bar, 2 cm.

(12) In females, the spinopostzygapophysial crest on 5–6c extends along the entire dorsal surface of the postzygapophyses; in males, it disappears short of reaching the edges of the postzygapophyses.

(13) In males, the spinopostzygapophysial crest on 6c is arched posteriorly; in females, it is almost straight and usually forms a tubercle at the edge of the postzygapophyses above the facet.

(14) In females, the long axis of the facet on the postzygapophyses of 8c is positioned at an angle of, at most, 35° to the longitudinal axis of the vertebral center; in males, the angle is at least 40°. In females, in the transverse plane, the facet on the prezygapophyses is at an angle of 40°–45° to horizontal; in males, the angle is 50°–55°.

(15) In all available specimens, the neuropophysis of the posterior cervical vertebra (9c) abruptly rises dorsally ahead of the spinous process from the prezygapophyses to the postzygapophyses. In females, it ascends abruptly (as a wall); in males, it is relatively gentle and occasionally reaches the middle of the base of the spinous process.

(16) In females, the facets of the prezygapophyses and postzygapophyses on 9c are at the same level; in

males, the facets of the postzygapophyses are located above the facet of the prezygapophyses.

(17) In females, the ilium curves more strongly than in males and the zone of curvature is at the base of the postacetabular process behind the acetabulum. The dorsal edge of the process curves laterally, and the curvature is especially strong at 5–6s. In males, the zone of curvature is poorly pronounced and falls on the acetabulum. The dorsal edge of a straightened postacetabular process is turned dorsally along the entire extent.

(18) In females, the postacetabular process is turned relative to the longitudinal axis of the ilium so that the lateral surface of the process is positioned at an angle of 45° to the sagittal plane, in contrast to those of males. Therefore, the conventional width of the pelvis in females is broader than in males, whereas the width of the sacral vertebrae at the pleurapophyses is approximately the same in either sex.

(19) The ischium in females is slightly arched externally in the middle part; in males, it is almost straight. Therefore, the apertura pelvis caudalis is wider in females than in males.

*Bagaceratops* sp. (Figs. 1a, 2c, 2d; 3g, 3h; 4g, and 4h) shows generally the same sexual differences as

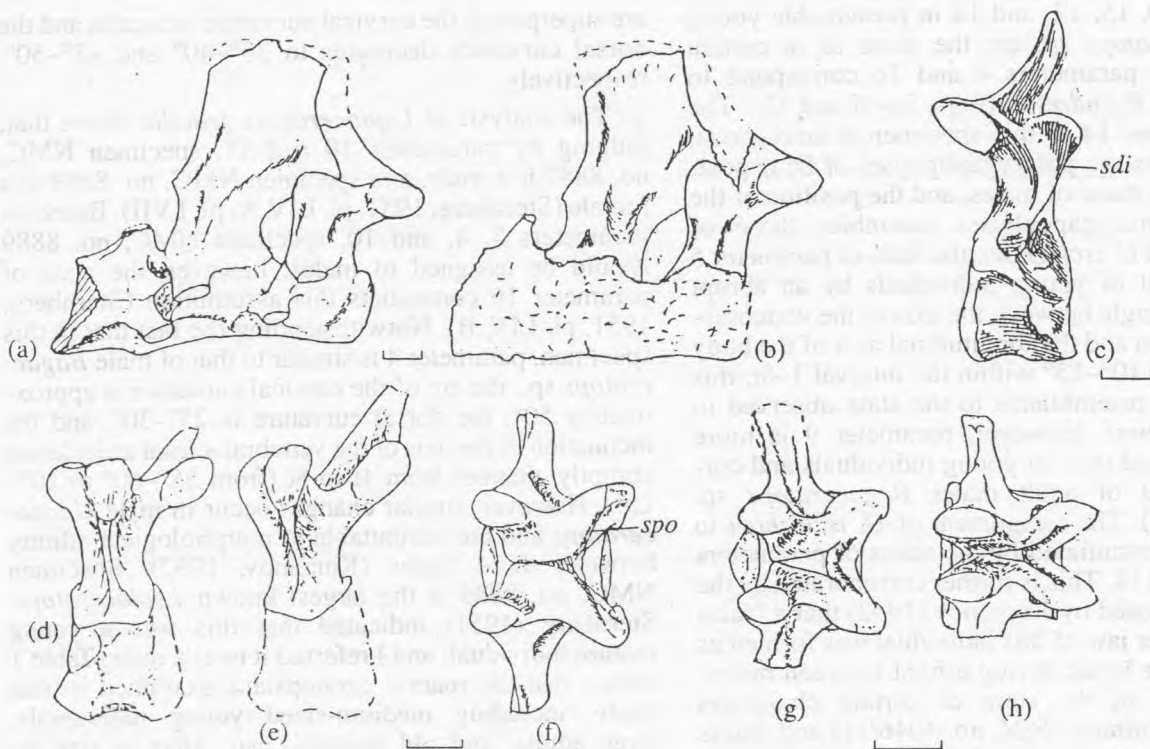


Fig. 4. Cervical vertebrae of Protoceratopsidae from the Upper Cretaceous of Mongolia: (a–f) *P. andrewsi*: (a) female, PIN, no. 3143/9; (b, e) male, PIN, no. 3143/5; (c) female, AMNH, no. 6418 (Brown and Schlaikjer, 1940); (d) female, PIN, no. 3143/7; and (f) female, PIN, no. 614/35; (g, h) *Bagaceratops* sp.: (g) male, PIN, no. 614/29 and (h) female, PIN, no. 4550/3; (a, b, d, e) Tugrikiin-Shire, Dzhadokhtskaya Formation; (c, f, g) Bain-Dzak, Dzhadokhtskaya Formation; and (h) Gilbertu, Barungiot Formation; (a, b) 1–3c; (c) 4c; (f) 6c; and (d, e, h) 8c; (a–e) lateral and (f–h) dorsal views. Designations: (*sdi*) supradiapophysial crest, (*spo*) spinopostzygapophysial crest. Scale bar, 1 cm.

*P. andrewsi*, although the state of parameter 14 is unknown, since the material is poorly preserved. The absence of the pelvic girdles of adult males prevented the estimation of sexual differences in its structure. The vertebral column of *Bagaceratops* sp. curves more strongly in the vertical plane than those of *P. andrewsi*. In particular, the arcs of the cervical and dorsal curvature are approximately equal to each other in adults; in the female specimen PIN, no. 4550/3, they are 40°–45° and 50°; in the male specimen PIN, no. 614/29, they are 55° and 65°–70°, respectively. In an immature female, the arc of the dorsum is 60°–65°. In female *Bagaceratops*, this arc probably decreased in length in the course of individual development. Parameters 6 and 7 are not characteristic of *Bagaceratops* sp.; however, parameters 4 and 9 are more strongly developed, since the spinous process on the 3t of males is inclined dorso-caudally at an angle of approximately 30°, and those of females, at 50°. In males, the distal endings of the spinous processes posterior to 6t are club-shaped; females lack this feature. The state of parameter 13 differs from those of *P. andrewsi*. In females, the spinopostzygapophysial crest on 6c disappears in the middle of the proximal half of the dorsal surface of the postzygapophyses, whereas males lack this crest.

*Udanoceratops* (Figs. 3i and 3j) is similar to *P. andrewsi* in most sexual characters. However, there are no data on parameter 19 in both available specimens. Parameters 10, 11, 15, and 16 in adult *Udanoceratops tschizhovi* (1–5c and the neural arch on 9c are absent); and parameters 12 and 13 in young *Udanoceratops* sp. (only prezygapophyses are preserved on 5–6c) are unavailable because of incomplete preservation of specimens. It appears impossible to estimate the applicability of parameters 6 and 7 to *Udanoceratops*, since, on the one hand, the inclination of the diapophyses abruptly decreases from 60°–65° to horizontal, and on the other hand, the diapophyses slightly curve ventrally on 1–4t in young individual (PIN, no. 4046/11) and on 7t in adults, as in female *P. andrewsi* (Fig. 3b). The same is true for parameter 8, since the presacral vertebrae of *Udanoceratops* are shorter than those of *Protoceratops* and *Bagaceratops*. The state of parameter 1 in adults (PIN, no. 3907/11) is uncertain, since the arc of the dorsal curvature is approximately 30°, whereas the arcs of the cervical and dorsal curvature in young individuals are 50° and 50°–55°, respectively. However, a similar decrease in the dorsal arc is observed in female *P. andrewsi* and *Bagaceratops* sp. This is a common feature of males and females of these species and other members of the Protoceratopsidae. The states of param-



eters 3, 5, 9, 10, 15, 17, and 18 in presumable young male *Udanoceratops* sp. are the same as in certain males, whereas parameters 4 and 16 correspond to those of female *P. andrewsi* (Figs. 3a–3f and 4b). The state of parameter 14 in this specimen is ambiguous, since the facet on the postzygapophyses of 8c is positioned similar to those of males, and the position of the facet on the prezygapophyses resembles those of females. In adult *U. tschizhovi*, the state of parameter 5 differs from that of young individuals by an abrupt decrease in the angle between the axis of the vertebral–costal articulation and the longitudinal axis of the body from 70°–65° to 10°–15° within the interval 1–8t; this shows a certain resemblance to the state observed in female *P. andrewsi*. However, parameter 9 is more strongly developed than in young individuals and corresponds to that of adult males *Bagaceratops* sp. (Figs. 3g and 3h). The assignment of *U. tschizhovi* to males is also substantiated by the states of parameters 3, 12–14, 17, and 18. This is further corroborated by the assumption proposed by Kurzanov (1992) that a “false joint” in the lower jaw of this individual was formed as a result of a bone break during a fight between males. The differences in the state of certain characters between young animals (PIN, no. 4046/11) and adults are probably associated with a dichronism in individual development (Geodakyan, 1991) of *Udanoceratops*. This ontogenetic rule of sexual dimorphism was corroborated on the basis of Recent material and states that the “female structure of a dimorphic character dominates at the beginning of ontogenetic development, whereas male structure, at the end” (Geodakyan, 1991, p. 66).

An attempt at sex identification in *P. andrewsi* that is featured in some monographs (Lull, 1933; Brown and Schlaikjer, 1940) confirmed the identification given by Brown and Schlaikjer, i.e., specimen AMNH, no. 6466 (Brown and Schlaikjer, 1940, fig. 24) is an adult male based on parameters 1 and 3–6. Specimen AMNH, no. 6417 is also an adult male based on parameter 10 (Lull, 1933, fig. 34). I determine specimen AMNH, no. 6418 (Brown and Schlaikjer, 1940, pl. 13, fig. 23) to be a young mature female based on parameters 10, 11 (Fig. 4c), 13, 16, and 17.

The analysis of the skeletal structure in *Montanoceratops cerorhynchus* (Brown and Schlaikjer, 1942, Fig. 2) shows that, judging by parameters 1 (?), 3–6, 9–11, and 17 (Fig. 1b), this is a large mature male. The state of parameter 8 in this specimen resembles those of adult male *Udanoceratops* and *Bagaceratops* (Figs. 3g–3j). A small cervical curvature and an overestimated dorsal curvature of *M. cerorhynchus* (approximately 30° and 55°, respectively) are caused by mounting the vertebral column in a curved position; this is evidenced by the fact that the prezygapophyses and postzygapophyses between 8–9c, 3–4t, and 11–12t are moved apart as much as possible (Brown and Schlaikjer, 1942, fig. 3). As the contours of the facets on the zygapophyses of the above-mentioned vertebrae

are superposed, the cervical curvature increases and the dorsal curvature decreases to 35°–40° and 45°–50°, respectively.

The analysis of *Leptoceratops gracilis* shows that, judging by parameters 10 and 17, specimen NMC, no. 8887 is a male, and specimen NMC, no. 8888 is a female (Sternberg, 1951, pl. LIV, A, pl. LVII). Based on parameters 3, 4, and 10, specimen NMC, no. 8889 should be assigned to males; however, the state of parameter 16 contradicts this assumption (Sternberg, 1951, pl. LIV, B). Notwithstanding the fact that in this specimen, parameter 4 is similar to that of male *Bagaceratops* sp., the arc of the cervical curvature is approximately 50°, the dorsal curvature is 25°–30°, and the inclination of the axis of the vertebral–costal articulation abruptly changes from 1t to 8t (from 55°–60° to 10°–15°). However, similar changes occur in male *Udanoceratops* and are attributable to morphological affinity between these forms (Kurzanov, 1992). Specimen NMC, no. 8889 is the largest known *Leptoceratops*. Sternberg (1951) indicated that this was a young mature individual, and I referred it to as a male. Table 1 shows that the mature ceratopsians examined in this study, including medium-sized young individuals, large adults, and old animals, can differ in size by approximately 1.5 times. Since the presacral part of *L. gracilis* NMC, no. 8889, is 96 cm long, including the head, the body, including the sacral and caudal regions, should be approximately 2.1 m long. An old animal should be approximately 3.2 m long, i.e., comparable in size to *M. cerorhynchus*. Consequently, *Leptoceratops* is a large protoceratopsid, approaching *Udanoceratops* from Asia in size (approximately 4 m long).

Thus, the ontogenetic development of sexual characters in the axial skeleton and pelvic girdle was similar in the protoceratopsids examined in this study. However, in *L. gracilis*, the fusion between three anterior cervical vertebrae and between the posterior sacral vertebrae occurs relatively late in ontogeny, probably in mature adults (Sternberg, 1951; Russel, 1970). Such fusion between the same cervical vertebrae probably occurred in *U. tschizhovi*, since these forms are morphologically similar (Kurzanov, 1992). Of the eight sacral vertebrae observed in *U. tschizhovi*, 4–7s become fused by the zygapophyses and partially by centers only at the adult stage rather than at the young mature stage, as in *P. andrewsi* (Table 2). Similar ontogenetic changes of the vertebral column in *L. gracilis* and *U. tschizhovi* and the differences from those of *P. andrewsi* (the body of which was at most 2.5 m long) are possibly attributable to large sizes. This may be associated with an increase in the duration of each age stage of large members of the Protoceratopsidae and, consequently, an increase in life span. The latter is well known with reference to large mammals where size increases directly proportionally to a general slowing of the reproductive rate (Foley, 1987). A similar pattern occurs in living reptiles; a decrease in the life span is accompanied by rapid changes of population structure

(Kamalova, 1977), and the duration of the young mature stage is minimized (Tereshchenko, 1991a).

An important, but currently poorly understood question, is the number of anterior caudal vertebrae that lack hemapophyses in the ceratopsians under study, these are the pygidial vertebrae after Hoffstetter and Gasc (1969). In *P. andrewsi* and *M. cerorhynchus*, the anterior chevron bone (hemapophysis) is located between 3 and 4cd (Brown and Schlaikjer, 1940, 1942). This is observed in female *P. andrewsi* PIN, no. 3143/7 and corroborated by a series of vertebral centers 1–3cd from other specimen of this species (PIN, no. 614/32). However, in male *P. andrewsi* PIN, no. 3143/16, *Bagaceratops* sp. PIN, no. 614/34, *Udanoceratops* sp. PIN, no. 4046/11, and specimen *P. andrewsi* PIN, no. 614/33, the first hemapophysis is located posterior to 4cd. Notice that in *M. cerorhynchus*, only the first anterior caudal vertebrae was in natural articulation with the posterior sacral vertebra, whereas 4–6cd were reconstructed by analogy with those of *P. andrewsi* (Brown and Schlaikjer, 1942). Taking into account the fact that in the original description, this dinosaur was assigned to the genus *Leptoceratops*, in which the first hemapophysis occurs on 5cd (Sternberg, 1951), the position of the first hemapophysis in *M. cerorhynchus* remains uncertain. Even if it is granted that *Leptoceratops* (like *Udanoceratops*) had eight sacral vertebrae rather than seven, the first hemapophysis of *Montanoceratops* would be located between 4 and 5cd. It is clear that different ceratopsian genera may possess different numbers of pygidial vertebrae; however, in the sample examined, the female *P. andrewsi* had two, and the male had at least three vertebrae. Different numbers of pygidial vertebrae in males and females of the same species occur in mammals (Cingulata), turtles, and crocodiles (White, 1939; Farlow 1995), and the males of these species have unpaired sexual organs. On the contrary, male lizards characterized by paired copulative apparatus possess the same number of pygidial vertebrae as females (White, 1939; Tereshchenko, 1991a).

#### Functional Interpretation of Sexual Differences

The absence of juveniles and pairs of young immature specimens of comparable sizes in the sample provides no way of tracing the changes of S-shaped curvature of the vertebral column in Protoceratopsidae at the early stages of formation. As the animals grew, constructive reorganization of the vertebrae occurred and the natural curvature of the vertebral column developed in such a way that the arc of the dorsal curvature became weaker in adult females than in males. Partial dorsal straightening increased the trunk length of mature females and, consequently, increased the volume of the abdominal cavity. The change of the orientation of the vertebral–costal articulation toward the direction of the thoracic region of the vertebral column, i.e., the change of the relatively vertical position for an almost horizontal position, occurs in mammals and is

associated with the ability for lateral movements of the ribs during breathing (Klimov, 1950). Consequently, a more inclined position of the vertebral–costal articulation and structural differences of the diapophyses (parameters 5 and 6) on the thoracic vertebrae may be associated with the adaptation of the female thorax for leveling the loads on ribs during breathing in the period of egg bearing. Since a protoceratopsid egg clutch includes 30–36 eggs (Brown and Schlaikjer, 1940), female weight prior to and within the reproductive period probably changed considerably. This increased the loads, not only on the ribs, but also on the vertebral column of females, particularly between the limb girdles. However, limited vertical mobility of the vertebral column, in particular between 4 and 8th (Tereshchenko, 1991b), impeded the flexure in females and gave a strong rigidity to the dorsum against extension during rapid locomotion in males. The higher spinous processes of males in comparison with those of females are probably attributable to a greater weight of muscles of the transversospinal system. In the thoracic region of males, the latter was subjected to a greater mechanical load than in females. This is corroborated by expanded distal endings of the spinous processes of these vertebrae in males in contrast to those of females.

Sexual differences in the cervical region consist mainly of the development of the cervical arc and should correlate with the structure of the axial skeleton. In protoceratopsids, they are observed in the arrangement of the facets on the prezygapophyses and postzygapophyses, the orientations of the latter, and the inclination of the spinous processes (parameters 9, 13–15). Two posterior cervical vertebrae are involved in the ascending part of the dorsal curvature, and the latter rises more abruptly in males than in females (Figs. 2a–2d). Therefore, the facet on the postzygapophyses of 8c in females is positioned at a smaller angle to the longitudinal axis of the center, and the difference between the levels of the facets on the zygapophyses of 9c is smaller than in males. At the same time, the rise of the anterior part of the neurapophysis between the prezygapophyses and the postzygapophyses of 9c in females occurs more abruptly than in males. The difference between males and females in the orientation of the spinous process of the axis (of almost the same height in either sex) becomes clear from the viewpoint proposed by Slijper (1946), who regarded the process as a lever that transmitted forces from the muscles and ligaments to other vertebrae. The inclinations of the spinous processes of the axis and anterior thoracic vertebrae are determined by the resultant of the epaxial muscle of the neck (*m. capiti-dorsi-clavicularis*) (Russel, 1935) applied to the processes at the most effective angle of 90°. The *capiti-dorsi-clavicularis* muscle should be similar in structure to the *spinalis cervicis* muscle of the neck of living tetrapods (Slijper, 1946; Gurtovoi 1978; Gurtovoi and Dzerzhinskii, 1992). A weak cervical curvature in female *P. andrewsi* provides the optimum angles between the muscular fascicles and the spinous pro-

cesses of 2c and anterior thoracic vertebrae (Fig. 2e). An increase in the cervical curvature in female *Bagaceratops* sp. requires an increase in the height of the spinous processes of 1t and 2t and a decrease in the height of the spinous processes posterior to 3t. In this case, a small increase in the angle between the muscular fascicles and the ending of the spinous process of 2c only slightly influences the efficiency of this muscle (Fig. 2g). If male *P. andrewsi* (similar to female *Bagaceratops* sp. in the development of the cervical arc) and male *Bagaceratops* (having a larger cervical arc) had the same structure of the axis as females (Fig. 2f, dotted line), the high spinous processes of the anterior thoracic vertebrae would have increased the angle between the muscle and the spinous process of 2c to 120–125°; this would have strongly decreased the efficiency of the muscle. Lest the working capacity of the epaxial muscle of the neck decrease, the spinous process on 2c in male protoceratopsids deviates cranially, and the spinous processes on three anterior thoracic vertebrae (particularly on 3t) deviate caudally; this decreases the angle between the muscle and the distal surface of the spinous process to the optimum (Figs. 2f and 2g). Thus, in *P. andrewsi*, the inclination of the spinous process of the axis depends not only on the height of the spinous processes of the thoracic vertebrae, but also on the length of the cervical curvature. In females, the latter is shorter than in males (Figs. 2a–2d).

This study has not conclusively resolved the problem of sexual dimorphism in Protoceratopsidae. However, the examination indicated rather reliable sexual characters, three of which are characteristic of all tetrapods (the spinous processes of the thoracic vertebrae are lower, the abdominal cavity is larger, and the pelvis is broader in females than in males). Further study aimed at the detection of sexual dimorphism in the skeleton of extinct vertebrates is of great importance, not only for the theory of sexual selection, but also for the differentiation between sexual features and taxonomic characteristics. In particular, notwithstanding the fact that Brown and Schlaikjer (1940), Dodson (1976), and the examination performed in the present study have identified specimen AMNH, no. 6466 as a male, the methods applied by the researchers for studying this type of variation in Protoceratopsidae are not irreproachable. The examination of sexual differences in postcranial skeletons performed independently of sex identification by cranial characters does not contradict the viewpoint stated by Dodson (1976) concerning the necessity of a critical revision of the genera and species belonging to advanced ceratopsians.

#### ACKNOWLEDGMENTS

I am grateful to V.B. Sukhanov for general supervision and to E.N. Kurochkin for perusal of the manuscript and valuable comments.

This study was supported by the Russian Foundation for Basic Research, project nos. 00-15-97754 and 00-04-49348.

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