

# Sexual Dimorphism in the Postcranial Skeleton of Dinosaurs

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**Abstract**—Sex-related variability in the tetrapod skeleton has regular patterns that reflect the different ontogenetic pathways leading to the formation of adult sexual features. In dinosaurs (as well as amniotes in general), these features are most pronounced in the morphology of postcranial bones. In males, sex-related traits reflect improved adaptations of the locomotor apparatus, while in females they are associated with the adaptation to hatching and laying eggs. Therefore, beyond the specifics of sex differences in different taxa of dinosaurs, there are also common patterns: in all adult males, neural spines are higher and limb bones are more robust than in females, while the volume of the abdominal cavity and the width of the pelvis are greater in females. The case study of ceratopsians (*Ornithischia*: *Neoceratopsia*) shows that knowledge of basic sex-related characters (those most constant in tetrapods) facilitates the search for accessory characters (more taxon-specific) that are correlated with basic ones, which provide a way to establish the limits of sexual variability typical for a given taxon.

**Keywords:** sexual dimorphism, postcranial skeleton, dinosaurs

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## INTRODUCTION

The problem of recognizing age dimorphism in the tetrapod skeleton has for a long time claimed the attention of paleontologists, who sought not only to separate sex-related characters from taxonomically important ones, but also to attain a better understanding of the role of sexual selection in the evolutionary development of characteristic morphobiological traits of individual forms and groups of animals. Dinosaurs are of special interest in this regard, and their sexual variability has been the subject of a great number of publications. However, judging from the reviews of Molnar (2005) and Mallon (2005, 2017), the problem of recognizing sexual dimorphism in fossil reptiles remains unsolved to this day. According to Mallon (2017), the main obstacles to establishing statistically significant sexual dimorphism traits in dinosaurs are: small sample size, insufficient control of results and a lack of a common methodology for solving the problem. Mallon further notes that there is no point in looking for sexual traits in the postcranial skeleton of modern reptiles which cannot be identified in fossil bones. In the same article, Mallon (2017) discusses mainly the skull and only partially the postcranial skeleton, leaving out of discussion the research on the sexual dimorphism in the axial skeleton of dinosaurs. This is surprising, considering that the same author had earlier (Mallon, 2005) positively evaluated the results of research into this question on the horned dinosaurs of the Upper Cretaceous of Mongolia

(Tereshchenko, 2001), pointing out that further study is required for their validation, but somehow ignoring the analysis of sexual variability in the postcranial skeleton of modern reptiles (Tereshchenko, 1980, 1991a) which preceded the attempt to solve the same problem for fossil ones (Tereshchenko, 1997; 2001). The combination of these two complementary lines of research had the objective of minimizing the difficulties of identifying the sex of dinosaurs which were later noted by Mallon. In this article we shall try to demonstrate the viability of this approach.

## MATERIAL

In discussing sexual dimorphism of the postcranial skeleton and its individual development in modern reptiles, we used the results of the study of 69 specimens of agamids (*Squamata*: *Lacertilia*), belonging to seven species and four genera: the steppe agama (*Trapelus sanguinolentus* (Pallas, 1814)), 13 males and 16 females; common agama (*Agama agama* (Linnaeus, 1758)), 2 males and 2 females; secret toadhead agama (*Phrynocephalus mystaceus* (Pallas, 1776)), 5 males and 5 females; Caucasian agama (*Laudakia caucasia* (Eichwald, 1831)), 5 males and 6 females; redbelly rock agama (*Laudakia erythrogaster* (Nikolsky, 1896)), 2 males and 1 female; Turkestan agama (*Laudakia lehmanni* (Nikolsky, 1896)), 3 males and 1 female; Himalayan agama (*Laudakia himalayana* (Steindachner, 1867)), 1 male and 4 females (Tereshchenko, 1991a). The discussion of the problem of rec-

ognizing sex and age-related variability of the postcranial skeleton in fossil reptiles (Ornithischia: Neoceratopsia) is based on the results of the study of 19 specimens (Tereshchenko, 2001) of protoceratopoids (*Protoceratops*, *Bagaceratops*, *Udanoceratops*) from Late Cretaceous Mongolian localities: Djadokhta Formation (Tögrökiin Shiree, Bayn Dzak, Udan Sayr, Baga Tariach) and Baruun Goyot Formation (Hermin Tsav, Gilbertu) (Lower to Middle and Middle to Upper Campanian: Alifanov, 2014). This material is housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN). Additionally, two skeletons of *Protoceratops* from the Kozłowski Paleobiology Institute of the Polish Academy of Sciences (ZPAL) were studied, and a cast of the *Leptoceratops gracilis* Brown, 1914 skeleton (PIN 4769/9), the original of which is housed in the former National Museum of Canada (NMC 8887), now renamed the Canadian Museum of Nature. In total, 23 specimens were studied, including eight likely females and 13 males (Table 1). The main focus of study was the axial skeleton and the pelvic girdle, since the shoulder girdle and the limbs were relatively poorly preserved.

In this study, the rock agamas of Eurasia are treated within the genus *Laudakia* (Panov and Zykova, 2003), rather than *Stellio*, where they were included previously (Tereshchenko, 1991a). In classifying the subclasses Lepidosauromorpha and Archosauromorpha, we follow the system of V.R. Alifanov (2012), except that in addition to the families Ceratopidae Marsh, 1889, Protoceratopidae Granger et Gregory, 1923, Bagaceratopidae Alifanov, 2003, we also include in the infraorder Neoceratopsia the family Leptoceratopidae Makovicky, 2001 (Tereshchenko, 2018).

## METHODOLOGY

In order to solve the problem of identifying sexual dimorphism in fossil tetrapods, it is necessary to draw on modern material, where a set of statistically significant characters can be established, typical for males and females respectively, which is impossible with fossil material not only due to the small number of specimens being compared but also because it is impossible to know what traits should be focused on. The reasons for this concern the different possibilities open to the student of modern and fossil material, respectively. A neontologist is working with specimens belonging to known taxa, for which sex and age can be established from the developmental state of the gonads, whereas the paleontologist is faced with the reverse problem, namely, to determine the age, sex and systematic affinity of available fossils based on the study of morphological characters of the skeleton (Tereshchenko and Sukhanov, 2009). Therefore, before considering sexual dimorphism of the postcranial skeleton in dinosaurs, we have to consider its manifestations in recent forms.

The study of sexual dimorphism in modern reptiles (Lacertilia: Agamidae) showed (Tereshchenko, 1991a), as expected, that the range of sexual traits and their expression both increase with age, reaching their maximum in adult, sexually mature individuals (Table 2). Therefore, in distinguishing sexes in agamid lizards, we used only those characters that significantly differed in adult, sexually mature males and females. The characters were considered significant whenever the difference between the means was equal or exceeded the maximum error over five or more measurements (Pomorsky, 1935). For characters observed on the first 14 or 15 caudal vertebrae, we calculated correlation coefficients and regressions; for every statistically significant character, theoretical regression lines were constructed from the regressions obtained. Sexual differences in the vertebral column were established by comparing identical vertebrae (i.e. of the same number), since vertebrae vary in morphology with their position in the vertebral column in both males and females. Pairs were selected based on similar individual length (from anterior margin of the head to the cloaca) for each age group, in order to eliminate size differences between males and females, since, as adults, males are larger than females and therefore also longer (Bannikov et al., 1977). Four age groups are generally recognized in lizards (Kamalova, 1971; Okulova, 1973): young of the year (small immature), young immature (=large immature), young mature (=small mature) and adult mature (=large mature). However, our study of the development of sexual differences during growth (Tereshchenko, 1991a) showed that clear separation of agamids into age groups (and even subgroups), in our case, into age stages, can be established based on the expression of sexual dimorphism in the postcranial skeleton (we recognized seven such stages, Table 2).

Review of published data and our results (Tereshchenko, 1980, 1991a) indicate that in most modern tetrapods there are four key indicators that can be fairly confidently used to distinguish the two sexes: in males, neural spines are higher than in females (Stromer, 1915; Slijper, 1946; Bogert, 1964; Sokolov, 1971; Barbadillo and Sanz, 1983); the volume of the abdominal cavity is larger in females than in males (Vorobyev, 1932; Porkert and Grosseova, 1984; Bauwens et al., 1997 among others); pelvic width is smaller in males than in females (Vorobyev, 1932; Dementyev, 1940; Klimov, 1950; Sokolov, 1971); in mammals, bones of the axial and appendicular skeleton are robust (stout, massive, thick) in males and more gracile in females (Vorobyev, 1932; Sokolov, 1971). In some birds (monogamous ones), however, the last character shows a reverse distribution, so that the skeleton is larger in females than in males (Molnar, 2005). In reptiles (Lacertilia: Agamidae), males have thicker limb bones (Table 2, character 8), and more gracile vertebrae, compared to females (Tereshchenko, 1991a). Whereas the sexually dimorphic pattern of bone

Table 1. Age and sex composition of the studied protoceratopoids

Age stages, taxon, collection number, sex							Family
Young immature		Young mature		Adult mature		Senescent	
smaller	large	small	large	small	large		
<i>Protoceratops andrewsi</i> PIN 3143/6	<i>Protoceratops andrewsi</i> ZPAL Mg D-II/3, ♀	Protoceratopidae gen. indet. PIN 614/61, ♂	<i>Protoceratops</i> sp. PIN 3143/5, ♂	<i>Protoceratops andrewsi</i> PIN 3143/16, ♂	<i>Protoceratops andrewsi</i> PIN 3143/12, ♂	<i>Protoceratops andrewsi</i> PIN 3143/9, ♀	Protoceratopidae
			<i>Protoceratops</i> sp. PIN 3143/7, ♀		Protoceratopidae gen. indet. PIN 614/30, ♀	Protoceratopidae gen. indet. ZPAL Mg D-II/4, ♂	
			Protoceratopidae gen. indet. PIN 614/35, ♀		<i>Protoceratops andrewsi</i> PIN 3143/14, ♂	Protoceratopidae gen. indet. PIN 3143/4, ♀	
	Bagaceratopidae gen. indet. PIN 3142/7, ♀			Bagaceratopidae gen. indet. PIN 614/34, ♂	Bagaceratopidae gen. indet. PIN 614/29, ♂	Bagaceratopidae gen. indet. PIN 614/53, ♀	Bagaceratopidae
	Leptoceratopidae gen. indet. PIN 4046/11, ♂	<i>Leptoceratops gracilis</i> PIN 4769/9, ♂ (NMC, no. 8887: Sternberg, 1951)			Bagaceratopidae gen. indet. PIN 4550/3, ♀	<i>Bainoceratops efreмовi</i> PIN 614/33, ♂	Leptoceratopidae

PIN and ZPAL collection numbers correspond to the following Mongolian localities: 614 and Mg D-II: Bayn Dzak, 3907: Udan Sayr, 3142: Hermin Tsav, 3143: Tögrökiin Shiree, 4046: Baga Tariach, 4550: Gilbertu.

**Table 2.** Development of some sexually variable, postcranial characters in the ontogeny of *Trapelus sanguinolentus* (Pallas, 1814)

No.	Character	Age stages (body length in mm)					
		Immature		Young		Mature	
		small (43–65)	medium (66–75)	large (76–85)	small (86–93)	large (94–108)	Senescent (109–115)
1	$h_{\delta} > h_{\varphi} - 3c - 2sc - 1 - 14cd$	3% 5%	10% 15%	20–25% 25–30%	15–20% 30–35%	2%	
2	$B_{\delta} > B_{\varphi} - 3c - 14cd$	No difference	No difference	3–4%	7–8%	15–20% 2–3%	
3	$Lc/Hc_{\varphi} > Lc/Hc_{\delta} - 4 - 14th$	No difference	2–4%	5–10%	10–15% 15–20%	2%	
4	$P_{\varphi} > P_{\delta} - 1sc$ $P/K_{\varphi} > P/K_{\delta}$	No difference	No difference	2% 3–5%	10–15% 20–25%	20–25% 15–20%	
5	Relief of the posterior surface of neuropophyses on 5–13th	Smooth	Smooth in ♂♂, in ♀♀ appears an inter-postzygapophyseal crest			♂♂ have an interpostzygapophyseal crest; in ♀♀ it is pyramid-shaped and passes dorsally in to the postspinal crest	
6	Ribs on cervical vertebrae immobilized	Ribs are free		5c (♀)	6c (♀) 5c (♂)	7–8c (♀) 6c (♂) 5–6c (♀) 5c (♂)	
7	Cervical ribs fuse with vertebrae						
8	Robustness of girdle and limb bones	No difference	In ♂♂ bones somewhat thicker than in ♀♀		Robust (thick) bones in ♂♂, gracile (thin) in ♀♀		
9	Articulation of pubis and ischium	Approximately equal mobility of epipubis and hypoischium in both sexes			More rigid in ♂♂ than in ♀♀	Onset of immobilization in ♂♂   in ♀♀	
10	Location of the ischial process on the ischium in ♀♀ and ♂♂	Approximately equal	Differences indistinct		Medially located in ♀♀, displaced towards the acetabulum and somewhat rotated towards the cloaca in ♀♀		
11	Degree of fusion of the epiphyses with the diaphyses in long bones	No fusion			Onset of fusion in ♂♂	Fused in both ♂♂ and ♀♀	
12	Crest at the base of the inner trochanter	Crest absent			Absent in ♀♀	Weakly developed in ♀♀	
					Weakly developed in ♂♂	Well developed in ♂♂	

Table compiled with data from Tereshchenko (1991a), omitting young of the year (smallest young immature individuals, 33–42 mm) since they do not show sexual differences in the postcranial skeleton. Abbreviations: **B** width of the vertebra across the postzygapophyses, **Hc** centrum height, **h** height of the neural spine, **K** width of vertebra at the precondylar neck, **Lc** centrum length, **P** length of the gap between pleurapophysis and the surface of the vertebra; see text for other explanations.

robustness found in mammals is called normal (Mallon, 2005), and the one found in monogamous birds (birds of prey and, likely, also waders) is called reverse (Molnar, 2005), the lizard pattern may be called combined: normal in the appendicular skeleton and reverse in the vertebral column. It should also be noted that the first sexual distinctive feature (the height of neural spines) corresponds to one character, whereas the second feature (robustness of postcranial bones) corresponds to two characters (one for the limbs and the other for the vertebral column), which can coincide with each other, merging into one character (as in mammals and some birds) or differ, i.e. appear as two characters (as in lizards). The dimorphism in the volume of the abdominal cavity, on the other hand, as well as pelvic width, is usually expressed as several characters, which may vary between taxa. Since characters such as “neural spine length” and “limb bone robustness” are the more permanent traits of sexual dimorphism, we classify these as *basic characters*, whereas the more individual sexual differences are classified as *accessory characters*. Knowing what the more consistent traits are for sexual dimorphism in tetrapods (the basic characters) simplifies the task of searching for the more specific sexual differences (accessory characters) which are correlated with the basic ones, thereby generating a fuller picture of the distinctive features of sexual variability typical for a given taxon. Applying this approach to the analysis of sexual differences in the fossil forms (Tereshchenko, 2001), we thereby follow the method of Nopcsa (1929), who studied sexual variability in ornithopods (Dinosauria: Ornithischia). Nopcsa established sexual differences “by establishing links between several characters, of which at least one was undoubtedly either a primary or secondary sexual character, thereby establishing the secondary sexual nature of the other linked characters” (Davitashvili, 1961, p. 482). We can, therefore, use as a significance test for sexual characters in dinosaurs (and for amniotes in general) not the available sample size, but the very fact of linkage between particular characters with certain sexual differences, independent of geographical variability in recent reptiles (Tereshchenko, 1991a) or stratigraphic separation in fossil ones (Tereshchenko, 2001, 2004a). Therefore, the identification of sexual variability in the postcranial skeleton of dinosaurs has to begin with the study of those basic differences between the sexes that have the most consistent manifestations in tetrapods and which we classified as the basic characters. These include, as already mentioned, features of neural spines, being higher in males than in females—a character observed already in young immature individuals (Table 2, character 1), the robustness of the girdle and limb bones, which, for mammals and, typically, for modern lizards (Table 2, character 8) are more robust in adult males than in females. After separating fossils according to these basic distinguishing characters, we can then try to find other characters linked to the

robustness of the bones of the axial skeleton, sexual differences in the volume of the abdominal cavity and pelvic width. By comparing sexual differences established this way among individuals belonging to several genera of the same family, it is then possible to establish common patterns. Further comparison of this pattern with patterns of sexual variability established for other families gives an idea of patterns of sexual differences at the order level etc.

Before identifying sexual dimorphism in dinosaurs, it is necessary not only to reconstruct the life position and order of skeletal elements, but also to determine the age composition of the available sample (Tereshchenko and Sukhanov, 2009, 2014), in order to separate young individuals (which are more weakly differentiated) from adult mature ones. The ordinal number of each vertebra in protoceratopoids (Protoceratopidae, Bagaceratopidae, Leptoceratopidae) was determined according to a key (Tereshchenko, 2007), which includes a system of measurements for vertebrae and their elements (centra and neuropophyses). The size of the damaged, deformed, and missing vertebrae, as well as the shape of the natural curvature of the spine, taking account of the intervertebral disks, were reconstructed according to specially developed methods (Tereshchenko, 1990, 1991b, 2015). Pairs were selected mostly based on the size of the specimens being compared within each age stage, in order to exclude this kind of differences in males and females, since it is believed that males, for instance, of *Protoceratops*, were larger than females (Brown, Schlaikjer, 1940).

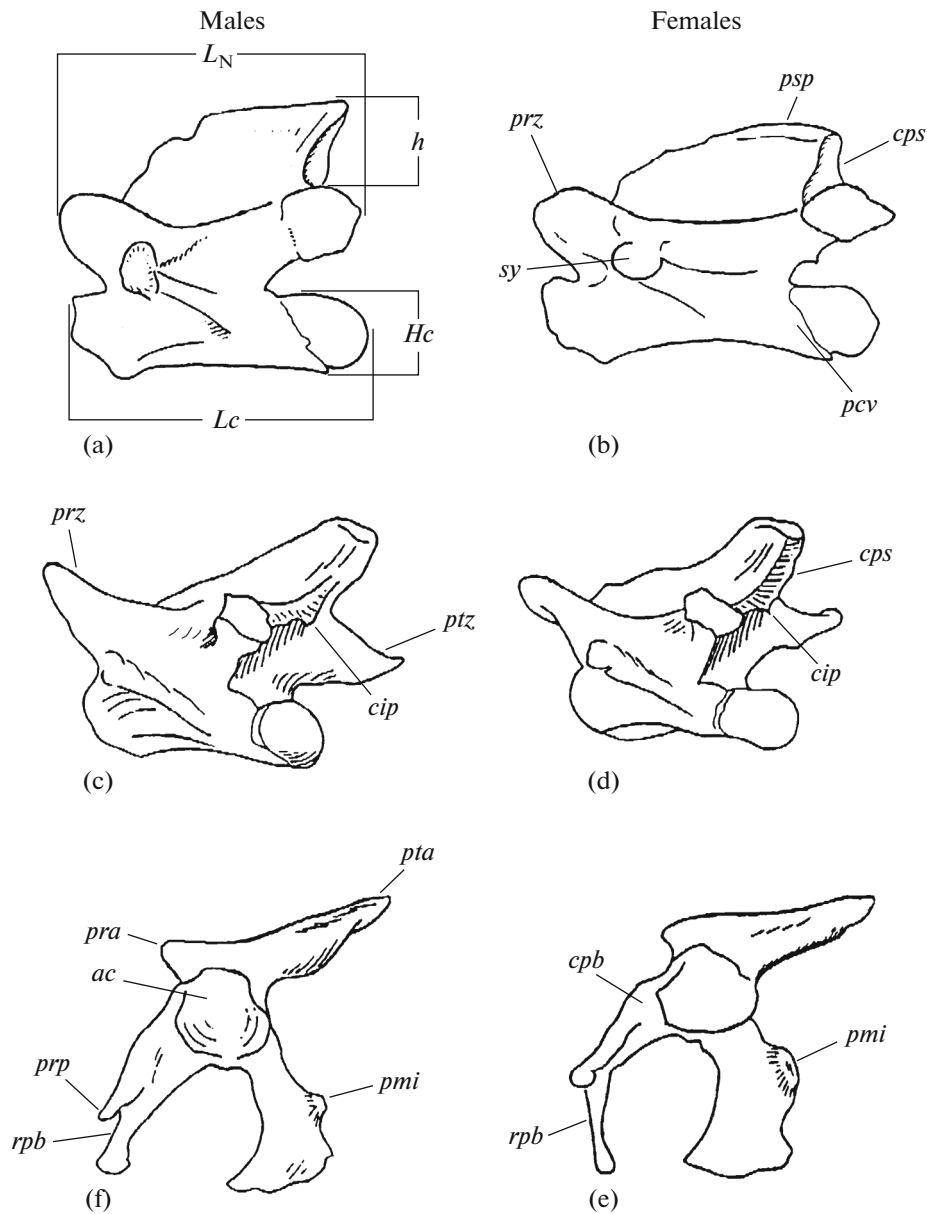
From the axial skeleton of ceratopsian dinosaurs, individual age is usually determined based on the degree of fusion between centra and neural arches (e.g., Gilmore, 1917; Bohlin, 1953; Romer, 1956; Chinnery, Weishampel, 1998). It is believed that in ceratopsians (as in archosaurs in general), the fusion of centra and neural arches forms a true neurocentral suture (Brochu, 1996). Our studies show however, that centra and neural arches in archosaurs (as in mammals) are connected not by a syndesmosis (a suture junction), but a synchondrosis (false suture, sutural spuria: Klimov, 1950). This is explained by the ability of reptiles to grow throughout life (Carroll, 1988); because of this, in ceratopsian dinosaurs, complete fusion of neural arches with centra does not occur even in old individuals (Tereshchenko, 2018). Therefore, based on the expression of this character, age variability can be assessed only in relative terms (Brochu, 1996). We selected characters (Table 3) for determining the age composition of our sample (Table 1) from both published data on age variability in the postcranial skeleton of ceratopsian dinosaurs (e.g., Brown, Schlaikjer, 1940; Sternberg, 1951; Coombs, 1980, 1982) and our own experience in studying this question (Tereshchenko, 2001, 2004a, 2008; Tereshchenko, Singer, 2013), including unpublished data. As the basic character, we selected the degree of size dif-

**Table 3.** Age-related changes in the vertebral column and the pelvic girdle of protoconeratopoids

Characters	Age stages						
	Young immature		Young mature		Adult mature		
	Small	Large	Small	Large	Small	Large	
Size differentiation of centra in precaudal vertebrae	None	Poorly developed	Well developed				Senescent
Arc length of cervical and dorsal curvature	?	15°–20° greater than in adults	10°–15° greater than in adults	Protoconeratopidae: 30°–45° and 40°–60° Bagaceratopidae: 45°–55° and 55°–70° Leptoceratopidae: 50°–55° and 30°–35°		15°–20° smaller than in adults	
Sequence of fusion in the first three cervical and sacral vertebrae (first centra, then zygapophyses) and sacral ribs to vertebrae*	Vertebrae and ribs separate, 1–3c and 1–8sc centra immobilized	Onset of fusion in 1–2c and 2–4sc	1–2c and 2–4sc fused; onset of fusion in 2–3c, 1–2sc and rib 3sc with centra 2–3sc	<b>Protoconeratopidae, Bagaceratopidae</b> 1–3c, 1–4sc, and rib 3sc fused; onset of fusion in 3–5sc and rib 4sc with centra 3–4sc  <b>Leptoceratopidae</b> 1–3c, 1–4sc, and rib 2sc fused; onset of fusion in 4–6sc and ribs 3, 4sc with centra 2–3–4sc		1–3c fused, 3 lm-7sc, and ribs 3–6sc; onset of fusion in 7–8sc, rib 7sc with centrum, and ribs 3–6sc with ilium	
Heterocoelous centra 1–5cd**	None	Poorly developed	Well developed		Well developed		
Neural spines of caudal vertebrae	Straight	Curved with the convex side of the arc facing posteriorly	<b>Protoconeratopidae, Bagaceratopidae</b> Noticeably on 9–11cd on 8–12cd  <b>Leptoceratopidae</b> Weakly on 9–11cd				Strongly on 7–14 cd
Ilium	Preacetabular process somewhat deflected laterally, postacetabular process straight, lateral surface of the ilium flat	Straight	Weakly on 9–11cd	Preacetabular process strongly deflected laterally, postacetabular process straight, lateral surface of the ilium somewhat concave	Weakly on 8–12cd		

\* In Neoceratopsia 23 vertebrae represent the original presacral part of the vertebral column, while vertebrae 24–27 are true sacral vertebrae (Sukhanov, Tereshchenko, 2004; Tereshchenko, 2004a, 2007). In protoconeratopoids, the first true sacral rib stands out in size and robustness. Its proximal end is connected ventrally with the centra of two adjacent vertebrae (23–24), and dorsally (without a gap) with the pedicle of the neural arch all the way to the diapophysis of the second of the two vertebrae. In protoconeratopoids, the number of “pre-sacral” vertebrae depends on the location of the sacrum as a whole relative to the primary sacral vertebra. For instance, in *Protoconeratops* and *Bagaceratops*, the sacrum is displaced by one vertebra compared with *Udanoceratops* and *Leptoceratops*. As a result, the sacrum, which includes eight vertebrae, contains some vertebrae of dorsal origin (two vertebrae in the first two genera, one vertebra in the second). There is also a difference in the primary sacral vertebra: 3sc in *Protoconeratops* and *Bagaceratops*, 2sc in *Udanoceratops* and *Leptoceratops*.

\*\* Heterocoelous form of centra 1–5cd in protoconeratopoids is, strictly speaking, the reverse of the form found in the presacral vertebrae of birds, is defined as a combination of opisthocelous morphology in the frontal plane and procelolous form in the sagittal plane (Tereshchenko, 2004b).

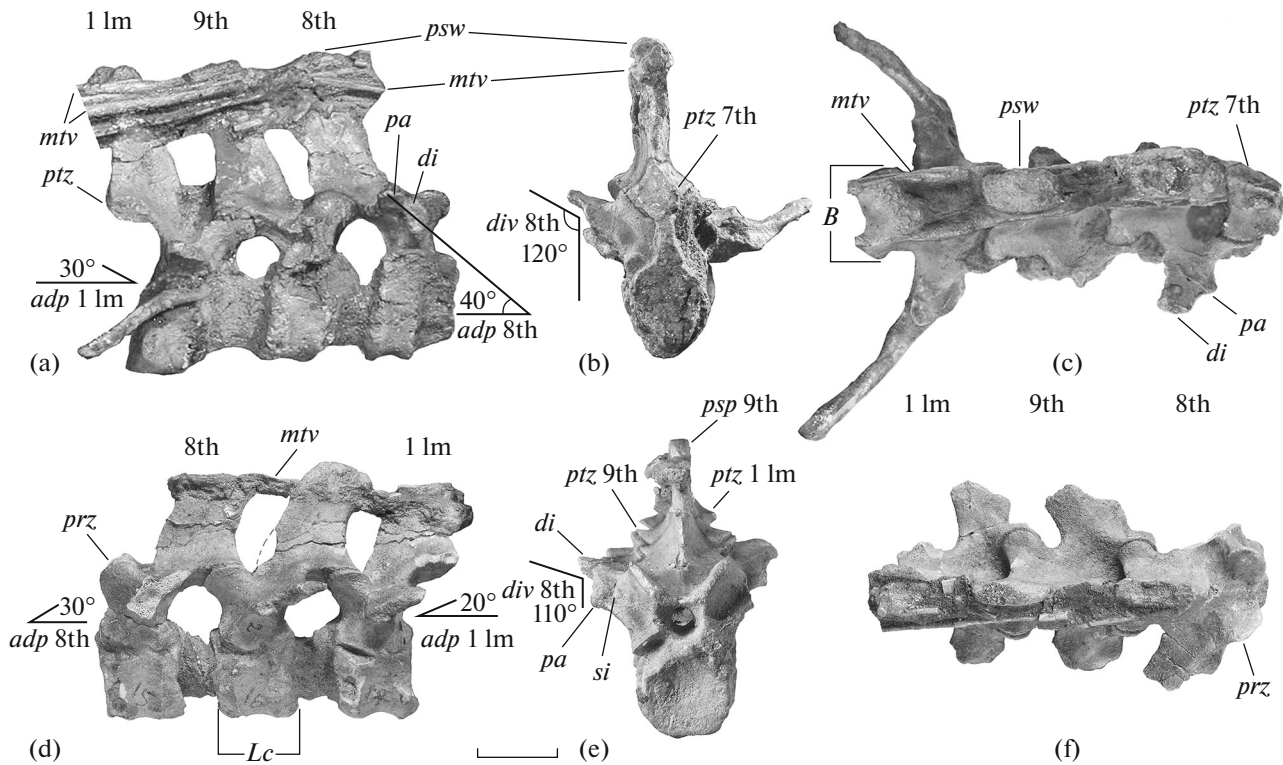


**Fig. 1.** Tenth dorsal vertebrae (a–d) and pelvic girdles (e, f) of agamid lizards (from Tereshchenko, 1991a, Figs. 1c–1f; 4c 4d): (a, b, e, f) *Laudakia caucasia* (Eichwald, 1831); (c, d) *Trapelus sanguinolentus* (Pallas, 1814); (a, b, e, f) left lateral view; (c, d) posterior and left lateral view. Abbreviations: *ac* acetabulum, *cip* crista interpostzygapophysialis, *cpb* corpus ossis pubis, *cps* crista postspinalis, *Lc* centrum length, *LN* neurapophysis length, *Hc* centrum height, *h* neural spine height, *pcv* precondylar constriction of the procoelous centrum, *pra* preacetabular process, *prp* prepubic process, *pmi* metaischadic process, *prz* praezygapophysis, *psp* processus spinosus neuralis, *pta* postacetabular process, *ptz* postzygapophysis, *rpb* ramus ossis pubis, *sy* synapophysis.

ferentiation in the centra of precaudal vertebrae (the change in the size of centra along the precaudal region of the vertebral column), which is much smaller in immature individuals compared with mature ones, both in modern (Tereshchenko, 1991a) and fossil (Coombs, 1980, 1982; Tereshchenko, 2001) reptiles.

During morphometric studies of sexual dimorphism in modern and fossil reptiles, we used both those parameters that are size-linked (linear measure-

ments, Figs. 1a, 2c) and those that are not (angular measurements, Figs. 2a, 2b). In processing osteometric data, we used, in addition to direct measurements, also ratios (indexes) of measurement pairs that most clearly reflect sexual differences in individuals irrespective of their sizes. These indexes can therefore serve as indicators of sexual characters that are difficult to identify on isolated bones. For instance, in order to show differences between direct measure-



**Fig. 2.** Eighth, ninth and tenth dorsal vertebrae (8th, 9th, 3 lm) of *Protoceratops* sp.: (a–c) PIN 3143/5 (male), (d–f) PIN 3143/7 (female); (a, d) lateral view: (a) right view, (d) left view; (b, e) anterior view; (c, f) dorsal view. Abbreviations: *adp* inclination of the axis of the costovertebral articulation, angle with the horizontal, *B* vertebral width across postzygapophyses, *di* diapophysis, *div* diapophysis inclination angle with the vertical, *mtv* mineralized tendons of *m. transversospinalis*, *pa* parapophysis, *psw* transverse expansion of the tip of the neural spine, for other abbreviations see Fig. 1. Note: in the notation for vertebrae, the abbreviation of the spinal region is followed by the number of the vertebra within that region. (a) postzygapophyses on 7th removed, (b) left rib on 1 lm removed. Scale 20 mm.

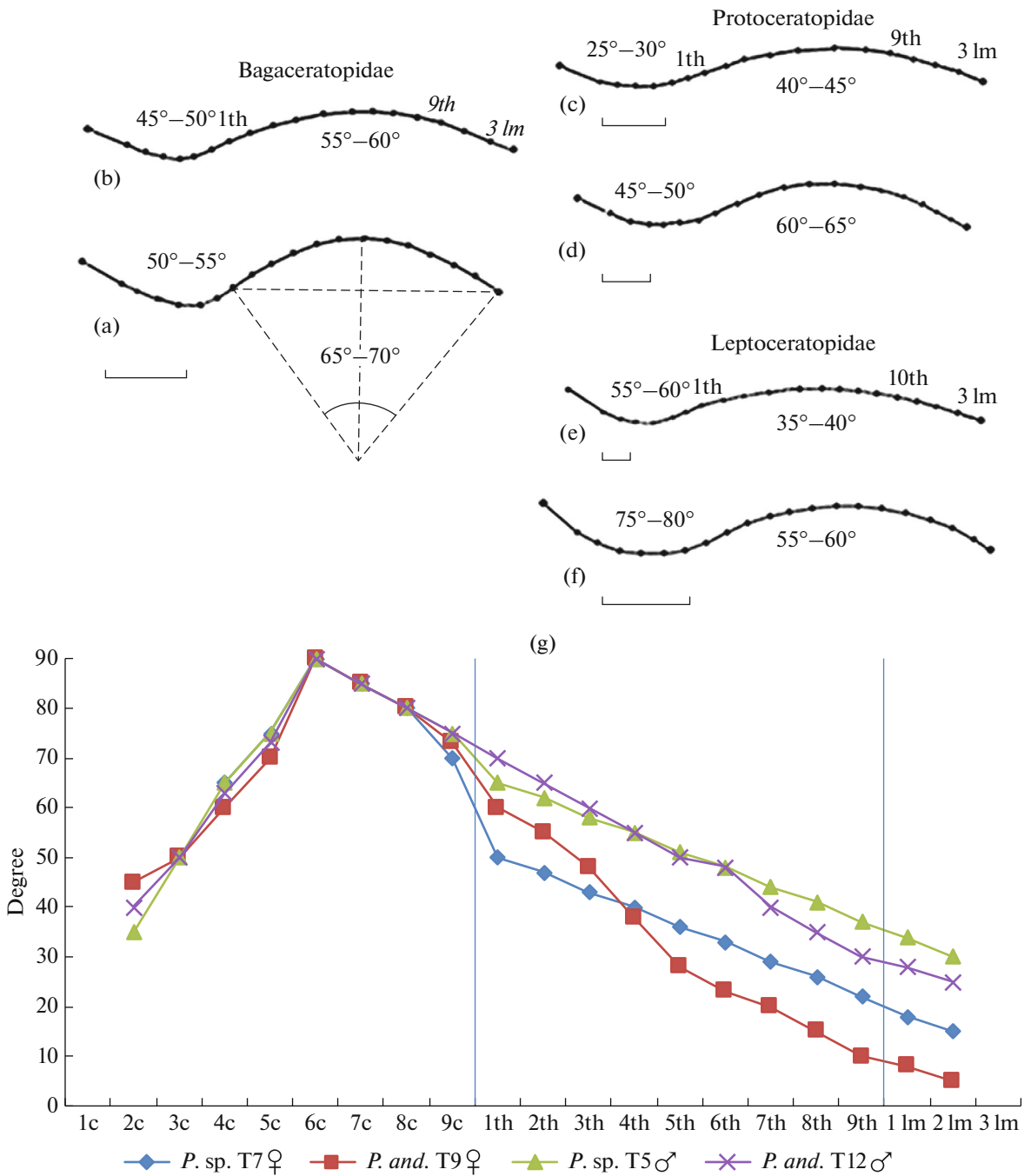
ments and indirect parameters (indexes) in agamid lizards linked to age-related changes in sacral width and therefore in the pelvic width between the right and left halves of the ilium (Table 2, character 4), we used the ratio between the width of the first sacral vertebra and the width of its centrum at the precondylar constriction (P/K). Differences in the relative centrum length were calculated in a similar way, i.e. as the ratio between centrum length and its width. In ceratopsian dinosaurs, the arc of the cervical (convex downward) and dorsal (convex upward) spinal curvature (Fig. 3a), as well as the curvature of the preacetabular process of the ilium and of the ramus of the ischium (Figs. 4a, 4e), were defined through the central angle of the arc in degrees. Since the sizes of individuals of the same age vary between members of different families of ceratopsian dinosaurs (Tereshchenko, 2001), relative indices of the height of the neural spine and the width of the centra were used, i.e. the ratio between the neurapophysis length (length of vertebra across the margins of prezygapophyses and postzygapophyses) and the height of the neural spine (LN/h) and the ratio between centrum width and centrum height (Bc/Hc).

In text, figures and tables, numbers denote the ordinal numbers of vertebrae in the following regions: c cervical, th dorsal, lm lumbar, sc sacral, cd caudal.

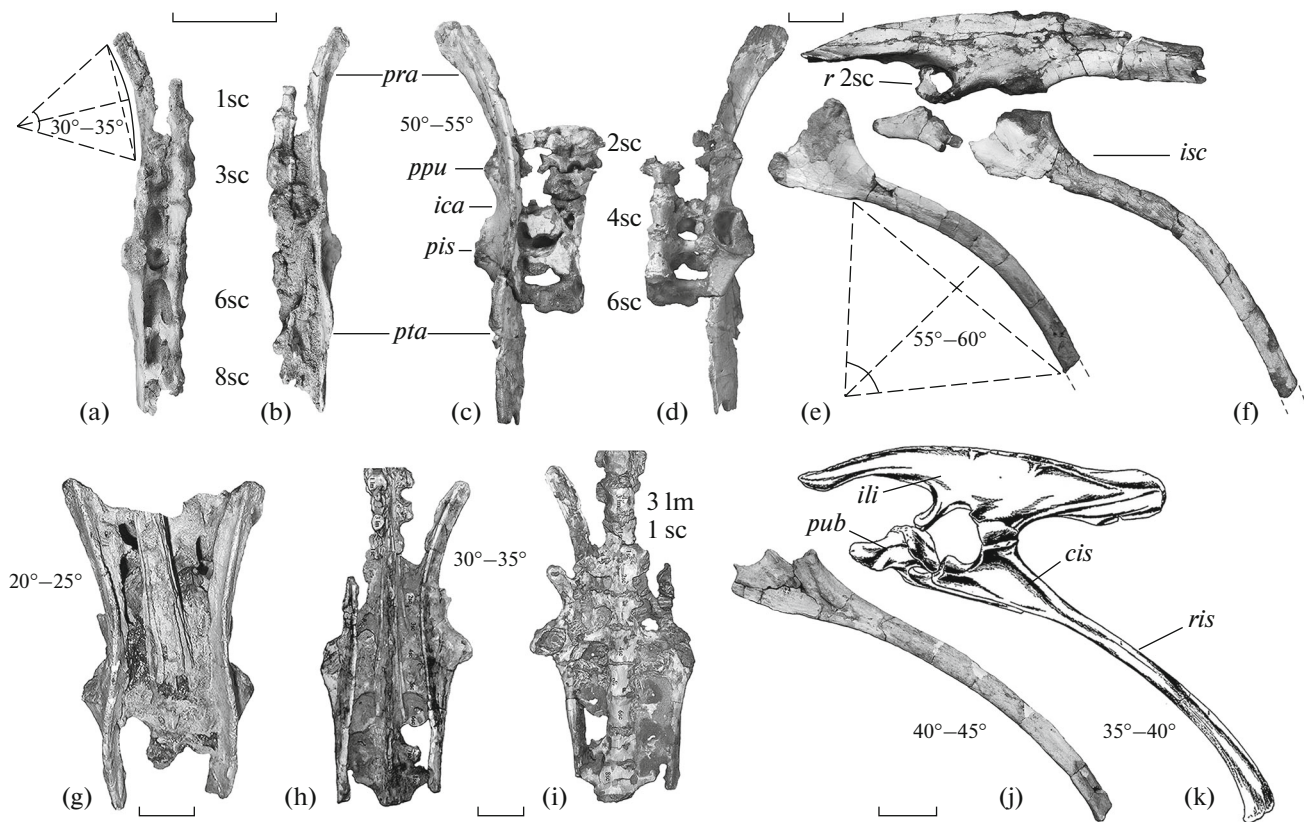
#### SEXUAL DIMORPHISM IN THE POSTCRANIAL SKELETON AND ITS VARIABILITY WITH AGE IN AMNIOTES

The patterns of sexual variability in the tetrapod skeleton reflect different ontogenetic directions leading to the specific characteristics of the sexes as adults. In modern amniotes (just as in dinosaurs) these aspects were most strongly expressed in the morphology of the bones of the postcranial skeleton, due to the different functions of the two sexes in life and reproduction. In females, the specialization of sexual characters is mostly directed towards adaptation to gestation and oviposition (bearing); whereas in males it is directed towards an improvement of the locomotor apparatus. Knowing the most typical differences of this kind between the sexes in modern amniotes, facilitates not only their recognition in fossil forms, but





**Fig. 3.** Outlines of natural curvature (a–f) and change in the inclination angles of the costovertebral articulation with the horizontal (g) of the presacral region of the vertebral column in protoceratopoids: (a, c) females, (b, d–f) males; (a, b) Bagaceratopidae gen. indet.: (a) PIN 4550/3, (b) PIN 614/29; (c, d) *Protoceratops* sp.: (c) PIN 3143/9, (d) PIN 3143/5, (e) *Udanoceratops tshizhovi* Kurzanov, 1992 (PIN 3907/11), (f) Leptoceratopidae gen. indet. (PIN 4046/11). Abbreviations: P. sp. T5 *Protoceratops* sp. (PIN 3143/5), P. sp. T7 *Protoceratops* sp. (PIN 3143/7), P. and T9 *Protoceratops andrewsi* Granger et Gregory, 1923 (PIN 3143/9), P. and T12 *Protoceratops andrewsi* Granger et Gregory, 1923 (PIN 3143/12). Note: (a–f) points on the curves indicate places of articulation between adjacent vertebrae, but the fused 1–3c are shown as a single link; (a) shows the method of calculating the arc of dorsal curvature where the chord connects the points of articulation between the cervical and the dorsal region with the point of articulation between the lumbar region and the sacrum; (g) labels on the x-axis indicate ordinal numbers of vertebrae, vertical lines correspond to spinal regions; see text for other explanations. Scale 80 mm.



**Fig. 4.** Protoceratopidae pelvic girdles: (a–f) females, (g–k) males; (a–d, h–k) *Protoceratops andrewsi* Granger et Gregory, 1923: (a, b) ZPAL Mg D-II/3, (c–f) PIN 3143/9, (h, i) PIN 3143/12, (j) PIN 3143/14, (k) AMNH 6466 (after Brown and Schlaikjer, 1940, text-fig. 31); (g) *Protoceratops* sp., PIN 3143/5; (a–c, g–i) ilium articulated with sacral vertebrae: (a, d, i) ventral view, (b, c, g, h) dorsal view; (e, j) right ischium, (f, k) pelvic girdle, left view. Abbreviations: *cis*—corpus ossis ischii, *iac*—incisura acetabularis, *ili*—ilium, *isc*—ischium, *pis*—pedunculus ischiadicus ossis ilii, *ppu*—p. pubicus ossis ilii, *pub*—pubis, *ris*—ramus ossis ischii, *r 2sc* fragment of rib 2sc leaning on pedunculus pubicus ossis ilii, for other abbreviations see Fig. 1. Note: (f, k) images scaled so that the ilia are of equal length, (h) in PIN 3143/12, the medial inclination of the right and left parts of the ilium obscures the small lateral deflection of the postacetabular process; see text for other explanations. See 40 mm.

also contributes to an understanding of the peculiarities in the formation of sexual characters in ontogeny.

#### *Sexual Dimorphism in Modern Amniotes*

The review below is based, primarily, on the results of our special studies (Tereshchenko, 1991a) on agamid lizards (Lacertilia: Agamognatha). Generalizations on the dimorphism in other modern reptiles, as well as in other amniote groups are drawn on more sparingly, from information found in published literature.

**Types of sexual characters.** Analysis of available data combined with the results of our studies (see the Methodology section, also Table 2) shows that three categories of characters can be recognized in the postcranial skeleton of modern animals that are shaped by the adaptation of the sexes to their life-functions. Category I includes characters associated with locomotor activity, which is generally higher in males than in females (Schmalhausen, 1969), Category II includes

characters shaped by the adaptation of females to gestation, and Category III includes traits associated with child-bearing (oviposition). It should be emphasized that Category I characters reflect mostly the morphological adaptation of males, which is recognized by comparing the later age stages of both sexes with the earlier age stages. The two other categories, on the other hand, characterize females, and can be developed to a different extent in amniotes. These latter characters are most strongly pronounced in reptiles, less strongly in mammals, and least of all in birds. This has to do with the different structure of the abdominal and pelvic cavities, which in reptiles are limited on one side by the vertebral column, and on the other side, by the ribs (fluctuating and/or sternal ribs) and pelvic bones respectively. In mammals, the abdominal cavity is open, but the pelvis is closed, as it is in reptiles, and this limits the size of the newborn (or eggs) and causes the tendency towards widening of the pelvic and ischial symphyses, as well as reducing the length of the pelvic cavity. In birds, the two cavities are open, which makes it

possible to gestate and lay large eggs without pronounced pelvic adaptations in females.

I. As noted previously, we treat as basic those characters associated with locomotor activity and involving sex differences in the height of the neural spines and the robustness of limb bones, since these characters are present in most amniotes, unlike the accessory characters typical for specific groups and forms. These differences are caused by the expanded attachment surface of limb muscles (Rowe, 1989) and spinal muscles (Tereshchenko, 1991a), as well as by the increased dynamic loading of limb bones (Lesgaft, 1892) and of neural spines (Slijper, 1946) by the musculo-ligamentous apparatus (Klimov, 1950). In agamid lizards, these characters are apparent in young individuals (Tereshchenko, 1991a), but the first one appears at the end of the immature stage (Table 2, characters 1, 8), whereas accessory characters mostly become recognizable in adult individuals (Table 2, characters 2, 6, 7, 10–12).

Neural spines are higher in males than in females. In reptiles (Lepidosauria: Squamata), this difference is pronounced in the precaudal (Figs. 1a, 1b) and the anterior caudal vertebrae (e.g., Stromer, 1915; Bogert, 1964; Tereshchenko, 1991a; Barbadillo and Sanz, 1983), whereas in mammals (Ungulata: Slijper, 1946; Sokolov, 1971 and Proboscidea: E.N. Mashchenko, personal communication) it is pronounced on the anterior thoracic vertebrae. In birds and turtles, dimorphism in this character is not pronounced, likely because in the immobile and shortened bird spine, neural spines on the cervical vertebrae are very low and almost equal in length, while in the turtle spine, lumbar and sacral vertebrae are fused with the carapace.

The bones of the mammal postcranial skeleton, as well as girdle and limb bones of some reptiles (Lacertilia: Agamognatha; Table 2, character 8) are massive in males and more gracile in females (Vorobyev, 1932; Sokolov, 1971; Tereshchenko, 1991a), whereas skeletal bones in some birds (Molnar, 2005) and vertebrae in agamid lizards (Tereshchenko, 1991a), are more robust in females than in males.

The appearance of reverse sexual dimorphism in the bones of the postcranial skeleton of females of monogamous birds is associated with flying and is a result of selection for “agility”, e.g. during hunting (Molnar, 2005). It should further be taken into account that in birds it is the limb bones of females that experience increased dynamic loading during the reproductive period: anterior limbs during flying and posterior limbs during locomotion over the substrate.

In considering the Type I accessory characters, it should be noted that the presence of normal sexual dimorphism in the axial skeleton of mammals and reverse dimorphism in lizards is likely explained by the differences in the structure of the dorsal region of the vertebral column. In mammals, the spine is arched, so that sagging during locomotion does not

present a problem in males or females, since the load experienced by the vertebrae decreases from the base of the arc to its top (Hesse, 1910) and the spine has the function of a shock absorber, dampening shocks and impacts from the posterior limbs that propel the body forward. In lizards, the spine is straight, which means that loading is increased not only at the middle of the spine, but also the entire posterior half of the spine. As a result, special adaptations must develop in females on these vertebrae to prevent sagging, especially during the maturation of oocytes and incubation of eggs when body mass is greater in females than males (e.g., Melkumyan, 1973; Shammakov et al., 1973; Panov and Zykova, 2003), so that vertebrae in females, combined with their low neural spines, look more massive compared to males (Figs. 1a–1d).

Several further accessory sexually dimorphic characters can be recognized in the skeleton. In males of elephants (Proboscidea: Elephantidae), including mammoths (*Mammuthus*), the tips of neural spines on the second and subsequent thoracic vertebrae have a club-shaped expansion, which is absent in females (E.N. Mashchenko, pers. comm.); in females of bovids (Bovidae: *Bison*), the scapula is shorter than in males (Sokolov, 1971). It is obvious that in bison, the length of the scapula is correlated with the height of the neural spines which are, as already mentioned, shorter in females than in males. In males of some galliform birds (Aves: Galliformes), unlike in females, there is a large spur on the tarsometatarsus (processus calcaris: Baumel and Witmer, 1993) which they use as a weapon. In males of some reptiles (Agamidae), the vertebral width across the postzygapophyses 3c–14cd is somewhat greater compared to females (Table 2, character 2), which, together with the high neural spines is explained by the increase in the attachment surface of the transversospinalis muscle in this region of the vertebral column. In females of some lowland agamas (Agamidae: *Trapelus*, *Agama*, *Phrynocephalus*), ribs 5–8c are more rigidly connected to the vertebrae (Table 2, characters 6, 7) and the dorsolateral process of the sternum (processus sternalis dorsolateralis) is almost twice as long as in males (Tereshchenko, 1991a, Figs. 3a, 3b). These differences in females can be associated with the action of the musculature of the anterior limbs in locomotion, display behavior (“nodding”)<sup>1</sup>, especially during the reproductive period, and in egg laying. In particular, the ventral and dorsal serratus muscles connect the inner surface of the scapula with the ends of the ribs 5–8c, suspend and fix the scapula to the axial skeleton, transmit some of the body weight onto the scapula, as well as vertical and horizontal stresses (Gurtovoi et al., 1978). The strength of scapula attachment to the axial skeleton depends directly on how rigidly the ribs in question are

<sup>1</sup> “Nods are a series of paired movements where the anterior body is lowered and raised by flexion and subsequent extension of the anterior limbs” (Panov and Zykova, 2003, c. 93).

attached to the vertebrae; in females this linkage is more rigid. The elongation of the sternum process in females is probably due to the fact that the force generated during the action of deltoid (*mm. deltoideus scapularis et clavicularis*) and subcoracoscapular muscles tends to deflect the scapula away from the axial skeleton and create conditions for dislocation at the sternocoracoid joint, which is counteracted by the internal sternal ligament (*ligamentum sterni internum*). This ligament originates from the articulation of the clavicle with the scapula and attaches to the dorsolateral process of the sternum. Therefore, the greater the loading of the sternocoracoid joint, the longer the dorsolateral process of the sternum. The greater length of this process in females compared to males can then be linked to higher loading of the sternocoracoid joint encountered not only during “push-ups” (“nodding”), but also while digging burrows to lay eggs (Bannikov et al., 1977; Polynova, 1982; Panov and Zykova, 2003). One further sexually distinctive character in males of agamid lizards is the medial position of the metaischiadic process on the ischium, the bone that is wider in females than in males, with the process located somewhat closer to the acetabulum and more rotated towards the cloaca (Figs. 1e, 1f Table 2, character 10). These differences of females are likely due to the structure of the musculature of the pelvic girdle and the femur, in particular, the expansion of the origin of *mm. puboischiofemoralis externus et internus* and *m. ischiotrochantericus*, as well as due to the way *m. hypoischiadicus* and *m. transversus cloacae cranialis* work (the first of these muscles extends the hypoischium upwards and together with the second muscle presses the cloaca from below: Gurtovoi et al., 1978). It should be noted that in males of mountain agamas, the tail (e.g., Rustamov et al., 1973; Ananjeva and Atayev, 1984) and posterior limbs (Ananjeva et al., 1990; Panov and Zykova, 2003; Tereshchenko, 1991a) are all longer than in females. Considering that the speed with which a lizard can run is increased by the length of the tail and posterior limbs (Snyder, 1954, 1962), these differences may be linked to the ability of males to run faster than females (Tereshchenko, 1991a).

Since mammals and the studied reptiles do not share any sexual characters from categories II and III, we classify these as accessory characters. An exception is the character reflecting the increased mobility of the pubic and ischiadic symphyses in adult females (Category III) which should be classified as a basic character.

**II.** The characters associated with egg retention (or gestation of fetus) in females are mostly related to the increase of the abdominal cavity (e.g., Vorobyev, 1932; Barbadillo and Sanz, 1983; Bauwens et al., 1997). In mammals, sexual differences can appear in the length and the width of the thorax which is, for instance, shorter and wider in human females than in males (Vorobyev, 1932; Alekseyev, 1966) and in the greater preacetabular pelvic width (the distance between the

margins of the wings of the ilium, *ala ossis ilii*) in females compared to males (Vorobyev, 1932; Klimov, 1950; Alekseyev, 1966; Sokolov, 1971). In females of some lizards (*Lacertidae*, *Agamidae*), the greater length of the abdominal cavity can be achieved through an increase in the length of dorsal vertebral centra (Table 2, character 3) (Barbadillo and Sanz, 1983), as well as sometimes their number (Porkert and Grosseova, 1984; Tereshchenko, 1991a). Also, the neck in adult males of agamas is longer and the back is shorter than in females (Tereshchenko, 1991a). In females of agamas, a massive crest forms with sexual maturity in the fossa between the postzygapophyses of each vertebrae in the posterior half of the back; in adults, the crest is pyramid-shaped and dorsally passes into the postspinal crest (Figs. 1b–1d, cps; Table 2, character 5). The postspinal crests form a series of braces that, through pads of connective tissue, enter into contact with the bases of the neural spines of the subsequent vertebrae, increasing the resistance of the vertebral column to sagging in the back. Additionally, compared to males, females of agamid lizards have an almost reduced preacetabular process of the ilium (Figs. 1e, 1f). This character can be explained by the fact that in females, due to the structure of intervertebral linkages, prevention of sagging in the posterior half of the back requires neither loading the quadratus muscle (*m. quadratus lumborum*) nor, for that reason, having a strengthened aponeurosis on the ilium, unlike in males. Also, the ramus of the pelvic bone is deflected ventrally and somewhat posteriorly in females, rather than anteriorly, as in males (Figs. 1e, 1f, rpb), which results in an increased length of the abdominal cavity and a decreased length of the pelvic cavity in females.

**III.** Characters associated with egg-laying or parturition in females of reptiles and mammals are usually related to increased pelvic width, reduced length of the pelvic cavity due to a shortened sacrum (Alekseyev, 1966) and convergence between the pelvic and the ischial symphyses together with an increased mobility in the articulation of pubis and ischium (e.g., Vorobyev, 1932; Klimov, 1950; Table 2, character 9). In birds, characters in this category are related to the distance between the caudal parts of the pubes, which is larger in females than in males (Dementyev, 1940). In reptiles and mammals, the maximum pelvic width usually corresponds to the level of the acetabula (acetabular pelvic width) which is greater in females than in males (Alekseyev, 1966; Sokolov, 1971; Tereshchenko, 1991a). In crocodiles (*Alligator mississippiensis*), this width is approximately equal in both sexes, but the height of the pelvic canal is greater in females than in males (Prieto-Marquez et al., 2007). Coming back to lizards, it should be noted that published data on the absence of sexual dimorphism in the pelvic girdle of iguanas (Prieto-Marquez et al., 2007) raises serious doubts. Our analysis of the data published by these authors (Prieto-Marquez et al., 2007, appendix 2),

shows that their conclusions are to a large extent determined by the predominance of immature individuals of iguanas (*Iguana iguana*) in their sample which contains only seven mature individuals out of 30 specimens with body length of 13–44 cm. Sexual maturity in males of *I. iguana*, it should be noted, occurs when body length is  $25.2 \pm 7.0$  cm in males,  $30.8 \pm 5.2$  cm in females (Meshaka et al., 2007). Also, in adult females of iguanas, the pelvis is 14% wider than in males, which is also true for small adult agamas (Table 2, character 4).

**A general assessment of features of sexual dimorphism in the postcranial skeleton of modern amniotes** was mainly done from data obtained during the study of sexual differences in modern agamid lizards which showed that most associated characters are relatively stable (Tereshchenko, 1991a). In particular, out of 15 sexual traits discovered in the adults of the steppe agama (*T. sanguinolentus*), 14 were found in most of the studied agamids of the same age.

Basic characters. (1) neural spines of the dorsal and anterior caudal vertebrae are higher in males than in females (Figs. 1a, 1b; Table 2, character 1); (2) girdle and limb bones are thicker in males than in females (Table 2, character 8); (3) pubic and ischial articulations are more mobile in females and more rigid in males (Table 2, character 9).

Accessory characters. (4) precaudal vertebrae are more massive in females than in males (Figs. 1a, 1b); (5) the width of the dorsal and the anterior caudal vertebrae across the postzygapophyses is greater in males than in females (Table 2, character 2); (6) centra of dorsal vertebrae are longer in females than in males ( $L/H\text{♀} > 1.0$ ,  $L/H\text{♂} < 1.0$ , especially for 4–14th, Table 2, character 3); (7) acetabular pelvic width in females is greater than in males ( $P/K\text{♀} \geq 2.0$ ,  $P/K\text{♂} < 2.0$ ; Table 2, character 4); (8) males have an interpostzygapophyseal crest on 5–13th, in females it is pyramid-shaped and passes dorsally into the postspinal crest (Figs. 1c, 1d, cip, cps; Table 2, character 5); (9) ribs 5c in males and 6–8c in females are immobilized (Table 2, character 6); (10) unlike males, in females rib 5c is fused with the vertebra (Table 2, character 7); (11) ramus of the pubic bone is deflected ventrally and somewhat posteriorly in females, ventrally and anteriorly in males (Figs. 1e, 1f, rbp); (12) ischial process on the ischium is medially positioned in males, closer to the acetabulum and somewhat rotated towards the cloaca in females (Figs. 1e, 1f, pmi; Table 2, character 10); (13) epiphyses of limb longbones in males fuse with diaphyses, which does not occur in females (Table 2, character 11); (14) crest at the base of the inner trochanter is found in males but absent in females (Table 2, character 12).

The specific manifestations of characters 9, 10, and 14, on the other hand, was found to be different in the several species studied in this family. In particular, character 14 is not typical for mountain agamas of

Eurasia (Agamidae: Agaminae) since males and females of the genus *Laudakia* lack a crest at the base of the inner trochanter. In *Ph. mystaceus*, ribs 5c and 6c do not fuse with vertebrae sequentially (first 5c, then 6c) as in *T. sanguinolentus*, *A. agama* and member of the genus *Laudakia* (characters 9, 10; Table 2, characters 6, 7), but rather simultaneously, first in adult females, then in old males. There are further sexually differentiated features (in the formation of the postcranial skeleton) that characterize larger groups of amniotes. For instance, immobilization of the pubic and ischial symphyses in mammals and reptiles occurs first in males, later in females (Vorobyev, 1932; Tereshchenko, 1991; Table 2, character 9). Also, epiphyses of limb long bones in reptiles, for instance, in agamas and iguanas (*Sceloporus grandaevus*), fuse to diaphyses first in males, then in females (Etheridge, 1962; Tereshchenko, 1991; Table 2, character 13) which, e.g., in *I. iguana*, grow slower than males (Meshaka et al., 2007). In mammals, on the contrary, epiphyses fuse to diaphyses of limb longbones, e.g. in bison (Sokolov, 1971) and in elephants (E.N. Mashchenko, personal communication) first in females, later in males. Such differences in the sequence of fusion of these skeletal elements in males and females are most likely associated with the fact that males reach maturity earlier than females in reptiles (Meshaka et al., 2007), but the opposite is true for mammals (Vorobyev, 1932).

The study of the development of sexual dimorphism in the ontogeny of the steppe agama (Table 2) and comparison of the expression of sexual differences in this species with other species of agamid lizards (in the characters listed above) allowed us to recognize several patterns in the formation of sexual traits in the postcranial skeleton of the group as whole (Tereshchenko, 1991a). The earliest sexual differences appear on the vertebrae of large young immature specimens (character 1) in which, in particular, the differentiation in the size of centra along the precaudal region of the spine is still poorly expressed. In medium-sized young immature individuals, the expansion of the sexual differences on the vertebrae (characters 1, 4, 8) continues, the first sexual trait appears in the limbs (character 2). Sexual dimorphism (characters 1–14) and size differentiation in the precaudal vertebrae are most pronounced in adult mature individuals, but with aging, some sexual traits become more difficult to recognize (characters 1, 3, 5, 6, 13). In other words, as soon as the animal starts reproducing, sexual differences quickly become apparent (first in the vertebrae, then in the girdles and in the limbs) and size differentiation of the centra accelerates. With continued participation in reproduction, sexual traits grow further apart for males and females. The loss of reproductive ability in senescence leads to a suppression of sexual differences although some (characters 7, 9, 10, 14) remain better expressed than others.

To summarize, knowledge of sexual traits and their different versions in the postcranial skeleton of modern amniotes which were exposed in the discussion of categories of sexual traits, define the direction to search for such traits in dinosaurs. The method of regular correlated sexual differences (see Methods above), on the other hand, provides an opportunity to recognize, with a high degree of reliability, sexual dimorphism in different dinosaur taxa despite differences in the structure of the postcranial skeleton.

### SEXUAL VARIABILITY IN DINOSAURS

The study is based mostly on our data on the study of sexual dimorphism of the axial skeleton and the pelvic girdle of protoceratopoids (Tereshchenko, 2001), including unpublished observations on the age variability of characters that were used to establish the age composition of our sample (See Methods, cf. Tables 1 and 3).

Our study shows that sexual differences recognized in the studied ceratopsians could be classified into the same categories of characters linked to the different function of the sexes during life and reproduction as for modern animals. For many sexual traits found in protoceratopoids, there are modern analogues; having studied these, we were able to discover a correlation between the basic (common to most amniotes) and newly discovered accessory (specific to groups and forms) sexual differences (see Methods). Recognizing sexual dimorphism in ceratopsian dinosaurs was also aided by some similarities in the structure of their postcranial skeleton with modern mammals and reptiles. In both dinosaurs and mammals, the back is arched (there is a cervical and a dorsal spinal curvature), the inclination of the axis of the costovertebral articulation in the sagittal plane changes in a similar way along the dorsal region of the spine, and there is a preacetabular process of the ilium. Similar to modern reptiles, dinosaurs have a well-developed postacetabular process of the ilium and, as in crocodiles, the acetabulum is located at the same level as the costal processes of the sacral vertebrae. These processes, pushing against the body of the ilium, brace the dome of the acetabulum from the inside (Borsuk-Bialynicka, 2008), which is also observed in dinosaurs (acetabular bar: Brown and Schlaikjer, 1940; Sukhanov and Tereshchenko, 2004). We should note that for protoceratopoids, we treat the last three dorsal vertebrae as part of the lumbar region which is both morphologically and biomechanically distinct from the anterior dorsal region (Tereshchenko, 2007).

In recognizing sexual variability in protoceratopoids, we based it first and foremost on the basic characters of category I, associated with locomotion of males and females, and category III, associated with egg-laying or parturition of females of modern reptiles and mammals and consisting of differences in the height of neural spines, robustness of limb bones, and

mobility of the pubic and ischial symphyses. Among the accessory characters of category I, we recognized differences in the expression of the club-shaped expansion on the tips of neural spines of dorsal vertebrae (as in elephants). Other characters taken into account were the differences in the length of the scapula and the width of the vertebrae across the postzygapophyses in the precaudal (as in bison) and the first 10–15 (as in agamas) caudal vertebrae. In characters of category II, which are associated with egg retention by females, we paid special attention to sexual differences in the robustness of bones of the axial skeleton, the length and width of the abdominal cavity of which the latter can be estimated from the preacetabular width of the pelvis. Notable among accessory characters of category III is the fact that in ceratopsian dinosaurs, as in crocodiles, the acetabular width of the pelvis is approximately equal in both sexes, but the height of the pelvic aperture (apertura pelvis caudalis) is greater in females than in males (Tereshchenko, 2001; Prieto-Marquez et al., 2007).

Research into sexual variability in agamid lizards has been important for its study in ceratopsian dinosaurs not only as a way of gaining experience establishing an approximate set of sexual characters and making a comparative analysis for different forms of the studied group, but also as it provided opportunity to apply to dinosaurs the patterns of change in sexual dimorphism through individual development first recognized in modern reptiles. In particular, we were able to use the observation that in the ontogeny of agamas, appearance of basic characters precedes the appearance of accessory ones. The first sexual differences were found in vertebrae (differences in neural spine height) in large young immature individuals (Table 2, character 1), then also in the limbs of young mature individuals (Table 2, character 8, including differences in the robustness of vertebrae), but the strongest dimorphism is found in adult specimens. Immobilization of the pubic and ischial symphyses occurs first in large adult mature males, then in older females (Table 2, character 9).

Paleontologists do not agree on the issue of robustness of the postcranial skeleton in males and females of dinosaurs. Some researchers consider the female skeleton more robust, as is observed in some reptiles (Sternberg, 1927; cited in Molnar, 2005) and birds (e.g. Raath, 1990; Dodson, 1996), but others disagree (Mallon, 2005; Molnar, 2005). Contrary to the opinion of Sternberg (1927), Mallon (2005), considers the male skeleton in ceratopsians to be more robust than in females, calling this condition normal, as opposed to reverse, sexual dimorphism. However, we did not exclude the possibility of finding combined sexual dimorphism in ceratopsians: normal in the limb skeleton and reverse in the vertebral column.

**Sexual dimorphism in ceratopsian dinosaurs (Ornithischia: Neoceratopsia).** By building on the

experience of studying sexual dimorphism in modern amniotes and based on both new (see Methods) and published data on age variability in the postcranial skeleton of ceratopsian dinosaurs, characters are determined that reflect the most typical structural changes at each age stage (Table 3). This, in its turn, contributed to an understanding of the probable development of sexual dimorphism in the ontogeny of the studied ceratopsians (cf. Tables 3 and 4).

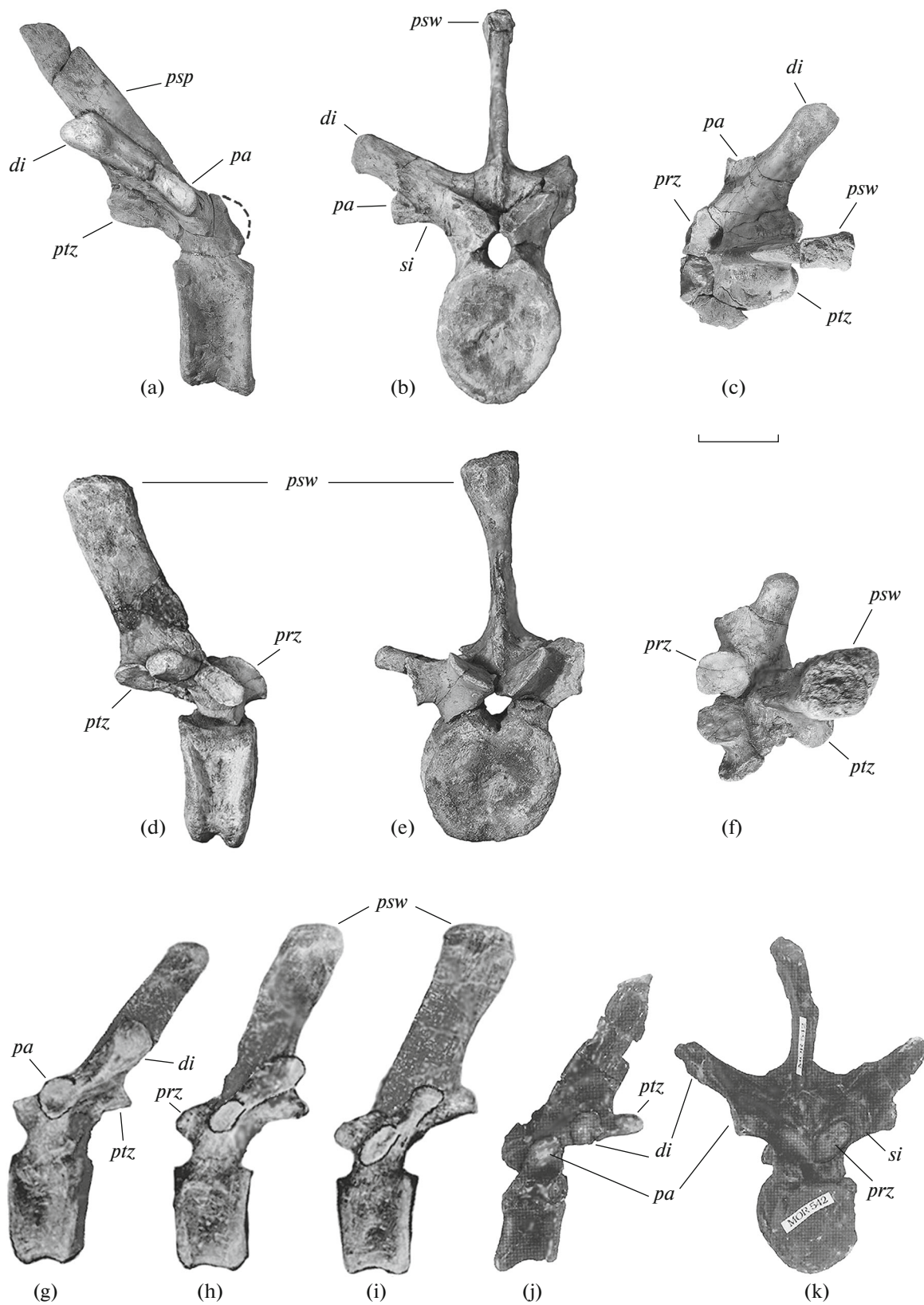
Recognition of sexual dimorphism in the postcranial skeleton of *Protoceratops andrewsi* led us to establish 19 sexual distinctions (Tereshchenko, 1997; 2001), of which 15 are found in most mature Protoceratopidae, Bagaceratopidae and Leptoceratopidae: *Udanoceratops tschizhovi* Kurzanov, 1992 (for convenience, we will refer to these taxa below as *Protoceratops*, *Bagaceratops* and *Udanoceratops*).

Basic sexual distinctions. **1.** Neural spines of the dorsal (1–9th and 1–3 lm) and likely, also sacral vertebrae in males are higher than in females (Figs. 2a, 2b, 2d, 2e). Relative height index for neural spines (LN/h) varies from 1.3 to 1.8 in females and from 0.8 to 1.2 in males. **2.** Girdle (Figs. 4c, 4g, 4h) and limb bones are thickened (robust) in males, relatively thin (gracile) in females. **3.** The mobility of the ischial symphysis (hypischium) is much greater in females than in males.

Accessory sexual distinctions. **4.** Precaudal and the first 13 (14) caudal vertebrae are stout (robust) in females, more gracile in males (Fig. 2). In particular, the centra of the 1–8th vertebrae are relatively wider (Bc/Hc) in females than in males. In *Protoceratops*, this index has a value of  $0.96 \pm 0.04$  in males,  $1.02 \pm 0.02$  in females; in *Bagaceratops*,  $0.68 \pm 0.07$  and  $0.82 \pm 0.05$  respectively. **5.** The anteroposterior width of the junctions between the bases of diapophyses and parapophyses of dorsal vertebrae is greater in females than in males (Figs. 2c, 2f). **6.** The diapophyses of dorsal vertebrae (5th–2lm) are more strongly deflected dorsally in males than in females (Figs. 2b, 2e, div): the angle of inclination of the diapophyses relative to the vertical decreases caudally from  $150^\circ$ – $155^\circ$  to  $100^\circ$ – $105^\circ$  in males and from  $135^\circ$ – $140^\circ$  to  $90^\circ$ – $95^\circ$  in females. **7.** Neural spines on 5th–3lm are distally expanded, club-shaped in males, unlike in females (Fig. 2, Fig. 5; Tereshchenko, 2001, text-fig. 3). The degree of this expansion increases in males from 5th to the last dorsal vertebrae (Fig. 5a–5f, 5g–5i), then decreases. **8.** The neural spine on 2c is directed dorsally and somewhat posteriorly in females, inclined anteriorly in males (Tereshchenko, 2001, text-figs. 4a, 4b). **9.** The arc of cervical and dorsal curvature is greater in males than in females (Figs. 3a–3d). For the back, the values for this curvature in adult males of *Udanoceratops*, *Protoceratops* and *Bagaceratops* are  $40^\circ$ – $45^\circ$ ,  $55^\circ$ – $60^\circ$  and  $65^\circ$ – $70^\circ$ , whereas in females the values are  $3^\circ$ – $35^\circ$ ,  $45^\circ$ – $50^\circ$  and  $55^\circ$ – $60^\circ$ . Therefore, the back and the abdominal cavity are approximately

10% longer than in males. **10.** The angle of inclination of the costovertebral articulation with the long axis of the centra (with the horizontal) is greater in males than in females (Figs. 2a, 2d, adp; 3g). This angle decreases from the first to the second last dorsal vertebra with values of  $60^\circ$ – $65^\circ$  to  $25^\circ$ – $30^\circ$  in males,  $45^\circ$ – $55^\circ$  to  $5^\circ$ – $15^\circ$  in females. **11.** The ilium is curved in the frontal plane so that the preacetabular process is deflected laterally, the postacetabular process is relatively straight, and the middle part (where the curve flattens) is at the level of 3–4sc in males (Figs. 4b 4g, 4h), 4–5sc and 5–6sc (Fig. 4c) in females of *Bagaceratops* and *Protoceratops*, respectively. **12.** The dorsal margin of the ilium at the flattening of the curve is oriented dorsally in males, somewhat deflected outward in females (Fig. 4b, 4c, 4g, 4g, 4h; Tereshchenko, 2001, text-fig. 1a). **13.** The preacetabular process of the ilium is curved (laterally deflected) more strongly in females than in males (Figs. 4a–4c, 4g–4i)). Because of this, the preacetabular pelvic width is greater in females. **14.** The postacetabular process of the ilium is paddle-shaped with the dorsal margin deflected laterally relative to the ventral margin (Figs. 4a–4c, 4g–4i). The angle of inclination of its lateral surface relative to the vertical varies from  $10^\circ$  to  $20^\circ$  in males and from  $25^\circ$  to  $50^\circ$  in females. As a result, the postacetabular pelvic width (the maximum width measured at the dorsal margins of these processes) is greater in females. **15.** The ramus of the ischium is arched some  $15^\circ$ – $20^\circ$  more strongly in the sagittal plane in males, especially in adult and old individuals (Figs. 4e, 4f, 4j, 4k). As a result, the functional axis of the ischium is more strongly deflected anteriorly in the females, resulting in a greater height of the pelvic canal compared to males.

Characters 1, 2, 4–8 can be placed in the first category; 9, 10, 13 in the second; 3, 11, 12, 14, 15 in the third. The sexual differences in the robustness of the vertebrae have a somewhat different pattern compared to the agamid lizards where vertebrae are more robust in females throughout the indicated region of the vertebral column. However, in protoceratopoids, this difference is most apparent in cervical, sacral, and anterior caudal vertebrae, and is less pronounced in the dorsal vertebrae. In particular, the robustness of these vertebrae is revealed in the increased size of the centra and the width at the fusion of the diapophyses and parapophyses (characters 4, 5), but the presence of club-shaped expansions on the tips of the neural spines (character 7) enhances the robust appearance. A certain reduction in the sexual differences in the robustness of the characters discussed here is likely due to the evolution of an arched back in ceratopsian dinosaurs (character 9) as it is observed in mammals, where males have more robust vertebrae compared to females (See the subsection Sexual dimorphism in modern amniotes). It should be noted that characters 5 and 6 cannot at present be extended to all protoceratopoids, because in our sample they were only registered



**Fig. 5.** Leptoceratopidae dorsal vertebrae: (a–i) males, (j, k) female; (a–f) *Udanoceratops tschizhovi* Kurzanov, 1992 (PIN 3907/11), (g–k) *Montanoceratops cerorhynchus* (Brown, Schlaikjer, 1942): (g–i) AMNH 5464 (after: Brown, Schlaikjer, 1942, Fig. 3), (j, k) MOR 542 (after: Chinnery and Weishampel, 1998, textfig. 4B); (a–c, g) 5th, (d–f, h) 8th, (i–k) 10th; (a, d) right view, (b, e, k) anterior view, (c, f) dorsal view, (g–j) left view. For abbreviations see Figs. 1; 2. Note: (g–k) images scaled so that centra are of equal height. Scale 40 mm.



**Table 4.** Development of some sexually variable characters of the vertebral column and pelvis in the ontogeny of protoцератопидов

Characters	Age stages					
	Immature		Mature		Senescent	
	Young		Young		Adult	
	large	small	large	small	large	
Neural spines of dorsal vertebrae higher in males than in females ( $L_N/h_q > L_N/h_\delta$ )	5–10%	15–25%	30–40%	45–60%	25–40%	
Length of the arc of cervical and dorsal curvature in $\delta\delta > \text{♀♀}$	5°–10°		10°–15°		15°–20°	
Inclination of the costovertebral articulation relative to the long axis of the centra of dorsal vertebrae in $\delta\delta > \text{♀♀}$	No difference	5°–10°	10°–15°	15°–20°	10°–15°	
Neural spines on 5th–3rd in $\delta\delta$ , unlike $\text{♀♀}$ , distally expanded in diameter	Poorly visible		Well visible		Very well visible	
Width of bases of diapophyses 5–8th in $\delta\delta < \text{♀♀}$	No differences	Poorly visible				
Inclination of the neural spine of the axis (2c)	Somewhat anterior in $\delta\delta$ of protoцератопидов and $\text{♀♀}$ of Bagaceratopidae, oriented dorsally in $\text{♀♀}$ of Protoцератопидов		Dorsally and somewhat posteriorly in $\text{♀♀}$ , anteriorly in $\delta\delta$		Posteriorly in $\text{♀♀}$ , somewhat anteriorly in $\delta\delta$	
Preacetabular process curved in $\delta\delta < \text{♀♀}$	10°–15°		15°–20°		20°–25°	
Curvature of the dorsal margin of the preacetabular process flattens	Before the acetabulum in $\delta\delta$ and $\text{♀♀}$		At the level of 3–4 sc in $\delta\delta$ , behind 4sc in $\text{♀♀}$			
Condition of the dorsal margin in the zone of flattening of the curvature	Directed dorsally in $\delta\delta$ , deflected laterally in $\text{♀♀}$ : <b>Bagaceratopidae</b> at the level of the acetabulum, <b>Protoцератопидов</b> behind the acetabulum					
Location of the lateral surface of the postacetabular process relative to the vertical in the transverse plane	Oriented vertically in $\delta\delta$ and $\text{♀♀}$		Dorsal often deflected laterally relative to ventral			
Ramus of ischium curved in the sagittal plane in $\delta\delta < \text{♀♀}$	No difference	10–15%	20–25%	55°–65° in $\text{♀♀}$ , 35°–45° in $\delta\delta$	30–40%	
	50°–55°					

Young of the year are omitted from the table since it has been impossible to assess sexual dimorphism from the single specimen in our sample (Table 1).

in *Protoceratops*, whereas in *Udanoceratops*, character 5 is absent.

Characters 9 and 10 may be typical not just for dinosaurs in general, but also for mammals (both modern and fossil) which have a natural curvature of the spine and a reduction in the angle of inclination of the costovertebral articulation along the dorsal region, resembling the studied ceratopsians. Character 15, on the other hand, is likely only valid for dinosaurs, despite the peculiarity of their pelvic girdle. Unlike modern reptiles (Figs. 1e, 1f) and most saurischian dinosaurs (Saurischia), in which pubic bones meet ventrally and limit the pelvic canal laterally, separating the pelvic from the more voluminous abdominal cavity, the ornithischian and some saurischian (Theropoda: Deinonychosauria, Segnosauria) dinosaurs have pubic bones that are aligned with the posteriorly directed ischium, and meet ventrally, only limiting the pelvic opening of the joint abdominal and pelvic cavities. Both groups, however, as well as crocodiles, share the same sexual differences in the height of the pelvic canal, which is greater in females than in males. However, these differences are achieved in different ways: in crocodiles the height of the pelvic canal is regulated by the length of the functional axis of the ischium (Prieto-Marquez et al., 2007), whereas in ceratopsians (character 15) and in theropods (Carpenter, 1990) it is regulated by its angle with the vertical, which is greater in females than in males.

**Age-related changes in the formation of sexual dimorphism.** Several accessory sexual distinctions found in protoceratopoids—characters 9, 10, 12, 14, and 15 (curvature of the ischium)—notably are not known in modern amniotes. Characters 8, 11 and 13 are not treated here, since the functional significance of character 8 has previously been discussed in a separate article (Tereshchenko, 2001), and patterns of change in characters 11 and 13 are readily apparent from Table 4. Analysis of age-related changes in the expression of characters 9 and 10 in the ontogeny of the studied ceratopsian dinosaurs (Tables 1, 3, 4) shows that there is a decrease with age in both the arcs of cervical and dorsal spinal curvature, and the inclination angles with the horizontal of the costovertebral articulation along the dorsal region of the spine (Figs. 3f, 3g; Table 3). This decrease occurs faster in females than in males (Table 4). Large, young, immature individuals likely lack sexual distinctions in these characters (Table 4). The decrease in the cervical and dorsal curvature and in the inclination of costovertebral articulation appears first in medium-sized, young, mature females, then in large, adult, mature males. For this reason, sexual distinctions in characters 9 and 10 appear more clearly in females than in males, whose condition remains unchanged until early senescence.

Details of age-related changes in the sexual dimorphism were also studied in the pelvic girdle

(characters 12, 14, and 15). If it is assumed that in males and in females of the year, the ilium at the level of 3–5sc and the lateral surface of the straight postacetabular process were oriented vertically, as in PIN 3143/6, then these characters were retained in males until sexual maturity. In females, on the other hand, the dorsal margin of the ilium (character 12) is deflected outwards at the stage of large immature individuals, at the level of 3–4sc in *Bagaceratops* and 5–6sc in *Protoceratops* (Table 4). With the advent of sexual maturity in males and females, the whole dorsal half of the ilium body at the level of 3–5sc starts deflecting laterally, so that its lateral surface becomes somewhat concave in large, young, mature individuals, preserving this state until senescence (Table 3). At the same time, in large, young, mature individuals, the lateral surface of the postacetabular process (Table 3) starts deflecting laterally relative to its ventral margin (character 14). This process advances faster in females than in males, so that in large mature and old females the angle of inclination of this lateral surface with the vertical becomes 2–2.5 times larger than in males (Table 4).

Quite a different pattern is observed in the age-related dynamics of sexual distinctions in the ischium (character 15). In immature males and females, this bone is arched in an arc of approximately 50°–55°. As the animal grows, the curvature remains almost the same in females (55°–65°), whereas in males it becomes reduced and by early senescence reaches 35°–45°. For this reason, sexual differences in this character are more easily recognized in males than in females, in which the state of this character remains almost unchanged throughout life (Table 4).

Comparing age-related differences in sexual characters in the skeleton of the studied dinosaurs on one hand and modern lizards on the other, shows differences in the pace of their appearance for several morphological structures. In particular, such differences in the vertebral column (characters 1, 8) and the pelvic girdle (characters 12, 13) in proceratopoids likely appear already at the late stage of medium-sized, young, immature individuals (young of the year) whereas in lizards they only appear in large, young, immature individuals. Sexual differences in the height of the neural spines (character 1) in protoceratopoid young of the year, on the other hand, do not exceed 5% as in lizards at the next age stage (cf. Table 2, character 1 and Table 4, first character in the list). No differences between males and females are expected to be found in the studied ceratopsian dinosaurs at the early stage of young of the year in the inclination of the neural spine of the axis (character 8), the maximum pelvic width measured across the dorsal margins of the ilium (character 12) and across the margins of the preacetabular processes (character 13). More or less the same condition is observed in lizards but at the age stage following the young of the year (Table 2). This is probably due to the growth rate of protoceratopoids which was

much higher (as also in non-basal theropods) than in non-dinosaur reptiles and was close to the growth rate of birds (Norell et al., 1995).

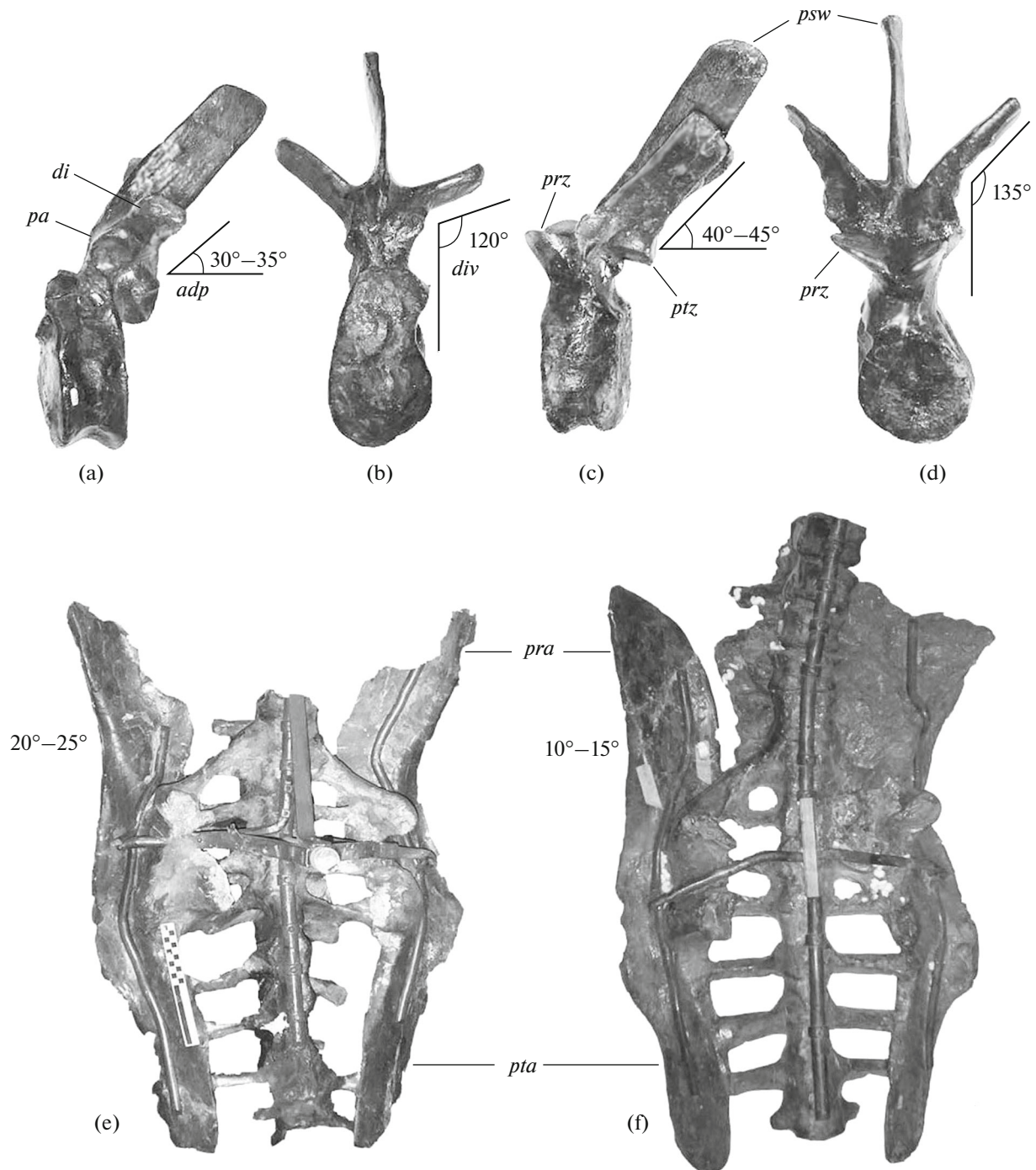
**Adaptive significance of some discovered sexual differences.** Adaptive significance is best discussed with the examples of dimorphism belonging to the second (characters 9, 10, 13) and third category (characters 11, 12, 14). The straighter back and greater preacetabular pelvic width in mature females (characters 9, 13) increased the length and width of the abdominal cavity. Accordingly, the more gently inclined costovertebral articulations in females (character 10), and, therefore, a more oblique inclination of the dorsal ribs facilitated their deflection dorsolaterally in the middle and almost laterally in the end of the dorsal region (Klimov, 1950). This morphology made it possible for females to breathe normally without limiting the additional increase in the width of the abdominal cavity during egg retention. The displacement of the inflection zone caudal of the acetabulum (character 11), associated with the deflection of the dorsal margin (character 12), and the outward inclination of the lateral surface of the postacetabular process (character 14) in females are associated with the increase in the cross-sectional area and, therefore, in the mass of *m. transversospinalis*. This multipennate muscle does not show any apparent changes in its passage from the trunk to the tail, preserving its ability to extend the spine vertically (Gurtovoi et al., 1978) and, therefore, to participate in raising the tail during egg-laying by the female. Since the cloaca in ceratopsians was located behind the ischial symphysis (Romer, 1927), then in order to expand it, it must have been necessary to raise the heavy tail at least 17 times to lay a single clutch (Tereshchenko and Singer, 2013) of 34–36 eggs (Brown and Schlaikjer, 1940).

**Assessment of some published data on sexual dimorphism in ceratopsian dinosaurs.** In this and a previous study (Tereshchenko, 2001), in comparing sexual differences found in Protoceratopidae with those in other protoceratopoids, we mostly used Bagaceratopidae because of a lack of females in our sample of Leptoceratopidae (Table 1). However, by analyzing specimens and illustrations in the studies by Brown and Schlaikjer (1942), Sternberg (1951), Chinnery and Weishampel (1998), and Chinnery and Horner (2007), we were able to extend the sexual characters discovered to all members of Leptoceratopidae (Table 4)<sup>2</sup>. In other words, our results enable us to assess the sex and age of Leptoceratopidae specimens pictured in the publications cited above. For instance, the structure of the vertebrae and the pelvic girdle of *Montanoceratops cerorhynchus* (Brown, Schlaikjer, 1942) indicates that based on characters 1, 7, 8, 10–15, AMNH 5464 is a large, adult, mature male (Figs. 5g–5i; Brown and Schlaikjer, 1942, text-figs. 3; 4; 7, B), while MOR 542,

based on characters 1, 7, 10–13, belongs to a young, mature female (Figs. 5j, 5k; Chinnery and Weishampel, 1998, text-figs. 4C; 8B). *Leptoceratops gracilis* (Sternberg, 1951) specimens NMC 8887 and 8888, based on the degree of fusion of sacral vertebrae (Table 3) and characters 8, 11, 13, 15 are both young, medium-sized, mature individuals, of which the first is a male, the latter a female (Sternberg, 1951, Plate LIV, A and Plate LVII). Specimen NMC 8889, which Sternberg considered a young mature individual, may, judging from the description and characters 1, 8, and possibly 10 (Sternberg, 1951, Plate LIV, B), turn out to be a large, young or small, adult, mature male. The same can be said about *Cerasinops hodgskissi* (MOR 300) based on characters 1, 7, and possibly 10 (Chinnery and Horner, 2007, text-fig. 4A, 4B, 4D, 4E), which has a transverse expansion of neural spines that is less pronounced than in large adult mature males of protoceratopoids (Figs. 2a–2c, compare with Figs. 5d–5f, 5h–5i).

Of special interest is Mallon's (2005) reassessment of sexual dimorphism in the postcranial skeleton of two specimens of *Chasmosaurus belli* Lambe, 1902 (Neoceratopsia: Ceratopidae), which had previously been identified by Sternberg (1927) as male (NMC 2245, length 4.93 m) and female (NMC 2280, length 4.95 m). Mallon concluded that the two specimens differ in the structure of the collar, the height of the neural spines, the length and orientation of diapophyses on dorsal vertebrae and the robustness of limb bones. Citing Tereshchenko (2001), Mallon agrees that based on characters discussed in this article as characters 1 and 2 (basic characters of neural spine height and robustness of limb bones) and character 6 (accessory character of inclination angle with the vertical of diapophyses), contrary to Sternberg's opinion, NMC 2280 should be classified as male, and NMC 2245 as female (Figs. 6a–6e). However, doubts about including character 2 with sexual characters and the necessity to confirm the presence of characters 1 and 6 in the skeleton of other species of *Chasmosaurus*, as well as the stratigraphic separation of the two skeletons (Dinosaur Park Formation, Alberta; Campanian) led Mallon to the conclusion that NMC 2280 belonged to *C. russelli*, while NMC 2245 belonged to *C. belli* (Mallon, 2005). In reaching this conclusion, he involuntarily accepted the results of our study on the possibility of extending sexual characters (characters 1, 2, and 6 in our case) to separate species of a given genus (*C. russelli* and *C. belli*), despite their stratigraphic separation. By analyzing the data in Mallon's study (Mallon, 2005, text-fig. 3.2, text-figs. 3.5A, 3.5C; Table 3.1) we were able to recognize additional sexual characters that were not observed by the author of that study: in the spine, characters 4, 7 a 10 (Figs. 6a, 6b, 6d, 6e compare with Figs. 2a, 2b, 2d, 2e; and Figs. 5d, 5e, 5h–5k), in the pelvic girdle, character 13 (Figs. 6c, 6f compare with Figs. 4c, 4d, 4h, 4i) and in the shoulder girdle (differences in scapula length which is lon-

<sup>2</sup> The applicability of characters 4–6 to members of the family Leptoceratopidae requires further study.



**Fig. 6.** Dorsal vertebrae (a, b, d, e) and pelvic girdle (c, f) of *Chasmosaurus belli* Lambe, 1902 (after Mallon, 2005, text-figs. 3.2C, 3.2D; 3.6A): (a–c) MNC, no. 2245, (d–f) MNC, no. 2280; (a, b) 10th, (d, e) 8th; (a, d) left view, (b, e) anterior view, (c, f) ventral view. For abbreviations see Figs. 2, 4. See text for explanations.

ger in NMC 2280 than in NMC 2245; see Mallon, 2005, text-fig. 3.5A). As a result, while in no way disputing Mallon's opinion on the attribution of specimens NMC 2280 and NMC 2245 to separate species, we are able to determine with a high degree of certainty that based on characters 1, 2, 4, 6, 7, 10, 13 and the length of the scapula, the first of these is a male while

the second is a female. The weakly developed expansion of the tip of the neural spine 8th (Figs. 6c, 6e) in the male (NMC 2280) and the small lateral deflection of the preacetabular lamina (Fig. 6c) in the female (NMC 2245), likely indicate their individual age as large, young, mature individuals. The correlation between the length of the scapula and the height of the

neural spines observed in *Chasmosaurus* is possibly typical for all ceratopsian dinosaurs, as this pattern is known in modern mammals (discussed above for *Bison*), where males have longer scapulae and higher neural spines than females.

The suggestion that there are similarities in the patterns of sexual differences between ceratopsian dinosaurs (Ornithischia: Neoceratopsia) and other dinosaur groups (Saurischia: Theropoda) is corroborated by Carpenter's (1990) and Osborn's (1916) studies on the variability of *Tyrannosaurus rex* Osborn, 1905. Carpenter, in discussing what we here called accessory sexual character 15, hypothesized that specimen AMNH 5027 was a male, while CM 9380 and TMP 81.6.1 were females. Comparing the cervical vertebrae between *T. rex* specimens BM(NH) R7994 and AMNH 5027, Carpenter notes that the first of these is more robust than the second (Carpenter, 1990, text-fig. 10.4) which suggests to us that if AMNH 5027 was a male, then BM(NH) R7994 must be a female. Molnar (2005), citing Osborn (1916), indicates that in the tyrannosaur female (CM 9380), the sacral vertebrae are more robust and the pelvis (at the level of the acetabulum) is wider than in the male (AMNH 5027). This shows that while ceratopsians and theropod dinosaurs show similar sexual differences in the robustness of the vertebrae and the height of the pelvic canal (characters 4 and 15), they have clearly different patterns of dimorphism in pelvic width. Sexual differences in the acetabular pelvic width, already discussed for modern mammals and lizards, in *T. rex* have values around 25%, according to our measurements from the figure in Molnar (2005, text-fig. 15.6B), which is comparable to values found in modern adult agamas (Table 2, character 4).

The study by Persons et al. (2015) on sexual dimorphism in the caudal vertebrae of two specimens of the oviraptorosaur *Khaan mckennai* (Theropoda: Oviraptoridae) from the Upper Cretaceous of Mongolia (Barungayot Formation, Uhaa Tolgod locality). Persons et al. indicate that specimen MPC-D 100/1002 is somewhat longer than MPC-D 100/1127 and both likely belong to adult individuals. Noting that in the first specimen, the haemal arches of the six anterior caudal vertebrae are longer and their ventral ends are more expanded anteroposteriorly compared to the second specimen, the authors conclude that MPC-D 100/1002 is a male, while MPC-D 100/1127 is a female. These sexual differences could be treated as accessory characters typical for the group in question if they were associated with one basic character or at least two accessory characters known for modern amniotes or neoceratopsians. In other words, the authors have demonstrated that sexual dimorphism in oviraptorosaurs exists, but could not prove their sex assignment.

We add to the above that in modern reptiles, the number of the first caudal vertebrae lacking haemal

arches (pygal vertebrae: Hoffstetter and Gasc, 1969) usually correlates with the structure of the copulative organ. In crocodiles and turtles their number is greater in males than in females (White, 1939), but is the same in lizards (Tereshchenko, 1991a) and, likely, snakes. The copulative organ in is unpaired in crocodiles; in lizards and snakes, it is paired, has the shape of two sacs lying below the skin at the posterior margin of the cloaca, originating from its wall and capable of being extruded (everted) (Schmalhausen, 1947; Naumov and Kartashev, 1979). In dinosaurs, males and females of protoceratopoids and oviraptorosaurs have the same number of pygal vertebrae, with the first haemal arch occurring between 2–3cd in *Khaan mckennai* (Persons et al., 2015), 3–4cd in *Protoceratops andrewsi* (Brown and Schlaikjer, 1940) and *Montanoceratops cerorhynchus* (Brown and Schlaikjer, 1942) and 5–6cd in *Leptoceratops gracilis* (Sternberg, 1951). Females of *Khaan* and *Protoceratops* laid a pair of very elongated eggs simultaneously (Brown, Schlaikjer, 1940; Persons et al., 2015), which was facilitated by the mobility of the pubic and ischial symphyses (character 3). It can therefore be deduced that in males of these dinosaurs, the sex organ was paired.

## CONCLUSIONS

This study shows that during functional specialization of sexual characters in both modern and fossil amniotes, males follow the path of increasing the adaptation of the locomotor apparatus, whereas females increase their adaptation to reproduction. Accordingly, three categories of sexual differences can be recognized in the postcranial skeletons of amniotes reflecting the adaptation of the sexes to their functions in life and reproduction. These include:

(I) Characters associated mostly with locomotor activity which is usually higher in males;

(II) Characters reflecting the adaptation of females to gestation (egg retention) which causes the abdominal cavity to be larger in volume than in males.

(III) Female traits associated with parturition or egg-laying, which result in a greater pelvic width and mobility of the pubic and ischial symphysis compared to males.

In particular, in dinosaurs, category I characters include higher neural spines on the dorsal vertebrae in males, and, most likely, also their distal transverse expansion (club shape), especially in the posterior back; the limb bones in males are more robust but the vertebrae more gracile than in females. Category II includes differences in the arc of the dorsal curvature of the spine and in the inclination angle with the horizontal of the costovertebral articulation (greater in males than in females), as well as differences in the preacetabular pelvic width (which is smaller in males). Category III includes, among other characters, differences in the postacetabular pelvic width and the incli-

nation of the functional axis of the ischium, which are both higher in females than in males.

The male sex organ of dinosaurs was likely paired, which is indicated by the same number of pygal vertebrae, as in modern lizards and snakes.

Establishing sexual dimorphism in the postcranial skeleton of dinosaurs has to proceed by searching for sexual characters specific to individual taxa based on their correlation with undoubtedly sexual characters, i.e. the most reliable for the group as a whole. We call the first accessory, and the latter, basic sexual characters.

Identifying characters of sexual variability and their transformations during ontogeny will greatly simplify the identification of taxonomically significant characters. We believe that this approach can be used in assessing the morphological diversity of any tetrapod group including dinosaurs.

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