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POSTCRANIAL ANATOMY OF *SAUROLOPHUS ANGUSTIROSTRIS* WITH COMMENTS ON OTHER HADROSAURS

(Plates 18—25)

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A supplementary description of the postcranial skeleton of a hadrosaurine dinosaur *Saurolophus angustirostris* ROZHDESTVENSKY is given, based on the material from the Upper Cretaceous Nemegt Formation at Altan Ula and N Nemegt localities, Nemegt Basin, Gobi Desert, Mongolian People's Republic. Articulated skeletons of *S. angustirostris* and of other hadrosaurs exhibit a comparatively strong ventral inclination of the cranial portion of the thoracic vertebral column. This may indicate a presence of spacious crop. Weight of the crop might necessitate a shortening of the body cranial to the acetabulum in order to shift backward the center of gravity of the heavy thoracic part. This inclination had the effect of shortening. It was important for counterbalancing the thorax by the tail during the bipedal progression with horizontally maintained thoracic portion of the backbone. During bipedal locomotion, the neck was held vertically and the head was thrust forth and back to adjust the center of gravity.

It is noticed that in *S. angustirostris*, as well as in, at least, several other hadrosaurs, the puboiliac contact was reinforced by anterior sacral ribs; similar bracing of this contact by sacral ribs is known in some other ornithopods. This made it possible for these hadrosaurs to assume and maintain an upward inclined stance during high-browsing and while surveying the surroundings. Hadrosaurs are considered here as terrestrial bipeds, which, however, occasionally moved around on all fours e. g. while in swamps or marshes, and while they rested grounding the food withdrawn from the crop.

Key words: Dinosauria, Ornithischia, Hadrosauridae, Cretaceous, Mongolia.

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ANATOMIA SZKIELETU POZACZASZKOWEGO *SAUROLOPHUS ANGUSTIROSTRIS*

Streszczenie. — Praca zawiera dalsze rezultaty badań autorek nad dinozaurami kaczodziobymi (Hadrosauridae). Dokonano uzupełniającego opisu szkieletu pozaczaszkowego *Saurolophus angustirostris* ROZHDESTVENSKY, 1952, opierając się na materiałach pochodzących z formacji Nemegt (górna kreda) w Ałtan Ule i Pn. Nemegcie (Kotlina Nemegt, Pustynia Gobi, Mongolska Republika Ludowa).

Zwrócono uwagę, że szkielet *S. angustirostris*, a także szkielety innych kaczodziobych, charakteryzują się silnym wentralnym nachyleniem przedniego odcinka tułowiowej części kręgosłupa i związanym z tym obniżeniem pasa barkowego, niespotykanymi u innych dinozaurów. Cechy te mogą wskazywać na występowanie u kaczodziobych dużego wola. Ciężar wypełnionego pokarmem roślinnym wola powodował, zapewne, konieczność skrócenia odcinka ciała znajdującego się przed punktem jego podparcia w panewce biodrowej, aby przesunąć ku tyłowi środek ciężkości. Nachylenie ku dołowi przedniego odcinka kręgosłupa tułowiowego powodowało takie skrócenie tej części ciała. Miało to duże znaczenie dla utrzymania równowagi ciała tych w zasadzie dwunożnych dinozaurów. Stosunkowo ciężka głowa musiała być trzymana w czasie lokomocji w górze, na pionowo ustawionej szyi, i zgodnie z przemieszczającym się środkiem ciężkości przesuwana odpowiednio do tyłu lub do przodu (fig. 5).

Wykazano, że połączenie kości krzyżowej z biodrowo-łonowym regionem miednicy było dodatkowo wzmocnione przez żebra krzyżowe u *S. angustirostris*, a także co najmniej jeszcze u kilku innych kaczodziobych dinozaurów (fig. 4).

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INTRODUCTION

The present paper reports further results of our investigations on Mongolian hadrosaurs (MARYAŃSKA and OSMÓLSKA 1979, 1981*a*, 1981*b*, 1983) collected by the Polish-Mongolian Paleontological Expeditions, carried on in 1963—1971. It is based mainly on the postcranial skeletons of four incomplete specimens of *Saurolophus angustirostris* from the Upper Cretaceous Nemegt Formation[1] found at the localities Altan Ula II, IV and N Nemegt, all within the Nemegt Basin, Gobi Desert, Mongolian People's Republic (for the geological setting see GRADZIŃSKI 1970, GRADZIŃSKI and JERZYKIEWICZ 1972: figs 1 : 27; 2 : 27). Of these specimens, that labeled as ZPAL MgD-I/159 represents a young individual and is the most complete. Its skull was described earlier (MARYAŃSKA and OSMÓLSKA 1981*a*). We were able to compare the postcranial skeletons of *S. angustirostris* housed in the Palaeontological Institute of the USSR Academy of Sciences in Moscow and in the laboratory of Stratigraphy and Palaeontology of the Academy of Sciences of the Mongolian People's Republic in Ulan-Bator. This has allowed us to supplement earlier morphological observations on *S. angustirostris* of ROZHDESTVENSKY (1957).

As demonstrated by EFREMOV (1955) the *Saurolophus* skeletons in the Nemegt Basin are very often found complete, or as the articulated portions of skeletons, for instance in the famous „Dragon's Grave" at the Altan Ula II locality (EFREMOV 1955: fig. 7), where over an area of 700 m^2 seven almost complete skeletons were found. It is characteristic that almost all the complete or partial articulated skeletons were preserved with skin imprints, independently of the locality or of the sediment type, both in strongly cemented sandstones of the „Dragon's Grave" and in almost loose sand of the N Nemegt (contrary to GRADZIŃSKI 1970: 212). It should be added here, that the skin imprints have never been found with skeletons of other

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[1] The age of the Nemegt Formation is disputable. According to GRADZIŃSKI *et al* (1977) it corresponds to the ?upper Campanian and/or ?lower Maastrichtian stages; recently KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO (1983) claimed on charophytan evidence that it is not younger than the early Campanian.

dinosaurs in the Gobi Desert, even with these occurring at the same localities and in the same sediment types as *S. angustirostris*. In fact, most of the known skin impressions of dinosaurs are found with articulated hadrosaur skeletons. Although the tuberculated hadrosaur skins evidently have no ossifications, it is clear that they had to be much more resistant and thicker than they were in most non-hadrosaurian dinosaurs.

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Abbreviations used:

AMNH — The American Museum of Natural History, New York;
PIN — Palaeontological Institute, USSR Academy of Sciences, Moscow;
GISPS — Geological Institute, Laboratory of Stratigraphy and Paleontology, Academy of Sciences of the Mongolian People's Republic, Ulan Bator;
ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

POSTCRANIAL SKELETON OF *SAUROLOPHUS ANGUSTIROSTRIS*

MATERIAL

N Nemegt locality:

ZPAL MgD-I/12 — fragmentary right ramus of mandible,
ZPAL MgD-I/13 — proximal part of left fibula,
ZPAL MgD-I/157 — incomplete posterior part of skeleton of adult individual including a series of 43 caudals, fragmentary ischium, left and right tibia, fibula and pes,
ZPAL MgD-I/160 — posterior portion of right tibia and astragalus,
ZPAL MgD-I/163 — left metatarsal IV,
ZPAL MgD-I/164 — pedal ungual,
ZPAL MgD-I/165 — fragmentary left metacarpal,
ZPAL MgD-I/169 — two caudals,
ZPAL MgD-I/170 — fragmentary skeleton of young individual including: 24 caudals, fragments of fore limbs,
ZPAL MgD-I/171 — fragmentary skeleton of young individual including: several damaged cervicals, dorsals and sacrals, proximal portion of right ulna.

Altan Ula II locality:

ZPAL MgD-I/87 — skin imprints,
ZPAL MgD-I/158 — left scapula, coracoid, humerus, radius, ulna and incomplete manus,
ZPAL MgD-I/166 — 5 dorsals of young individual,
ZPAL MgD-I/168 — nearly complete pelvis lacking postacetabular processes to the ilia and shafts of ischia, sacrum, 8 or 9 posterior dorsals, with 4 fragmentary ribs.

Altan Ula III locality:

ZPAL MgD-I/69 — fragment of right maxilla.

Altan Ula IV locality:

ZPAL MgD-I/159 — almost complete skeleton of young individual including: skull (described by MARYAŃSKA OSMÓLSKA 1981a), first 8 cervicals, series of 18 dorsals, sacrum including 9 vertebrae, first 3 caudals, complete and right scapula, proximal portion of the left one, right and left coracoid, 2 fragmentary sternal bones, fragmentary cervical and thoracic ribs, ilia (the left one incomplete), right and left prepubis, ischia lacking shafts, proximal portion of right femur, numerous skin imprints.

Tsagan Khushu locality:

ZPAL MgD-I/162 — fragments of skull,
ZPAL MgD-I/167 — proximal portion of right tibia.

DESCRIPTION

Vertebral column (pls. 18, 19: 1—3, 21 : 1, 22, 23: 1—9, table 1). The neck of S. *angustirostris* was comparatively short. A preserved series of cervicals in ZPAL MgD-I/159 includes first eight neck vertebrae out of the 12 (ROZHDESTVENSKY 1957) characteristic of the species.

The atlas (fig. 1). An intercentrum, two halves of the neural arch and a centrum joined to the axis in the form of an odontoid process are preserved. The intercentrum is semilunate, short craniocaudally, with an excavated upper edge for reception of the odontoid. The surface for reception of the occipital condyle is larger and more concave than that for the contact with axis. On the ventral surface of the intercentrum, on each side, runs an oblique, caudolaterally directed furrow which differentiates a tubercle which may correspond to the parapophyses of the remaining cervicals, including the axis. Each half of the neural arch consists of two wings: the vertical wing displays two articular surfaces, one for the contact with intercentrum caudomedially and one for reception of the occipital condyle craniomedially. The dorsal surface of the horizontal wing is somewhat concave craniocaudally. The wing is directed slightly medially to meet the thickened cranial end of the opposite horizontal wing. A postzygapophyseal articular facet is well developed on the ventral side of caudal portion of the wing, at the medial edge. At the lateral edge, the caudal portion of horizontal wing bears a distinct facet which looks like a rib facet. Similarly shaped neural arch of the atlas seems to be developed in *Corythosaurus casuarius* (AMNH 5338; Ostrom 1961: pl. 5) in which similar horizontal wings

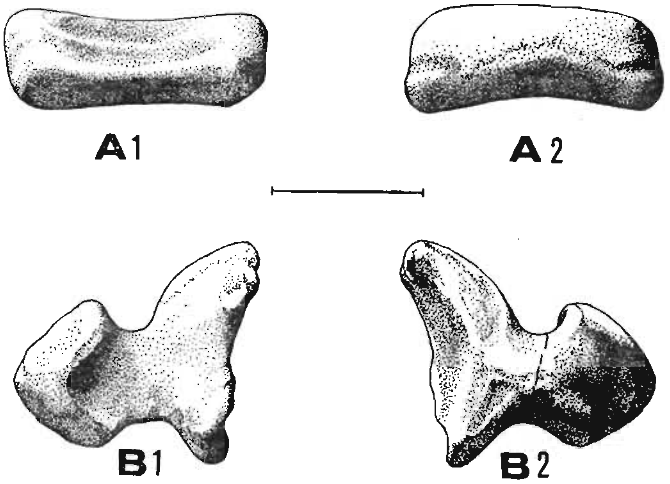

Fig. 1
Atlas of *Saurolophus angustirostris* Rozhdestvensky ZPAL MgD-I/159: A_1 intercentrum, dorsal view, A_2 intercentrum, ventral view; B_1 right half of neural arch, medial view, B_2 right half of neural arch, lateral view. Scale equals 3 cm.

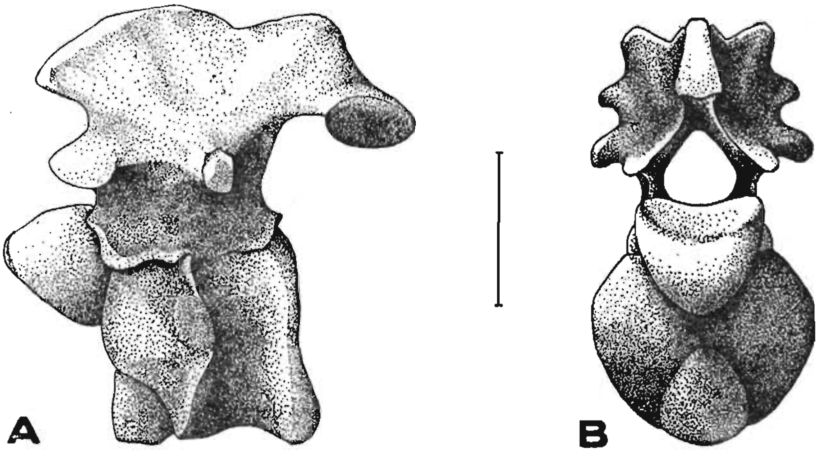

Fig. 2
Axis of *Saurolophus angustirostris* Rozhdestvensky ZPAL MgD-I/159: *A* left lateral view; *B* anterior view. Scale equals 3 cm.

Table 1

Measurements (in mm) of vertebral column of *S. angustirostris* in ZPAL collection

Vertebra number	Length of centrum *		Maximum width of centrum		Maximum height of centrum		Height of neural spine		Width of neural spine (antero-posteriorly)	
	MgD-I/157	MgD-I/159	MgD-I/157	MgD-I/159	MgD-I/157	MgD-I/159	MgD-I/157	MgD-I/159	MgD-I/157	MgD-I/159
Axis	—	20	—	46	—	41	—	31	—	60
C_3	—	25	—	48	—	44	—	—	—	—
C_4	—	27	—	50	—	44+	—	—	—	—
C_5	—	26	—	49	—	49	—	—	—	—
C_6	—	27	—	52	—	47	—	—	—	—
C_7	—	27	—	54	—	45	—	—	—	—
C_8	—	25	—	—	—	49	—	—	—	—
D_4	—	31	—	—	—	—	—	—	—	—
D_5	—	42	—	—	—	—	—	—	—	—
D_6	—	46	—	—	—	—	—	—	—	—
D_8	—	50	—	—	—	—	—	—	—	—
D_{12}	—	48	—	55	—	55	—	—	—	—
D_{14}	—	50	—	58	—	60	—	—	—	—
D_{15}	—	49	—	62	—	65	—	—	—	—
D_{16}	—	46	—	66	—	68	—	—	—	—
D_{20}	—	38	—	82	—	82	—	—	—	—
S_1	—	50	—	78	—	76	—	—	—	—
S_2	—	44	—	—	—	—	—	—	—	—
S_3	—	59	—	—	—	—	—	—	—	—
S_4	—	54	—	—	—	—	—	100	—	51
S_5	—	47	—	—	—	—	—	—	—	—
S_6	—	50	—	—	—	—	—	104	—	52
S_7	—	50	—	—	—	—	—	111	—	52
S_8	—	46	—	—	—	—	—	—	—	—
S_9	—	35	—	85	—	69	—	—	—	—
Ca_1	—	35	—	78	—	68	—	—	—	—
Ca_2	—	32	—	77	—	—	—	—	—	—
Ca_3	—	32	—	74	—	68	—	—	—	—
Ca_5	50	—	105	—	115	—	—	—	—	—
Ca_6	50	—	100	—	116	—	—	—	—	—
Ca_7	53	—	—	—	117	—	—	—	—	—
Ca_{11}	52	—	90	—	—	—	220	—	41	—
Ca_{12}	52	—	94	—	98	—	214	—	41	—
Ca_{13}	50	—	94	—	98	—	195	—	39	—
Ca_{14}	50	—	94	—	92	—	165	—	37	—
Ca_{24}	49	—	79	—	74	—	—	—	—	—
Ca_{34}	46	—	66	—	67	—	—	—	—	—
Ca_{41}	38	—	56	—	58	—	—	—	—	—
Ca_{47}	32	—	46	—	39	—	—	—	—	—

* Measured without articular surfaces.

are elongated forwards and contact each other cranially; there also seems to be a caudolateral articular facet in this specimen, as illustrated by OSTROM.

The axis (fig. 2). The centrum of axis is shorter than in the other cervicals. Its cranial face is very convex, especially dorsally, and is divided by a vertical median groove. Ventrally, a subconical, prominent intercentrum adheres to the cranial face of the centrum. The ventral side of the intercentrum is flat, the dorsal apex of the intercentrum does not reach half the height of the centrum. Dorsally, a large, subhemispherical odontoid process attaches to the cranial face of the axis centrum, reaching down half the height of the centrum. The intercentrum of axis and the centrum of atlas (odontoid) are separated suturally from each other by a significant distance. The odontoid is still well separated from the cranial face of the axis centrum. The neural arch of axis is very high and long, the postzygapophysis extending far backward. The arch is distinctly sutured to the centrum. The pedicel of the arch is very long craniocaudally, somewhat invading the convex cranial face of centrum, unlike the more caudal cervicals where the pedicels end at the border between the lateral side of centrum and the convex cranial face. The axial spine is still longer, its cranial apex protruding in front of the projection of the pedicel, and ending above the cranial limit of the prezygapophysis. Caudally, the axial spine divides into two high plates, each of which surmounts the postzygapophysis. The diapophysis is prominent and tuber-like, closer to the midline than those of the succeeding cervicals. It is situated at the level of the prezygapophysis.

Cervical vertebrae 3—8 have about equally long centra, which are somewhat longer, however, than that of the axis. They are strongly opisthocoelous, the convex cranial faces extend very far caudally on the ventral side. The centra are laterally concave, and their caudal edges form kind of a lip-like margin around the deeply concave caudal face of each centrum. The parapophyses are well marked, placed craniodorsally just beneath the suture with the pedicel. The pedicels are distinctly shorter than those of the axis. The postzygapophyses are long, massive, dorsally rounded, with large articular facets which face ventrolaterally; they gradually elongate on each successive cervical. The prezygapophyses are short and gradually shorten slightly along the cervical series; only that of cervical 3 is longer than the others. Instead of the neural spine, cervical 3 bears a low, median ridge; on the successive cervicals, the neural spines are not preserved in our specimen. They were probably low ridges, similar to those in *S. osborni*. The transverse process on cervical 3 is short, similar to that of the axis; beginning with cervical 4, the processes become stronger and longer; however generally they are rather short along the whole preserved cervical series.

The dorsal vertebrae. An almost complete series of dorsals, except probably two most cranial ones, is preserved in ZPAL MgD-I/159. The preserved cranial centra of the dorsals are short and are strongly concave laterally as well as ventrally. They become longer backward up to dorsal 8; beginning with dorsal 15 they shorten toward the sacrum. A ventral ridge is present on all preserved dorsal centra, being especially sharp on the centra of dorsals 9 to 13. The height of the dorsal centra within the preserved series increases significantly backward. The transverse diameters of the first nine preserved centra (3—11) are about equal, they increase gradually further on. In connection with the increase in width of the dorsal centra, the shape of the

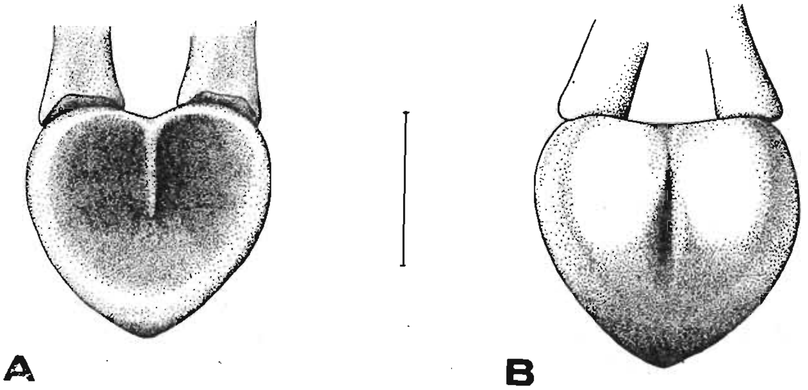

Fig. 3
Saurolophus angustirostris ROZHDESTVENSKY ZPAL MgD-I/159: *A* posterior articular face of centrum of ninth dorsal vertebra; *B* anterior articular face of centrum of tenth dorsal vertebra. Scale equals 3 cm.

articular faces changes from the heart-like and vertically elongated toward a subcircular shape. Although all the dorsals are opisthocoelous, they become less so toward the sacrum. The caudal face of the centrum of dorsal 9 has a peculiar vertical median ridge, which fits into a corresponding groove on the cranial face of centrum 10 (fig. 3). This feature is certainly absent between the more posterior centra; whether or not was it present between the centra preceding these two cannot be stated, because the vertebrae within this portion of the column, as preserved, are difficult to separate. A similar ridge was observed on the last dorsal centrum in *Hypsilophodon* by GALTON (1974*a*). The neural arches of the dorsals are mostly badly damaged in our specimen. As could be observed, the transverse processes were steeply rising outwards as far as the sacrum.

The sacrum of ZPAL MgD-I/159 includes nine sacrals which are already fused in this young skeleton but less so between sacrals 4 and 5, and, 7 and 8. It measures 440 mm in length and 225 mm in the height (maximum). As seen ventrally, the first sacral is strongly concave on its sides and has a very strong longitudinal ridge. Sacral 2 is transversely wider than the sacral 1 and it is strongly concave craniocaudally on the ventral side, although it has there a weakly pronounced longitudinal median ridge. Sacral 3 has an almost flat ventral surface devoid of any ridge. Sacrals 4—6 are transversely narrower than the more cranial and more caudal ones; sacrals 4 and 5 bear a deep median ventral longitudinal groove which shallows distinctly and widens along sacrals 6 and 7. The ventral surfaces of sacrals 8 and 9 are generally convex transversely, but nevertheless they bear a median, longitudinal depression. Sacral 9 is the shortest of the series and its shape resembles a caudal. The neural arches and sacral ribs are slightly distorted and damaged in ZPAL MgD-I/159, which does not permit full description. The distal ends of seven sacral ribs do not fuse to form a continuous acetabular bar. Sacral rib 1 is deep, flattened craniocaudally at the sacral centrum and thickens distally, displaying a large, subtriangular distal articular surface. This rib is directed obliquely backward but still its distal articular surface is well in front of the pubic peduncle of the ilium, so that it could not contact the latter bone (pl. 21: 1, fig. 4a). On the left side of the pelvis in ZPAL MgD-I/159, it is only sacral rib 2, that contacts the pubic peduncle of the ilium. However, on the right side of the same pelvis, there are two sacral ribs (1 and 2), the distal articular facets of which are in front of the pubic peduncle of the ilium. The sacropelvic region in this specimen is slightly deformed, but it seems that the arrangement visible on the right side is the normal one, as such an arrangement, with two ribs (1 and 2) in front of the acetabulum, is visible in ZPAL MgD-I/168 (pl. 25: 1). Sacral rib 7 arises from the cranial portion of the lateral surface of sacral centrum 8. This rib is plate-like, deep, directed obliquely forward and it contacts the ilium opposite the caudal margin of the antitrochanter. It is the last rib taking part in the formation of the acetabular bar. The distal extremities of the transverse processes of sacrals 2 to 5 are rounded, tuber-like. As preserved on both sides of the sacrum of ZPAL MgD-I/159, the ends of the transverse processes are placed on the upper surface of the dorsal iliac margin, an apparently natural condition, because it is also observed to some extent in ZPAL MgD-I/168 (pls 21: 1; 22: 1a; 25: 1a). The last three sacral transverse processes are thin craniocaudally and each still displays a sutural contact with its respective rib below, as in the case of the proximal caudals (see below). The neural spines of the sacrals are comparatively high, flat transversely, rectangular and equally thin along their entire height. They are well separated from each other and perpendicular to the long axis of sacrum. The cranial surface of sacral centrum 1 is very weakly convex. The caudal surface of sacral centrum 9 is somewhat concave transversely.

ROZHDESTVENSKY (1957) reported eight vertebrae in the sacrum of *S. angustirostris*. The same number is given by BROWN (1913a) for the sacrum of the *S. osborni* type specimen. The sacrum of our youngest individual ZPAL MgD-I/159 includes, without any doubt, nine vertebrae; ZPAL MgD-I/168 seems, however, to include eight vertebrae, although this cannot be stated for sure because of the state of preservation of this specimen.

The caudal vertebrae. Only three most proximal caudals are preserved in ZPAL MgD-I/159. They are nearly amphiplatyan, very short with subquadrate articular faces and craniocaudally concave lateral sides. Ventrally, the centra are concave longitudinally but flat transversely. The caudal ribs are short, inclined downward, with the inclination increasing toward the rear. Caudal rib 1 is flattened craniocaudally while the next ones are flattened dorsoventrally. These ribs are fused with the corresponding centra and transverse processes, but the suture between the rib and the process remains well visible in this specimen. The transverse processes are thin, perpendicular plates angularly terminated dorsodistally, above the contact with respective ribs. They diminish toward the rear. BROWN (1913*b*, fig. 3) illustrated a similar transverse process in a caudal of *Hypacrosaurus altispinus* but the shape and direction of rib is different in this species than in *S. angustirostris*. The sutural connection between the proximal caudal ribs and respective transverse processes was also noted by WIMAN (1929) in an unidentified hadrosaur from Shantung, China.

Another specimen of *S. angustirostris* in our collection, ZPAL MgD-I/157, displays an almost complete series of forty three caudals (probably caudals 5—47). The first three or four caudals in the preserved series are distinctly opisthocoelic, but more posteriorly they become gradually less so, attaining the amphiplatyan condition at about the level of caudal 20. The neural spines are flat transversely, equally wide craniocaudally, strongly inclined backward, but somewhat curved forward at the top. Caudal ribs were present on fourteen proximal caudals preserved, but at least last three of them were but small knobs. The first four chevrons slant backward much more strongly than the succeeding ones, which is characteristic for the chevrons located just above the shaft of ischium in hadrosaurs. The first seven chevrons of the series are very narrow in lateral view; beginning with chevron 8 they become broader laterally. The chevron located between the caudals 11 and 12 is abnormally developed (pl. 23 : 8, 9); its left ramus has a posterior process which fits into a facet on the corresponding ramus of the successive chevron. The chevrons on the proximal caudals are somewhat longer than corresponding neural spines.

Shoulder girdle (pls. 19: 1; 20: 1—5; 24: 1, table 2). *The scapula* is convex externally and it widens backward; the upper and lower margins of scapular blade are curved, the lower more so. The acromion inclines slightly downwards; it is subtriangular, prolonging backward and downward into an indistinct ridge, which ends close to the lower border, before reaching half the length of the scapular blade. More than half of the glenoid fossa is formed by the scapula.

The coracoid is short, typical of hadrosaurs, and was described in detail by ROZHDESTVENSKY (1957). At the sutural surface of the coracoid, on its internal side, close to the glenoid there is a deep notch. It is worth to mention that already in the young individual (ZPAL MgD-I/159) on the upper coracoid margin there is developed a strong knob. The knob provided an extensive attachment surface, probably for the origin of a tendon of biceps.

The sternal bones of the typical hadrosaurian shape, are incompletely preserved in ZPAL MgD-I/159. Their median blades are damaged as are the distal ends of the shafts. The sternal shaft is distinctly curved outward. In comparison with the sternals in *Anatosaurus annectens* (LULL and WRIGHT 1942 : fig. 21) that in *S. angustirostris* has a more curved shaft, a median blade that is less expanded caudally and cranial end that is less expanded dorsolaterally.

Fore limb (pls. 20 : 6, 7; 24 : 2—5; table 2). The most complete fore limb in our collection is represented by ZPAL MgD-I/158. *The humerus* is distinctly sigmoid and displays a subquadrangular deltoid process, although the latter is rather subtriangular in the humerus of the younger individual ZPAL MgD-I/159. Generally, the bone is typical of hadrosaurs. The same may be said of the radius and ulna. The antebrachium is shorter than the humerus.

The manus preserved in ZPAL MgD-I/158 is very incomplete. As far as can be stated, it con-

Table 2

Measurements (in mm) of scapulocoracoid, pelvis and limbs of *S. angustirostris*

	ZPAL MgD-I/159	ZPAL MgD-I/158	PIN 551—8 ROZHDESTVENSKY 1957 : 136
Scapula			
length	450+	770+	900
proximal width	105	210	—
distal width	122	190+	250
Coracoid			
length	80	—	—
proximal width	80	145	—
Humerus			
length	—	630	600
proximal width	93	165	—
distal width	—	125	—
Ulna			
length	—	565a	630
proximal width	—	110	—
Radius			
length	—	515a	530
proximal width	—	80	—
Metacarpal II			
length	—	238	250 *
Metacarpal III			
length	—	—	280
Metacarpal IV			
length	—	—	280 *
Metacarpal V			
length	—	120	110 *
Ilium			
length	540	—	960
maximum height	125	—	—
height above acetabulum	110	—	—
preacetabular length	196	—	—
postacetabular length	160	—	—
postacetabular height	93	—	—
length of acetabulum	115	—	—
width of antitrochanter	95	—	—
Prepubis			
length (from acetabulum)	247	—	470
maximum width	105a	—	260
Ischium			
length	—	—	1130
Femur			
length	—	—	1200
Tibia			
length	—	—	1000
Fibula			
length	—	—	870
Metatarsal III			
length	—	—	330

a — approximate

* — calculated from ROZHDESTVENSKY 1957, fig. 3

forms to the description given by ROZHDESTVENSKY (1957); however, it did not allow us to recognize whether digit IV has four phalanges, as the latter author suggests (1957 : fig. 3), or three, as is typical of most hadrosaurs. *S. angustirostris* differs in the structure of the digit IV of manus from all other hadrosaurs in having the phalanx IV—1 strongly asymmetrical; this caused strong lateral divergence of this digit. A smaller but distinct divergence of this digit is observed in most hadrosaurs, but there it seems to be caused by a curvature of the metacarpal IV. While reconstructing the manus in *S. angustirostris*, ROZHDESTVENSKY (1957 : fig. 3) placed the subtriangular phalanges II—2 and III—2 so that their apices are directed laterally; in other hadrosaurs, in which such subtriangular phalanges occur, the apices are directed medially so that a slight medial divergence of the unguals in these digits results (comp. *Lambeosaurus clavinitialis*: STERNBERG 1945; *Parasaurolophus walkeri*: PARKS 1922). The only specimen of *S. angustirostris* which we have found in the field displaying a natural arrangement of the bones within the fore limbs (GI SPS, pl. 20: 8) seems to indicate that this phalanx, at least in the digit II, has the apex directed medially.

Pelvic girdle (pl. 21: 22; 25; fig. 4, table 2). The pelvic girdle, preserved in ZPAL MgD-I/159 and 168, is deep, the acetabulum is oval and craniocaudally elongated. The prepubis extends cranially and laterally beyond the preacetabular process of ilium. The long axis of the shaft of the ischium is at a small angle to the longitudinal axis of the acetabulum. The region of the puboiliac contact is additionally strengthened by sacral ribs.

The ilium is similar in the shape to that described by LULL and WRIGHT (1942) for *S. osborni*. The differences concern the preacetabular process, which is shorter in *S. angustirostris* extending forwards along two — three posterior most dorsals, and the postacetabular process which is subrectangular in the later species while tapering backward in *S. osborni* (comp. ROZHDESTVENSKY 1957: fig. 4 and here pl. 21: 1). The pubic peduncle of the ilium is very narrow transversely and the surface for contact with the pubis occupies only its apex. The entire concavity between this apex and the ischiac peduncle forms the upper margin of the acetabulum; this is also confirmed by the size of a femoral head. Thus, in this respect, the illustration of the pelvis of *S. angustirostris* given by ROZHDESTVENSKY (1957: fig. 4), showing a laterally

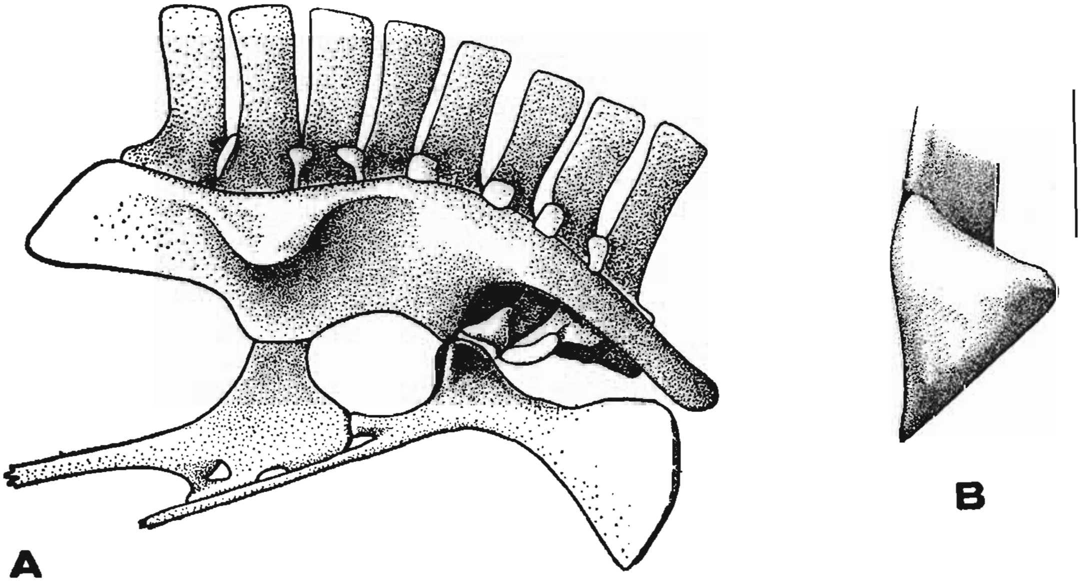

Fig. 4
Saurolophus angustirostris ROZHDESTVENSKY, *A* reconstruction of right side of pelvis and sacrum based on ZPAL MgD-I/159 and 168; *B* dorsal view of iliac peduncle of pubis, ZPAL MgD-I/159. Scale equals 3 cm.

broad pubic peduncle which contacts the pubis along the extensive surface, is incorrect. The antitrochanter is well developed and its upper surface slants slightly downward and outward.

The pubis generally resembles that in *S. osborni* but the prepubis widens more rapidly distally. The peduncle for contact with the ilium is very low, thick and long. It provides dorsally a subtriangular surface, which slightly slopes at the medial side (fig. 4b). A strong vertical lip bounds cranially the acetabular surface of the pubis which is directed toward the inside of the acetabulum, at an angle to the lateral surface of the main body of the pubis. The ischiac peduncle is long and slender. The pubic shaft separates from the main body of pubis at about a mid-length of the acetabulum. It is dorsoventrally flattened and separated from the ischiac peduncle by an obturator notch.

The ischium displays a high, straight and massive iliac peduncle, which is triangular in cross-section. The pubic peduncle is high, comparatively thin, higher than the corresponding ischiac peduncle of the pubis. The pubic and iliac peduncles of the ischium form an angle of about 90°. The plate-like portion of the ischium has a sinusoidal lower margin and contains a large opening, that is completely closed ventrally. This opening which is closed in ZPAL MgD-I/159 and MgD-I/169, corresponds to the notch visible on the illustration of the ischium given by Rozhdestvensky (1957: fig. 4) and to the closed foramen in the type specimen of *S. osborni* (Brown 1913*b*: fig. 1). The shaft of ischium is dorsoventrally flattened along its preserved proximal portion. All the specimens of this species which we have seen were either devoid of any hammerlike widening at the distal end of the shaft, or this portion of the shaft is missing.

Hind limb (pl. 23 : 10, 11; tables 2 and 3). There is no complete hind limb in our collection of *S. angustirostris*. The femur, tibia and fibula, as preserved, do not display important differences with other hadrosaurs.

The astragalus-calcaneum complex entirely covers the distal surfaces of tibia-fibula, all these elements are free. The astragalus displays cranially an ascending process in the form of an uneven triangle, the lateral side of which is less than three times as long as the medial one. The lateral edge of the astragalus underlies the fibula slightly. The calcaneum barely overlaps the tibia caudally.

The pes in *S. angustirostris* was described in detail by Rozhdestvensky (1957). We may only add, that in ZPAL MgD-I/157 there is a deep, sharp-edged excavation on the plantar surface of the phalanges 2 and 3 of all the digits, which is only slightly shallower on the phalanx II—2.

Table 3

Measurements (in mm) of pes of *S. angustirostris*

ZPAL MgD-I/157	Length	Width	
		proximal	distal
Metatarsal II	235	73	113
Phalanx II-1	85	76	83
II-2	44	75	68
II-3	88	58	72
Metatarsal III	280	130	125
Phalanx III-1	102	125	113
III-2	23	110	112
III-3	28	93	90
III-4	85	83	106 max.
Metatarsal IV	260	110	90
Phalanx IV-1	65	100	88
IV-2	19	76	
IV-3	14	75	
IV-4	20	65	
IV-5	85	60	74

As may be seen from the shapes of articular surfaces between the penultimate phalanges and the unguals, the marginal unguals were inclined so that their edges (the lateral on ungual IV and the medial on ungual II) were closer to the substrate. The unguals have the usual hadrosaurian hoof-like form and their serrated and rough anterior margins suggest indeed a presence of solid horny hoof.

As compared with the pes in *S. osborni*, that in *S. angustirostris* is proportionally shorter, thanks to a shortening of the phalanges.

Skin imprints (pl. 19 : 4, 5). Skin imprints are preserved especially well on some parts of the skeleton of ZPAL MgD-I/159. The pelvic region and the thigh are covered by small, rounded tubercles of a uniform size, with scarce, somewhat larger tubercles being dispersed among them. The tubercles on the inner side of the thigh are smaller and are all of uniform size.

SYSTEMATIC POSITION OF *SAUROLOPHUS ANGUSTIROSTRIS*

Saurolophus BROWN, 1912 is considered by some authors as being well allocated within the subfamily Hadrosaurinae LAMBE, 1918 (e. g. STERNBERG 1953) while others assign it to the subfamily Saurolophinae BROWN, 1912 (e. g. OSTROM 1961). As commonly understood, Saurlophinae *sensu* GILMORE, 1924 include the genera: *Saurolophus* BROWN and *Prosaurolophus* BROWN. Some authors included here also *Brachylophosaurus* STERNBERG (OSTROM 1961), *Kritosaurus* BROWN, *Jaxartosaurus* RIABININ and *Tsintaosaurus* YOUNG (YOUNG 1958). HOPSON (1975) following STERNBERG (1953) did not recognize the subfamily Saurolophinae, considering the saurolophines as an informal group within the Hadrosaurinae (see below). Although the hadrosaurs are well characterized by the structure of their heads, due to the modifications of the narial region (HOPSON 1975), and can be divided on this basis into several well defined morphological groups, their postcranial anatomy is relatively alike and only three characters (the length of neck, the structure of sacrum and of the ischium) allow their subdivision into two subgroups. These are: the „lambeosaurines" with long necks, ridged sacra and footed ischia and the „hadrosaurines" with short necks, grooved sacra and non-footed ischia. In respect to these three characters, the „saurolophines" conform very well to the „hadrosaurines" with the sole exception for *Tsintaosaurus*, which combines the seemingly *Saurolophus*-shaped crest (but tubular in fact, see below) with the „lambeosaurine" postcranial sacropelvic characters. This is why *Tsintaosaurus* has been assigned to the Lambeosaurinae in our earlier paper (MARYAŃSKA and OSMÓLSKA 1981*a*).

Trying to find some postcranial characters which could help in separating the hadrosaurines, saurolophines and lambeosaurines, we have here calculated some indices supplementing those provided by GALTON (1970). The results, including those of GALTON, are presented in table 4. As may be seen, these indices do not help in a separation of the subfamilial taxa. Some seemingly important indices (e. g. radius to humerus ratio), may be quite different between two species of the same genus (0.95 in *Parasaurolophus walkeri* and 1.03 in *Parasaurolophus cyrtocristatus*), and the differences between them may be greater than between the species assigned to different genera representing separate subfamilies (1.04 in a hadrosaurine *Edmontosaurus edmontoni* and 1.08 in a lambeosaurine *Corythosaurus casuarius*). Some of these indices, on the other hand, may be of an importance for evaluating the locomotory abilities of respective hadrosaur species, from the mediportal to subcursorial ones (COOMBS 1978).

In this situation, there is no practical means to divide hadrosaurs into more than two subfamilies: the Hadrosaurinae and the Lambeosaurinae. However, following HOPSON (1975), one can recognize several informal groups of genera on the basis of the morphology of the narial region. Within the hadrosaurinae these groups are: the edmontosaurs with *Edmonto-*

Table 4

Scapula and limbs ratios in hadrosaurs*

Ratios	Lambeosaurinae	Hadrosaurinae	"saurolophines"
Scapula width/length	0.22—0.29	0.23—0.30	0.24—0.28
Humerus length/scapula length	0.64—0.74	0.62—0.91	0.66—0.70
Radius length/humerus length	0.95—1.22	0.75—1.04	0.82—1.02
Mtc III length/humerus length	0.39—0.51	0.36—0.54	0.47—0.54
Tibia length/femur length	0.93—0.98	0.81—0.90	0.86—0.89
Mtt III length/femur length	0.29—0.38	0.26—0.36	0.28—0.37
Hind limb length/fore limb length	1.65—1.74	1.62—1.70	1.40—1.79
Hind limb length/trunk length	1.42—1.44	1.22—1.44	1.15—1.33

* — calculated from data in Lull and Wright 1942, ROZHDESTVENSKY 1957, present paper; some ratios after GALTON 1970

saurus LAMBE, *Anatosaurus* LULL and WRIGHT, *Tanius* WIMAN; the saurolophs with *Saurolophus* BROWN, *Prosaurolophus* BROWN, (?) *Lophoroton* LANGSTON; the kritosaurs with *Kritosaurus* BROWN, *Aralosaurus* RIABININ, *Brachylophosaurus* STERNBERG. Within the Lambeosaurinae one can distinguish: the lambeosaurs with *Lambeosaurus* PARKS, *Corythosaurus* BROWN, "*Procheneosaurus*" (="*Procheneosaurus*" *convicens* ROZHDESTVENSKY, 1968; comp. MARYAŃSKA and OSMÓLSKA 1981*a*), *Jaxartosaurus* RIABININ, *Hypacrosaurus* BROWN; the parasaurolophs with *Parasaurolophus* Parks; the tsintaosaurs with *Tsintaosaurus* YOUNG. The lambeosaurs are characterized by the presence of a hood built from the premaxillae 1 and 2 and from the nasals which are shifted dorsocaudally. The parasaurolophs have a tubular crest, different from that in lambeosaurs, which is built almost exclusively from the premaxillae, the nasals participating to a slight extent in its formation (RUSSELL 1946). The tsintaosaurs have also the tubular crest, which (unlike the parasaurolophs), is formed exclusively of the nasals (YOUNG 1958). There may be still one more informal morphological unit distinguished within the Lambeosaurinae, including a still undescribed genus found by the Soviet-Mongolian Joint Expedition at the Bayshin Tsav locality (KRAMARENKO 1974; Guide to the Paleontological Exhibition of the USSR Academy of Sciences in Japan 1979: 26; TSYBIN and KURZANOV 1979).

Saurolophus is so far one of two Upper Cretaceous transcontinental dinosaur genera (the other one is poorly known *Archaeornithomimus* — see RUSSELL 1972), known from North America and Asia, the North American representative being *S. osborni* and the Asian one *S. angustirostris*. The answer to the question whether or not these two hadrosaurs are really congeneric seems to be of some importance. However, we have not had an opportunity to compare directly *S. angustirostris* and *S. osborni*; unfortunately the latter species is not sufficiently described to allow a detailed comparison. Based on the published data concerning *S. osborni* (BROWN 1912b, 1913*a*, 1913*b*; LULL and WRIGHT 1942; STERNBERG 1953; OSTROM 1961; RUSSELL 1967: figs 6, 7; MORRIS 1973: fig. 2) and the photographs of the type specimen kindly provided by Mr. M. BRETT-SURMAN (George Washington University, Washington D. C.) we were able to supplement to some extent the list of differences noticed by ROZHDESTVENSKY (1957) between the Asian and North American *Saurolophus* species in question. The skull of *S. angustirostris*, as compared with that of *S. osborni* (see MARYAŃSKA and OSMÓLSKA 1981*a*), is narrower as a whole, the dental battery relatively longer, the external narial opening shorter, the lacrimal shorter, the jugal has a long anterior process, the quadrate is more bowed caudally. This list of differences does not include some very important characters, but the structures in which the eventual differences might be manifested, are inadequately known in *S. osborni* and their interpretation by different authors varied, or they could not be investigated because of the state of preservation. Among these may be mentioned: the presence of supraorbitals separating the frontal from the orbital margin, a significant participation of frontals and prefrontals in the formation of the crest, the presence of a longitudinal ridge on the dorsal (rostral) surface of each nasal; all these features are characteristic of *S. angustirostris* but it is impossible to state if they occur in *S. osborni*. The differences between the postcranial skeletons of the two species are listed in table 5.

Table 5

Comparisons of postcranial skeletons of *S. osborni* and *S. angustirostris*

	S. osborni	*S. angustirostris*
Scapula	straight	curved
Radius length/humerus length ratio	radius almost equals humerus	radius shorter than humerus
Sacrum		
number of vertebrae	8	9 *
neural spines	inclined backwards	perpendicular to long axis of sacrum
Pelvis		
preacetabular process	long, curved	short, weakly curved
postacetabular process	tapering backwards	subrectangular
prepubis	lower and upper edges gently bowed	anteriorly rapidly broadening
Pes as a whole	relatively long, about a third of femur length	about a fourth of femur length
Mtt III/femur ratio	0.31	0.27
Ph III-2/ph III-1 ratio	0.31	0.23

* but comp. p. 125

There is a character in the postcranial skeleton of *S. angustirostris* not mentioned in table 5, which was not so far described in *S. osborni*, namely a peculiar structure of pelvis with the sacral ribs keying the puboiliac region (comp. p. 125), and with the sacral diapophyses embracing the dorsal border of ilium. We consider, however, that this character might not be noticed previously in *S. osborni*, as it was not in *S. angustirostris*, and it may be not the exclusive character of the latter species; this is why we did not list it in table 5.

As *S. angustirostris* has not so far been formally diagnosed, we think it useful to provide below a diagnosis, including the specific characters distinguished by ROZHDESTVENSKY (1952, 1957) and by us (MARYAŃSKA and OSMÓLSKA 1981a, and the present paper):

Skull narrow, especially across the snout; external narial opening short, its caudal border above the first maxillary tooth; frontal with long vertical anterior process propping caudally lower half of nasal crest; prefrontal propping caudolaterally base of nasal crest; rostral surface of nasal within the crest bearing a longitudinal ridge or covered with irregular, bony chambers; two supraorbitals included in the orbital rim; jugal elongated rostrally into a sharp process wedged between maxilla and lacrimal; quadrate strongly bowed caudally; sacral neural spines perpendicular to long axis of sacrum, two first sacral ribs not contacting the ilium but reinforcing the puboiliac contact; scapula curved; radius shorter than humerus; postacetabular process of ilium broad, subrectangular; pes about a quarter of femur length; length ratios of: Mtt III to femur — 0.27, pedal phalanx III-2 to pedal phalanx III-1 — 0.23.

Considering all the cranial and postcranial differences between *S. angustirostris* and *S. osborni*, one can conclude that they are of the same rank as are those between e. g. *Tarbosaurus bataar* and *Tyrannosaurus rex*, *Saurornithoides mongoliensis* and *Stenonychosaurus inequalis*, *Velociraptor mongoliensis* and *Deinonychus* sp. etc., from the Upper Cretaceous of Asia and North America respectively. The generic and specific criteria are not clearly established for dinosaurs, as is generally the case for other fossil vertebrates, and this is also true for the hadrosaurs. Either the two hadrosaurine species compared here are not congeneric, or on the contrary, pairs of the above quoted theropod species, as well as many other Upper Cretaceous dinosaurs, should be considered congeneric. We decided here, that *S. angustirostris* is a *Saurolophus*, because we do not think it reasonable, at the moment, to change the generally accepted views concerning a content of this genus, without revising other, non-hadrosaur genera, which is beyond the scope of the present paper.

SOME ANATOMICAL STRUCTURES OF HADROSAURS

STRENGTHENING OF THE SACROPELVIC REGION

As was already noticed by several authors (LULL and WRIGHT 1942, GALTON 1970), a typical character of all hadrosaurs is a general lightness of the pubic peduncle of the ilium. As may be seen on some articulated hadrosaur skeletons, the pubis is often not connected with the ilium, although the contact of the ischium with the ilium is close and not deformed (e. g. BROWN 1916: pl. 14, PARKS 1935: pl. 6.1). The pubic peduncle of the ilium is also weak in our specimens of *Saurolophus angustirostris*. However, it may be easily noticed (pl. 27: 1 b) that the acetabular bar is longer than the portion of ilium above the acetabulum provided for contact with the sacral ribs. It causes that at least the first and most often also the second sacral rib included in this bar is placed cranially to the pubic peduncle of the ilium (p. 125). This peculiar arrangement is to be noticed on the illustrations of many other articulated hadrosaur skeletons (e. g. BROWN 1913a: pl. 63 — *Saurolophus osborni*, BROWN 1916b: pl. 14 — *Corythosaurus casuarius*, PARKS 1935: pl. 6: 1, 2 — *C. intermedius* and *C.* cf. *intermedius*). In *Parasaurolophus walkeri* (PARKS 1922: pl. 1), the same sacral ribs, similarly directed, may be observed. In the latter species they also contact the pubic process of the ilium, but this process differs in that it is unusually elongated, overlapping the iliac process of the pubis. In *S. angustirostris* (ZPAL MgD-I/159) the iliac process of the pubis is very massive, broad transversely (pl. 21: 2; fig. 4a), in contrast to the light, transversely narrow pubic process of the ilium (pl. 21 : 1). There is a large, roughly triangular dorsomedial surface present on the iliac process of the pubis, which could not come in contact with the ilium. It is more probable that this surface might be joined during the life of animal with the second sacral rib (pl. 25 : 1 b; fig. 4a) while the first sacral rib might additionally strengthen the puboiliac contact and, as well, spread cranially the thrust on the second rib.

It is generally believed that the weakest contact of the hadrosaur sacropelvic region was that between the pubis and ilium and that the pelvis joined the vertebral column exclusively by the ilium. As we were able to state, the pelvis had the additional contact with the sacrum by the junction between the pubis and one of the cranialmost sacral ribs, at least in some hadrosaurs. The modification of the sacropelvic junction in ornithischians is nothing new, as it also occurs in the pachycephalosaurs (MARYAŃSKA and OSMÓLSKA 1974), in which the additional contact between the sacrum and ischium is present.

GALTON (1974*a*, 1974*b*) noticed that in some conservative ornithopods (e. g. in *Hypsilophodon* and *Thescelosaurus*) the first sacral rib braces the pubis. He concluded that in the result of such a reinforcement of the puboiliac region these ornithopods „could have stood in a more upright posture than was probably the case for hadrosaurs" (GALTON 1974*b*: 1058). As we have shown, this reinforcement was also present in the hadrosaurs, thus GALTON'S supposition that hadrosaurs were not able to achieve the upright posture, may not be valid (see also NORMAN 1980: 68). MORRIS (1981) considered that weak connections between the pelvic elements of some hadrosaurs speak (among others) in favor of their aquatic habits. As stated above, the seemingly weak connections between the pelvic bones do not necessarily mean that the sacropelvic region was weakened. To the contrary, these hadrosaurs which had additional connection between the pubis and sacrum (as e. g. *S. angustirostris*) had, in our opinion, the more strongly bound sacropelvic region. Thus, for stating whether the pelvic girdle was „weak" or „strong" it is necessary to know how the pelvis was connected with the vertebral column. We believe that the hadrosaurs possessing the above mentioned reinforcement were essentially terrestrial, habitually bipedal forms. In our opinion the elongation of the suspension line of the pelvis on the sacrum, which took place in these hadrosaurs, might have adaptative significance only during terrestrial locomotion. The strong dorsal bracing of the ilium by sacral transverse processes, found only so far in *S. angustirostris*, additionally fixed the pelvis to the vertebral column and prevented a vertical dislocation of the former. Such an adaptation seems to be only explicable in the terrestrial animals and thus we do not share ROZHDESTVENSKY's opinion (1957 : 144) that *S. angustirostris* was essentially an aquatic form.

NATURAL CURVATURE OF VERTEBRAL COLUMN AND ITS IMPLICATIONS

The majority of the complete, articulated hadrosaur skeletons found in North America and Asia demonstrate a uniform, characteristic arrangement of the vertebral column: vertically positioned neck with the U-shaped bend (the bottom of „U" at about the shoulder joint), a series of first eight or nine dorsals gradually rising backward, at about 30° to the horizontal. It is worth of reminding here that between the centra of dorsals 9 and 10 there occurs, in *S. angustirostris*, an additional structure (comp. p. 125), which might have prevented any lateral dislocation of the thoracic vertebral column on the boundary between its downward inclined cranial portion and that horizontal, more caudal one. The latter portion of dorsal series, sacrum and the proximal caudals form an almost horizontal line in the articulated hadrosaur skeletons. Our specimen of *S. angustirostris* ZPAL MgD-I/159, as found in the field, presented the same arrangement of the vertebral column as that mentioned above; the contacts between the successive dorsal centra proved that this was a natural curvature of the vertebral column, as should be also the case of many other hadrosaurs. As is well known, the strongly opisthocoelic cervicals of hadrosaurs allowed great mobility of their necks. The mobility between the dorsals was much more limited, and in fact, the „hump" within the dorsal series, caused by the inclination of the cranial series of dorsals, probably could be never entirely „straightened". This opinion, although to our knowledge expressed verbally only lately by BAKKER (1978), was shared by several authors (e. g. LULL and WRIGHT 1942: figs 27, 28, 31, 41; RUSSELL 1977: 83, 95, 99) judging from the reconstructions given, which show the presence of the „hump". It should be added here, that inclination of the cranial portion of the dorsal series of the vertebral column had also caused another modification in the skeleton, namely within the rib cage. The first several ribs in hadrosaurs are directed caudoventrally which results in the ventral convergence of the dorsal ribs.

We believe that the curvature of the vertebral column has its explanation in the static of the skeleton during bipedal progression. According to GALTON (1970), hadrosaurs were bipedal runners which during locomotion held the vertebral column horizontally. GALTON's (1970: fig. 5) reconstruction of *Anatosaurus annectens* does show a much smaller forward sloping of the thoracic portion of the vertebral column than it can be seen in the naturally arranged other hadrosaur skeletons.

The sloping of the thoracic vertebral column certainly resulted in the effective shortening of the hadrosaur trunk region and caused the shift of the center of gravity backward, closer to the hip joint. On this way, with the vertically held neck and the short deep trunk, the preacetabular weight of the animal could be much more easily counterbalanced by the horizontally held tail during bipedal locomotion (fig. 5c). It should also be added that while the hadrosaurs run or walked bipedally, they might regulate the shift of the center of gravity by thrusting the head back and forth, as do some walking birds (DAGG 1977: 93). The downward bend of the cranial portion of the thoracic vertebral column had still another effect: it caused a lowering of the shoulder joint and shifted backward the sternum. This might enable the fore limbs an easy reach to the ground (BAKKER 1978), which might have a certain significance for some locomotoric and feeding habits, among others (fig. 5b).

Taking into account the size of adult hadrosaurs their habitual (although not obligatory) bipedality (p. 134) and their capacity to raise the vertebral column to the upright position (p. 133), they might use a considerably high reach to obtain food (fig. 5a). Contrary to BAKKER (1978: 663), it seems that they might be high-browsers although low-browsing played possibly also a role in their feeding habits. Since hadrosaurs were very large herbivores with an efficient grinding apparatus (OSTROM 1964), it seems worth-while to reconsider some possible consequences of these facts. The dental batteries of hadrosaurs were well adapted to prepare a resistant plant matter for extracting much more nutritive substance than it was possible for any other dinosaur plant-eater, except the ceratopsians. This adaptation certainly made it possible for hadrosaurs to attain large body size. Whatever efficiency their grinding apparatus had, fragmenting of the rather resistant plant tissue (KRÄUSEL 1922; OSTROM 1964) had to be a time-consuming process, especially when one contrasts the relative narrowness of the buccal passage and the significant amount of food to be processed. Hadrosaurs were defenceless animals, moderately fast running, most probably slower than the contemporaneous large carnivores. Thus, it seems unlikely that they could safely grind the large quantities of the browsed vegetation on site. More probably, they collected and stored the food without much processing, and later, while in the shelter, they retracted the food to the mouth, by means of the antiperi-

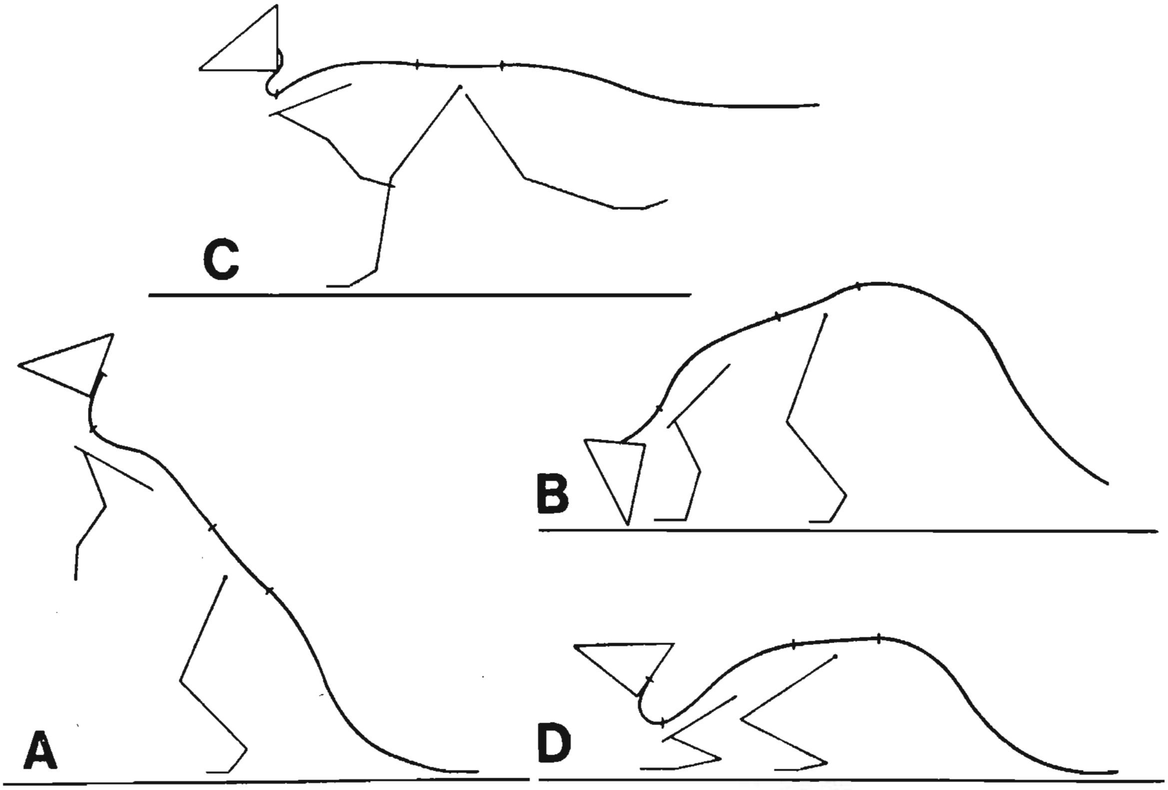

Fig. 5
Diagrammatic reconstruction of *Saurolophus angustirostris* ROZHDESTVENSKY in: *A* high-browsing stance; *B* low-browsing stance; *C* running stance; *D* resting pose. Based on ZPAL MgD-I/159 and PIN 551—8.

staltic movements of the esophagus, in order to grind it thorougly. This would require the assumption that hadrosaurs had either a highly specialized stomach similar to that in the ruminants, which seems to be less probable, or a large crop, as has e. g. a leaf-eating bird *Opisthocomus*, serving as a food storage. However, the very large crop, such as might be necessary to fulfill the requirements of food storage of an animal of the hadrosaur size, would cause the loss of balance of any biped, if it were placed far forward from the point of support of the body at the acetabulum. In our opinion, there is some osteological evidence that the crop in hadrosaurs might have been present and shifted far backward to meet the demands of stability. One evidence is the downward curvature of the cranial portion of the thoracic vertebral column discussed above (p. 134). Another character, common to all hadrosaurs, which results partly from the downward curvature just mentioned, is the backward shift of the sternum (comp. p. 135) and a backward direction of first dorsal ribs (which confirms a more caudal location of the sternum). A similar curvature of the cranial portion of the dorsal vertebral column and the backward shifting of the sternum is observed in hoatzin (*Opisthocomus*; see above). The crop in the leaf-eating hoatzin is, however, not only for storage, as postulated here for the hadrosaurs, but for the obvious reason (lack of dentition) it takes also part in the mechanical fragmentation of the food.

The crenulated bill of hadrosaurs was considered by MORRIS (1970) as best adapted to filtering and it was thought by this author to be too thin and „too weak to be of use in browsing on fibrous or woody plants" (MORRIS 1970: 12). However, taking into account the fact that many of Recent herbivorous mammals crop fibrous grass using their soft lips or tongue, it may be accepted that hadrosaurs for browsing did not necessarily need a thick, strong beak. As to the undulation of the inner surface of the bill, it might be as well a good adaptation for cropping the leaves of terrestrial plants. The presence of a strong hyoid apparatus in hadrosaurs speaks for the presence of a strong, efficient tongue, which could transport the food cropped by the bill to the rear of mouth.

As was mentioned above, hadrosaurs had to retreat to places where they would not be threatened by carnivores, in order to grind their food. The swamps, marshes or quaggy river banks might constitute such safe shelters for hadrosaurs, which (thanks to their „weblike", or more properly „snow-shoe-like" manus) could in this environment more easily move around on all fours than could the heavy, obligatorily bipedal carnosaurs.

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EXPLANATIONS OF THE PLATES 18—25

PLATE 18

Saurolophus angustirostris Rozhdestvensky, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia; ZPAL MgD-I/159

1. Right half of neural arch of atlas, lateral view, × 1/2.
2a. Second (axis) to fourth cervical vertebrae, left lateral view.
2b. Same vertebrae, dorsal view.
2c. Same vertebrae, ventral view.
3a. Fifth to eighth cervical vertebrae, left lateral view.
3b. Same vertebrae, dorsal view.
3c. Same vertebrae, ventral view.
4a. Tenth to twelfth dorsal vertebrae, the tenth with a fragmentary rib, right lateral view.
4b. Same vertebrae, dorsal view.
4c. Same vertebrae, ventral view.
5a. Thirteenth to sixteenth dorsal vertebrae, partly with fragmentary ribs, right lateral view.
5b. Same vertebrae, dorsal view.
5c. Same vertebrae, ventral view.

2—5 stereophotographs, × 1/4

Photo: W. Skarżyński

PLATE 19

Saurolophus angustirostris Rozhdestvensky, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. Block containing right scapula in lateral view, fragmentary ribs, third to ninth dorsal vertebrae in left dorsolateral view.
2a. Seventeenth to twentieth dorsal vertebrae, left lateral view.

2b. Same vertebrae, dorsal view.
2c. Same vertebrae, ventral view.
3a. First to third caudal vertebrae, right lateral view.
3b. Same vertebrae, dorsal view.
3c. Same vertebrae, ventral view.
4. Skin imprint from the dorsocaudal region, × 1.

Figs. 1-4: ZPAL MgD-I/159

5. Skin imprint; ZPAL MgD-I/157, × 1.

2 and 3 stereophotographs. All, except 4 and 5, × 1/4

Photo: *W. Skarżyński*

PLATE 20

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, Gobi Desert; Mongolia

1a. Right coracoid, external view.
1b. Same coracoid, internal view.
2. Left scapulocoracoid, lacking distal half of scapula, dorsal view.
3. Right scapulocoracoid, internal view.
4a. Fragmentary left sternal bone, external view.
4b. Same bone, internal view.
5a. Fragmentary right sternal bone, external view.
5b. Same bone, internal view.
6a. Proximal part of right humerus, lateral view.
6b. Same humerus, medial view.
7. Proximal part of left humerus, anterior view.

Figs. 1-7: ZPAL MgD-I/159; Altan Ula IV

8. Right half of fragmentary, articulated skeleton as found in the field, internal view; approx. × 1/20. IG SPS, N Nemegt.

All, except 8 stereophotographs, × 1/4

Photo: *W. Skarżyński*

PLATE 21

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia; ZPAL MgD-I/159

1. Right ilium attached to sacrum, lateral view.
2a. Right prepubis, lateral view.
2b. Same prepubis, medial view.
3a. Right ischium lacking shaft, lateral view.
3b. Same ischium, medial view.

All stereophotographs, × 1/4

Photo: *W. Skarżyński*

PLATE 22

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia; ZPAL MgD-I/159

1a. Sacrum with right and fragmentary left ilium attached, dorsal view.
1b. Same sacrum, ventral view.

Both stereophotographs, × 1/4

Photo: *W. Skarżyński*

PLATE 23

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, N Nemegt, Gobi Desert, Mongolia; ZPAL MgD-I/157

1. Anterior portion of tail as found in field, left lateral view, approx, × 1/20.
2. Fifth (?) to seventh (?) caudal vertebrae of the same tail, right lateral view, × 1/8.
3. Tenth (?) to fourteenth (?) caudal vertebrae of the same tail, right lateral view, × 1/8.
4. Fifteenth (?) to twenty-first (?) caudal vertebrae of the same tail, right lateral view, × 1/8.
5. Twenty-second (?) to twenty-ninth (?) caudal vertebrae of the same tail, right lateral view, × 1.
6. Thirtieth (?) to thirty-seventh (?) caudal vertebrae of the same tail, right lateral view, × 1/8.
7. Thirty-eighth (?) to forty-seventh (?) caudal vertebrae of the same tail, right lateral view, × 1/8.

8a. Chevron of the eleventh (?) caudal, same tail, posterior view, × 1/4.
8b. Same chevron, anterior view, × 1/4.
8c. Same chevron, left lateral view; stereophotograph, × 1/4.
8d. Same chevron, right lateral view; stereophotograph, × 1/4.
9a. Chevron of twelfth (?) caudal, same tail, posterior view.
9b. Same chevron, anterior view, × 1/4.
9c. Same chevron, left lateral view; stereophotograph, × 1/4.
9d. Same chevron, right lateral view, stereophotograph, × 1/4.
10a. Distal part of left tibia and fibula with proximal tarsals attached, anterior view; stereophotograph, × 1/8.
10b. Same specimen, posterior view; stereophotograph, × 1/8.
10c. Same specimen, lateral view; stereophotograph, × 1/8..
11a. Right pes, dorsal view, × 1/8.
11b. Same pes, ventral view, × 1/8.

Photo: *W. Skarżyński* 1—10
L. Dwornik 11

PLATE 24

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula II, Gobi Desert, Mongolia; ZPAL MgD-I/158

1a. Left scapula lacking distal end, medial view.
1b. Same scapula, lateral view.
1c. Same scapula, dorsal view.

2a. Left humerus, anterolateral view.
2b. Same humerus, posteromedial view.
2c. Same humerus, posterior view.
3a. Damaged left ulna, medial view.
3b. Same ulna, posterior view.
4a. Left radius, medial view.
4b. Same radius, posterior view.
5a. Bones of left manus. From the left, upper row: metacarpal V, phalanx III-1, metacarpal II; lower row: phalanx IV-2, phalanx II-2, ungual II; all dorsal views.
5b. Same bones and arrangement, ventral views.

2—5 stereophotographs, all × 1/8

Photo: W. Skarżyński

PLATE 25

Saurolophus angustirostris ROZHDESTVENSKY, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula II, Gobi Desert, Mongolia; ZPAL MgD-I/168

1a. Block containing damaged pelvis, sacrum and posterior dorsals in articulation, right lateral view.
1b. Same specimen, lateroventral view showing relation of sacral ribs to ilium and pubis; iliac peduncle of pubis slightly dislocated towards medial axis of skeleton.

Both stereophotographs, × 1/8

Photo: W. Skarżyński

2a

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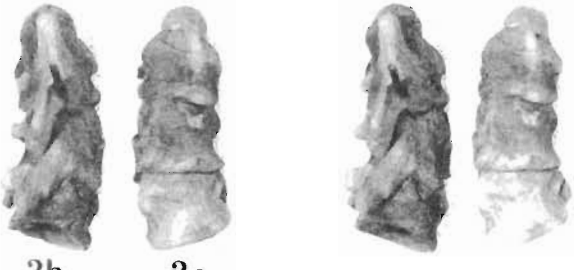

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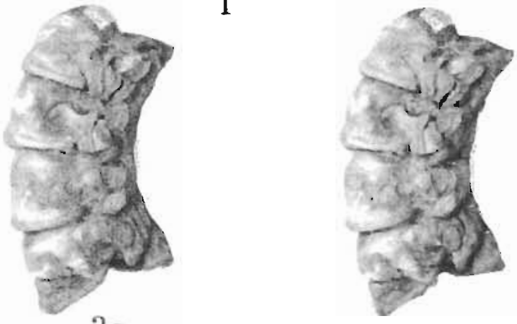

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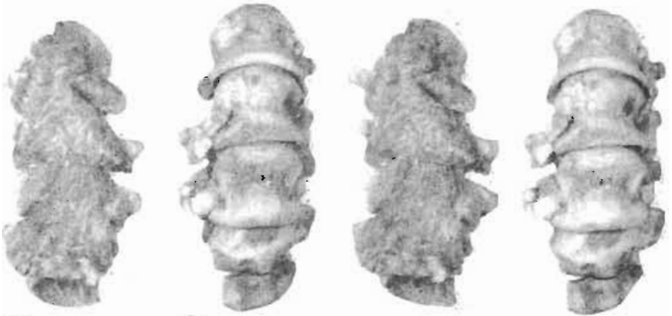

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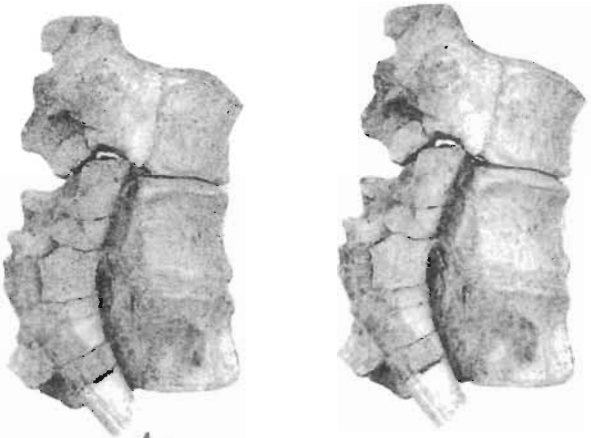

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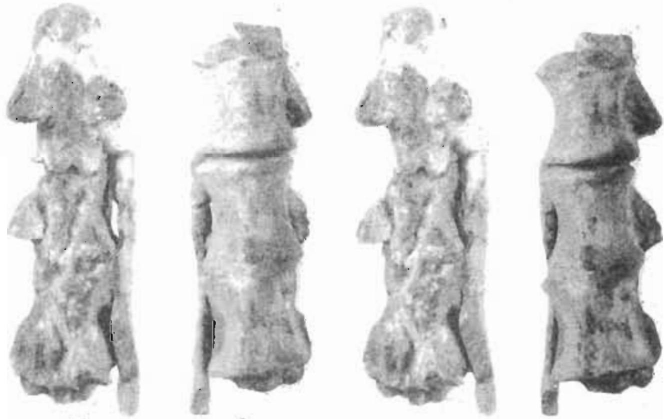

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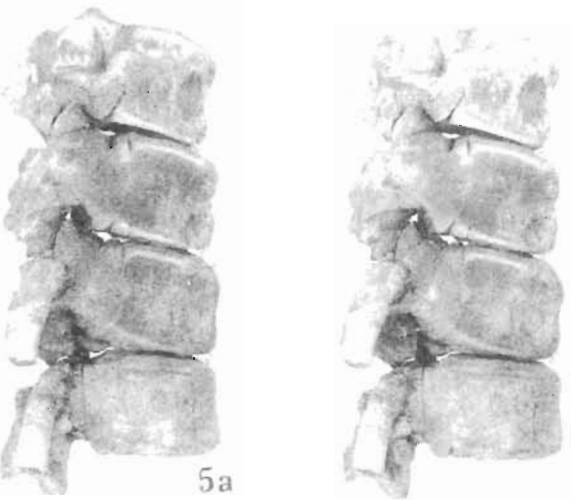

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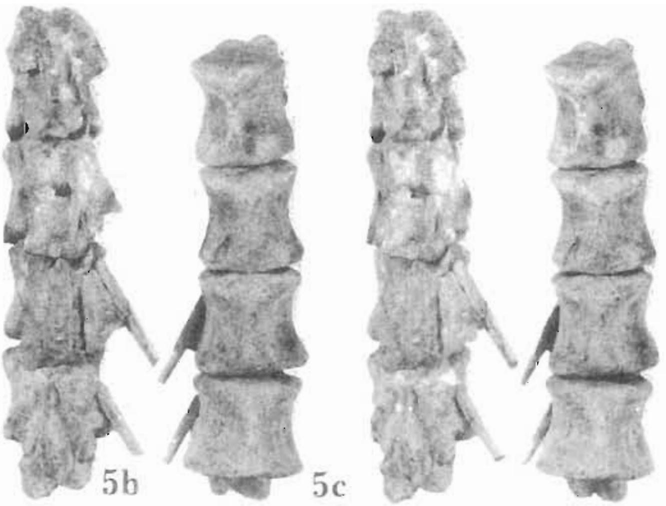

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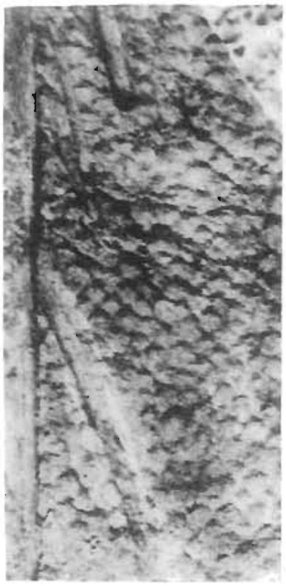
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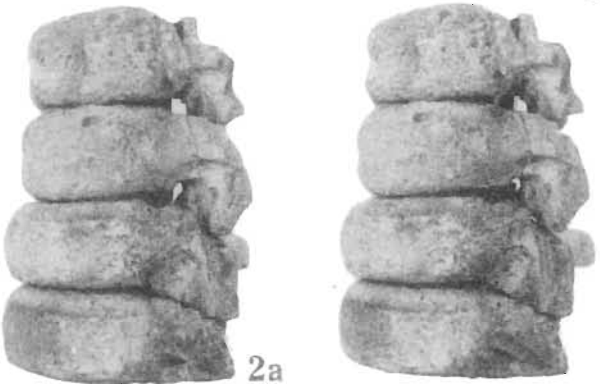
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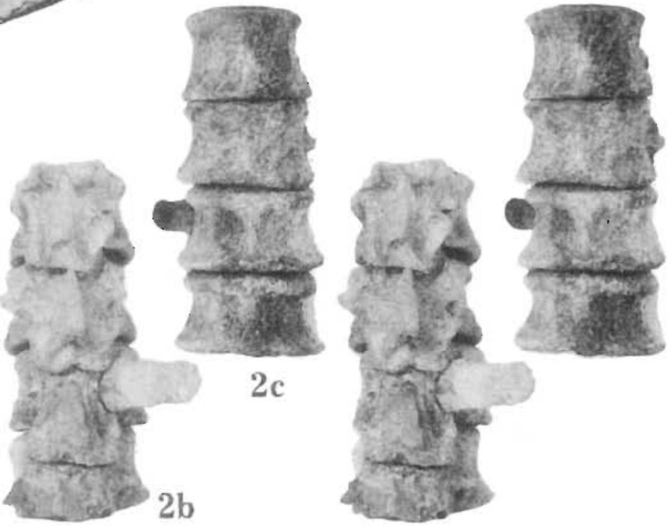
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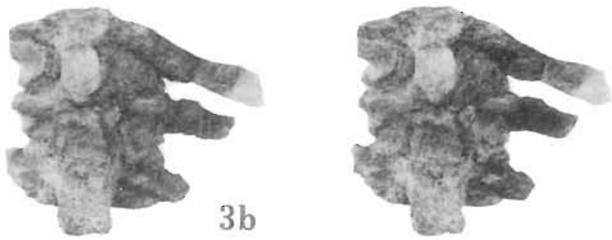
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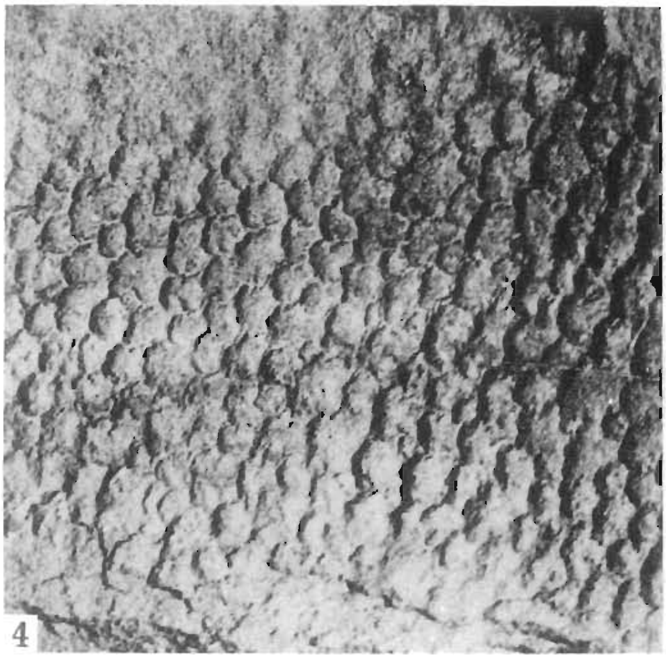
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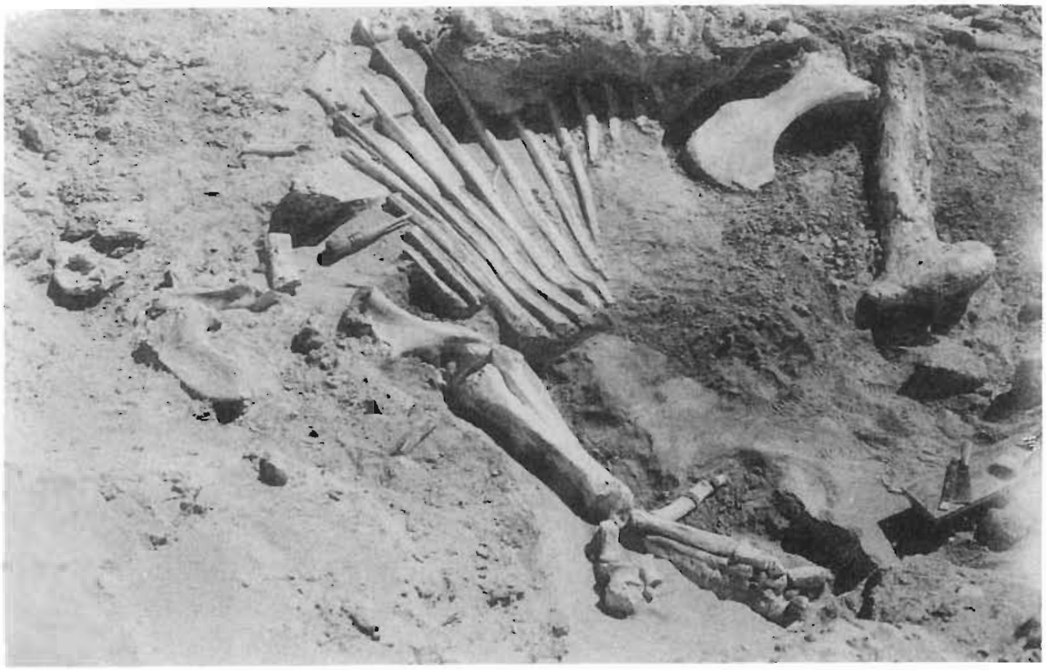

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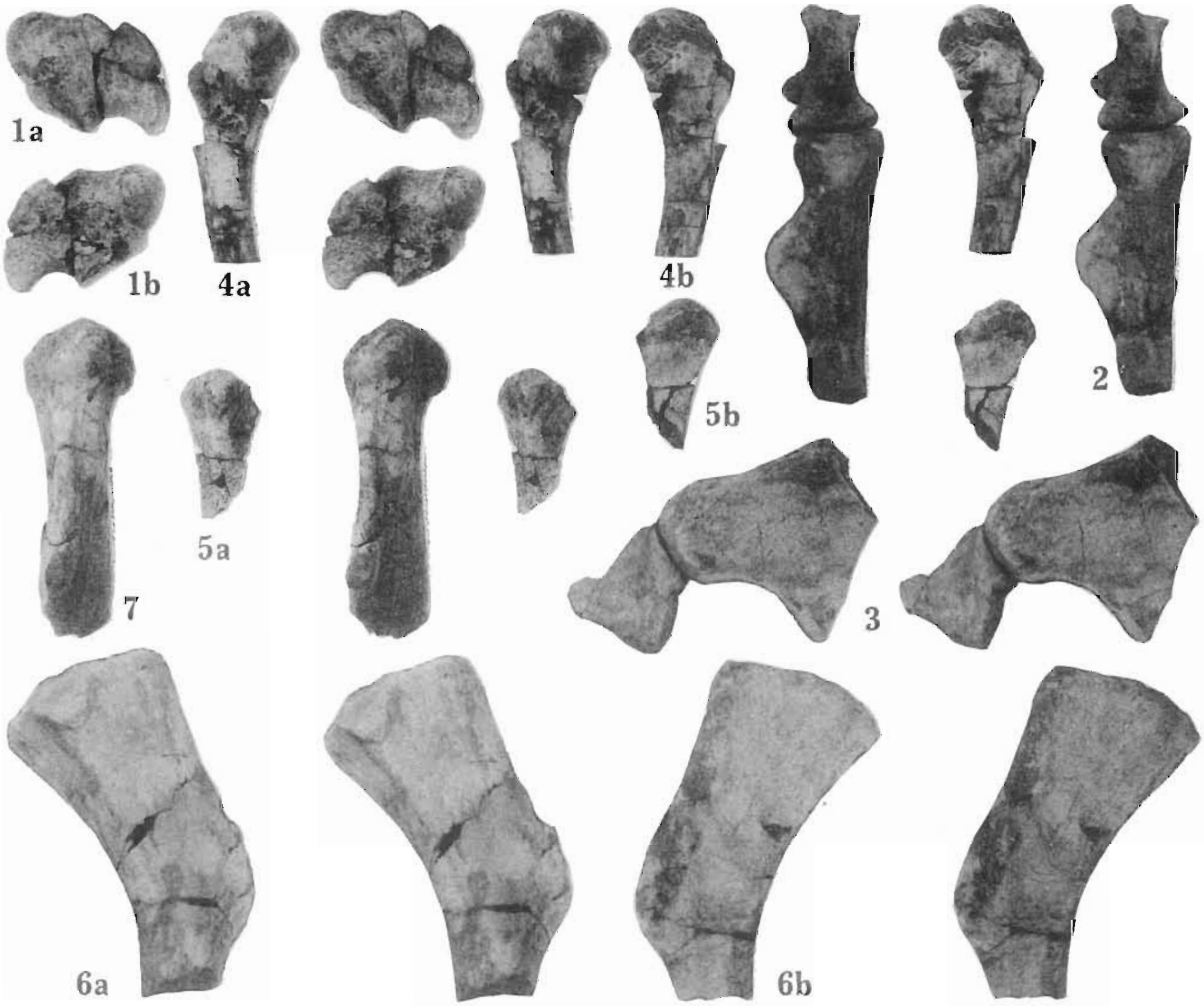

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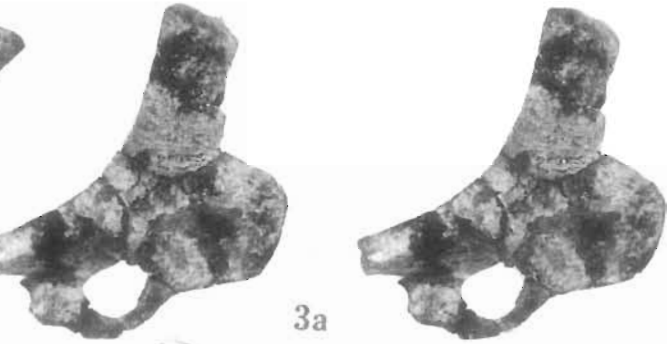

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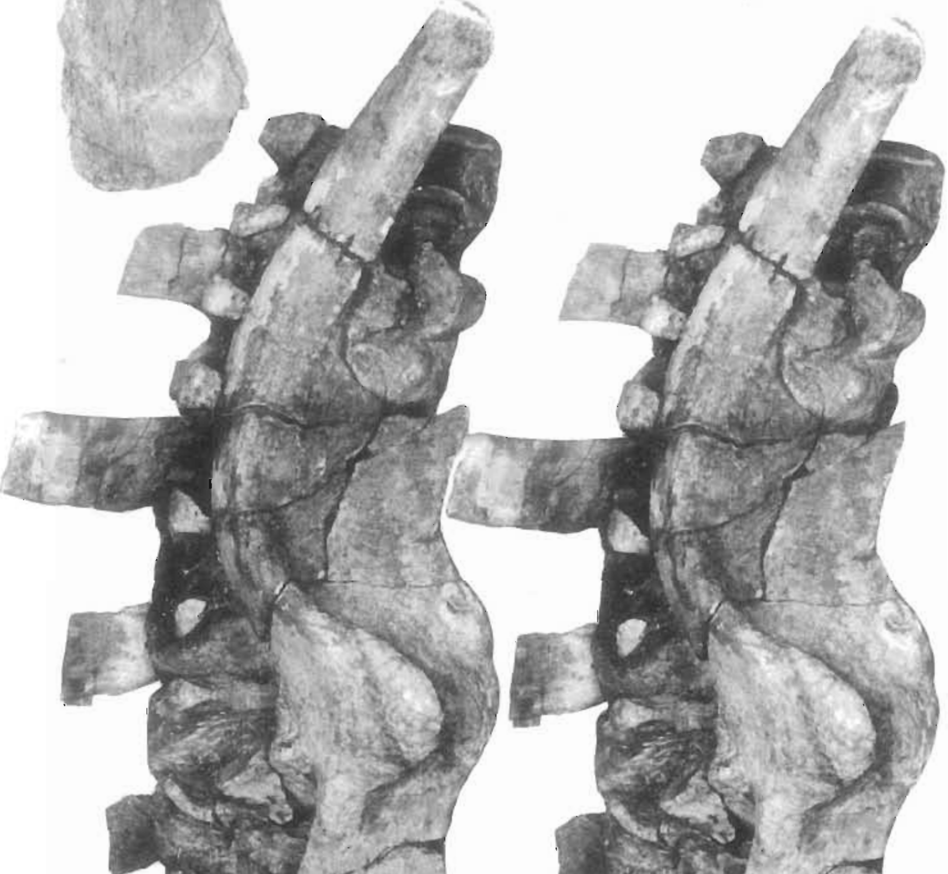

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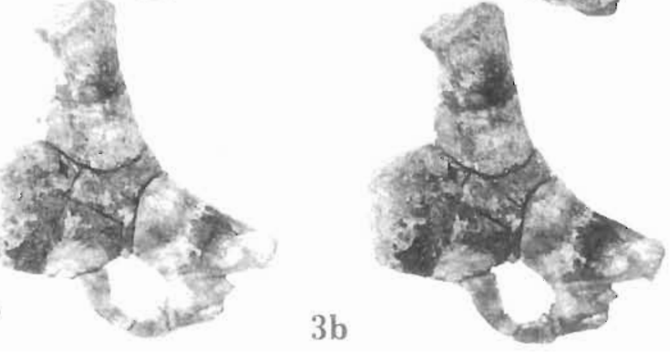
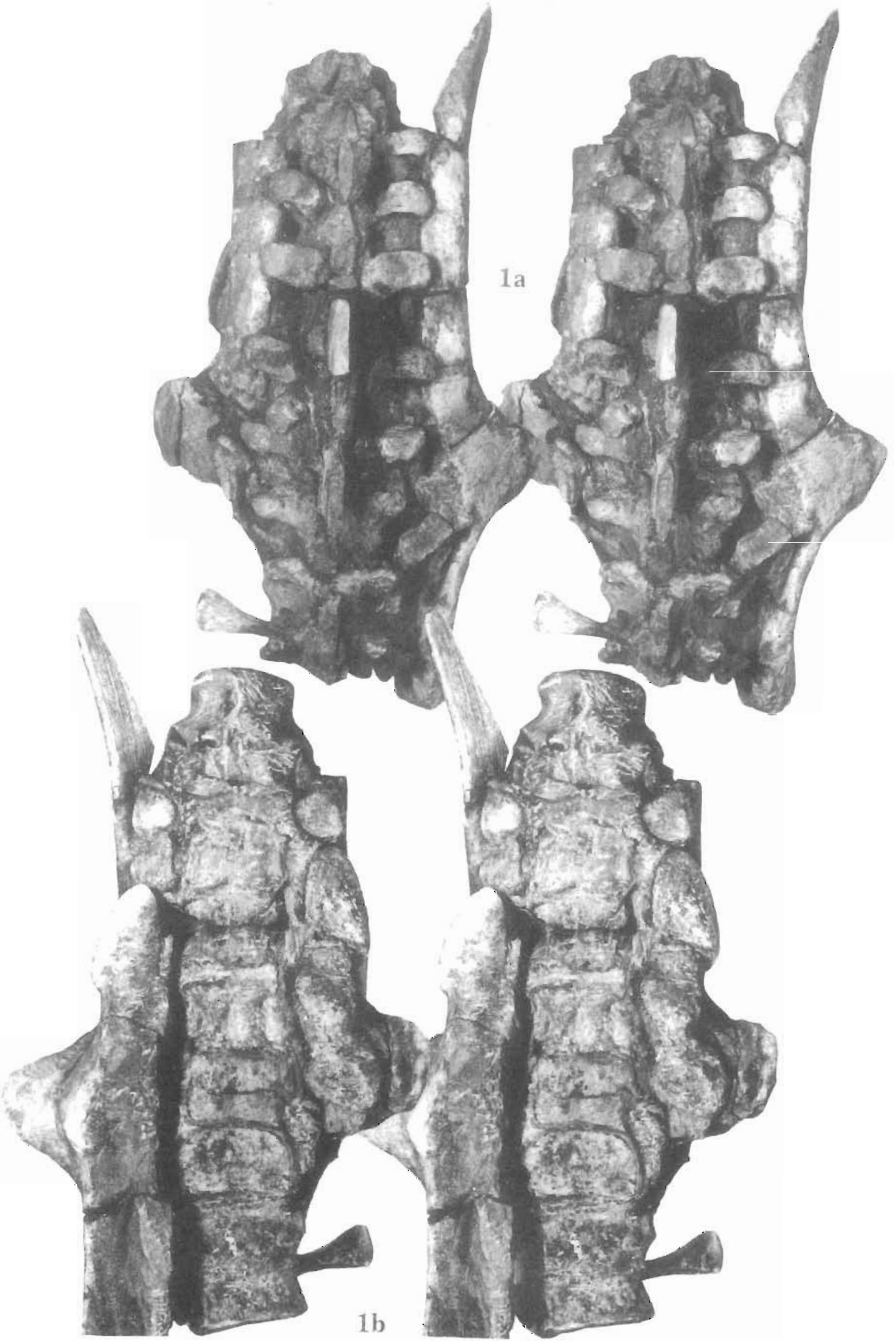


3b

T. Maryańska & H. Osmólska: Anatomy of *Saurolophus*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8c 8d 9c 9d

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9a

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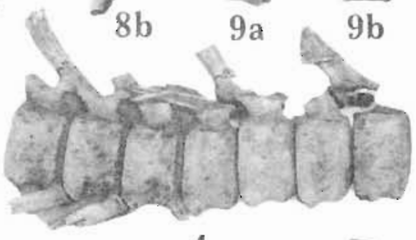

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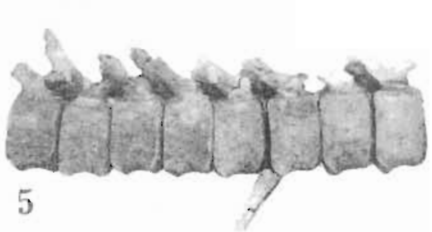

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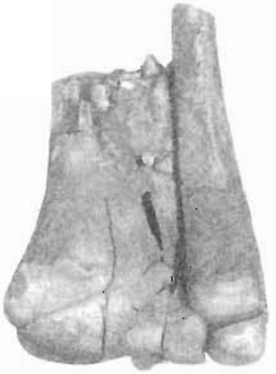

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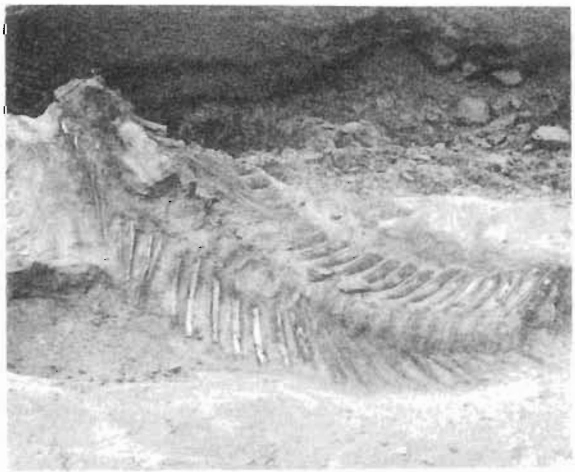
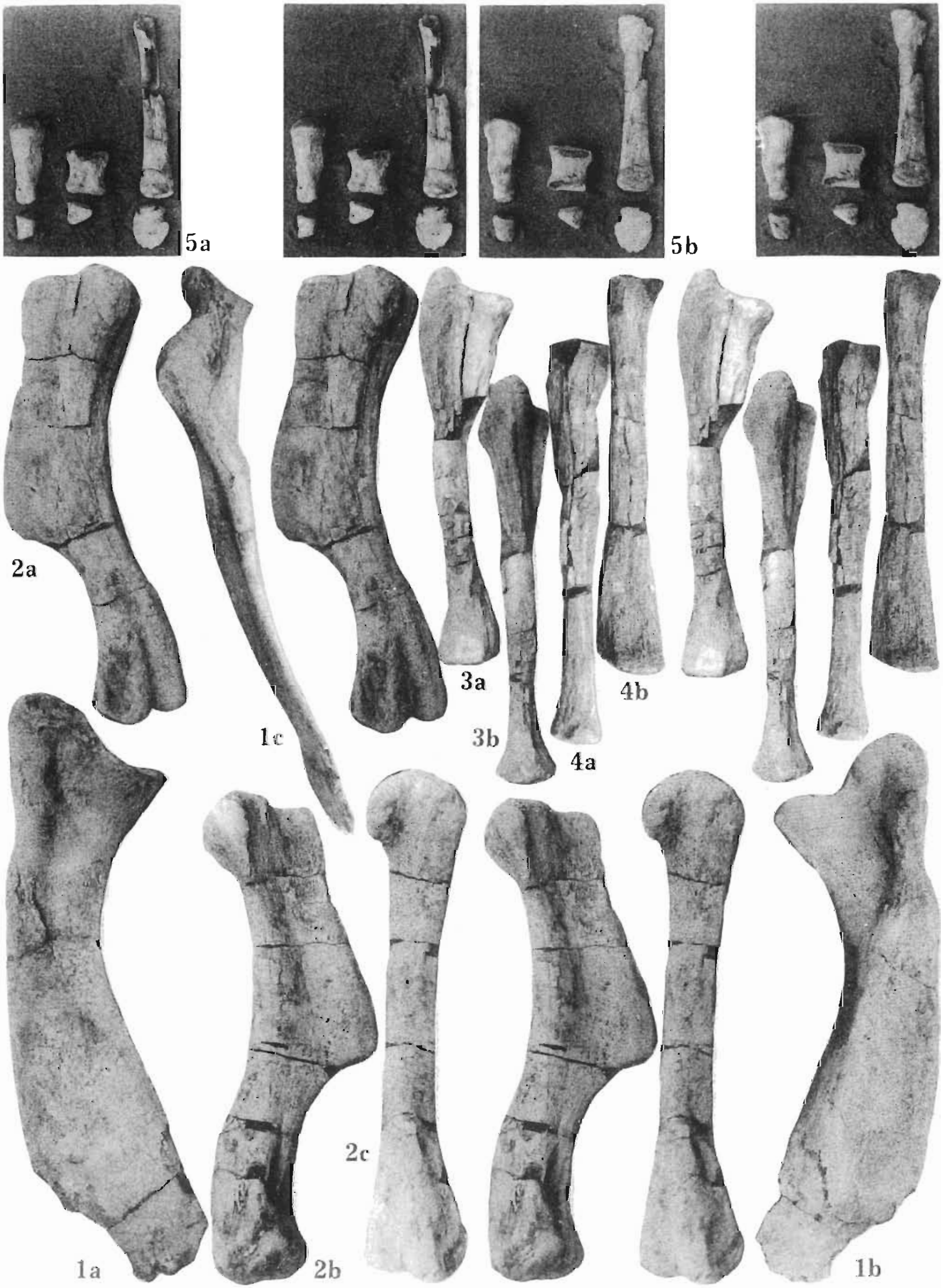
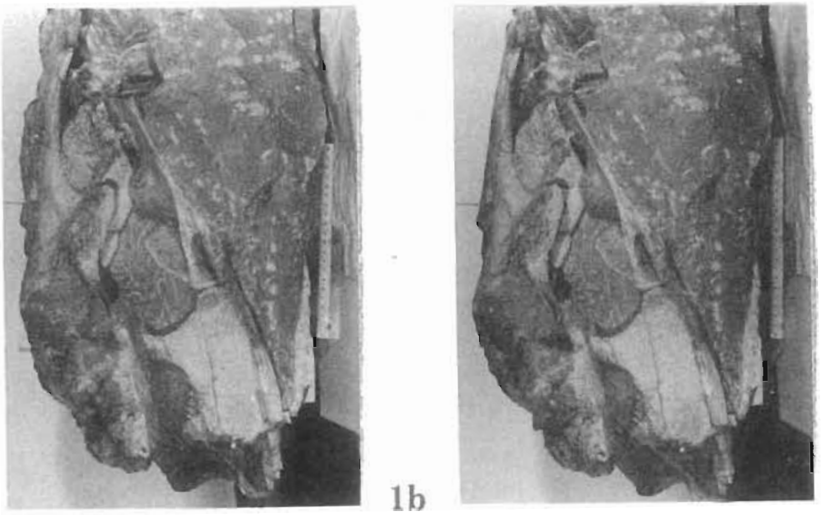
11b

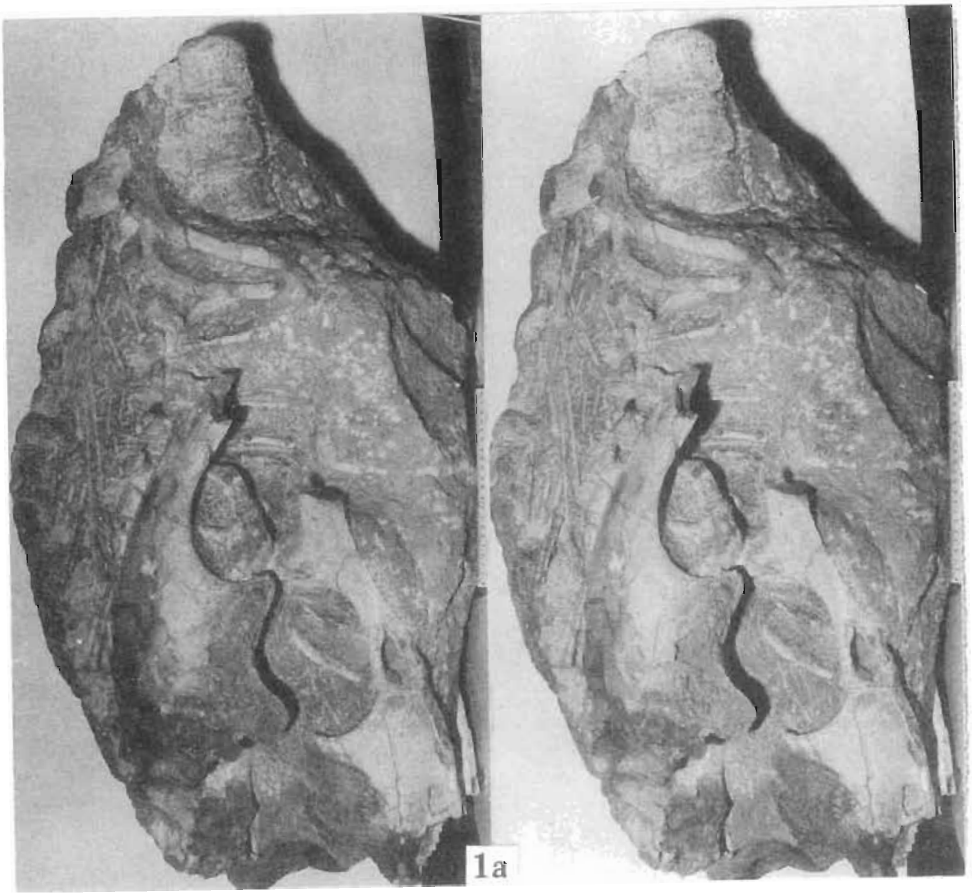


1

11a


5a
5b
2a
1c
3a
3b
4a
4b
1a
2b
2c
1b


1b


1a