An unusual theropod dinosaur from the Late Cretaceous Nemegt Formation of Mongolia

HALSZKA OSMÓLSKA

An incomplete skeleton of a theropod dinosaur, *Bagaraatan ostromi* gen. et sp. n., was found in the Nemegt Fm. at Nemegt, Mongolia. The mandible in *B. ostromi* has a shallow but massive dentary, relatively deep postdentary portion with two surangular foramina and somewhat elongated retroarticular process; on the lateral surface of the postacetabular process of the ilium there are two large depressions for muscle origins separated by a crestlike projection; the fibula is fused distally with the tibiotarsus and the coalesced astragalocalcaneum. *Bagaraatan* represents the Tetanurae and displays some synapomorphies with the Avetheropoda, however, incompleteness of the skeleton of *B. ostromi* does not allow to determine its more precise affiliation. *Bagaraatan* was about 3.0–3.5 m long, had a relatively small head and slender hind limbs. The presence of strongly developed hyposphenes in a long series of anterior caudals rendered its tail only slightly flexible proximally.

Key words: Dinosauria, Theropoda, Tetanurae, anatomy, habits, relationships.

Halszka Osmólska, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

During the Polish Mongolian Expedition in 1970, a fragmentary skeleton of a medium sized theropod dinosaur was found in a sand layer of the Nemegt Formation (?mid-Maastrichtian: Jerzykiewicz & Russell 1991) at the Nemegt locality. The specimen includes the incomplete left mandible, 25 caudals of the proximal and medial part of the tail, a fragmentary pelvis and the left hind limb lacking most of the pes. The aim of the present paper is to describe these remains, because in spite of its incomplete nature, the skeleton provides many distinctive features, which justify the erection of a new genus and species, *Bagaraatan ostromi*.
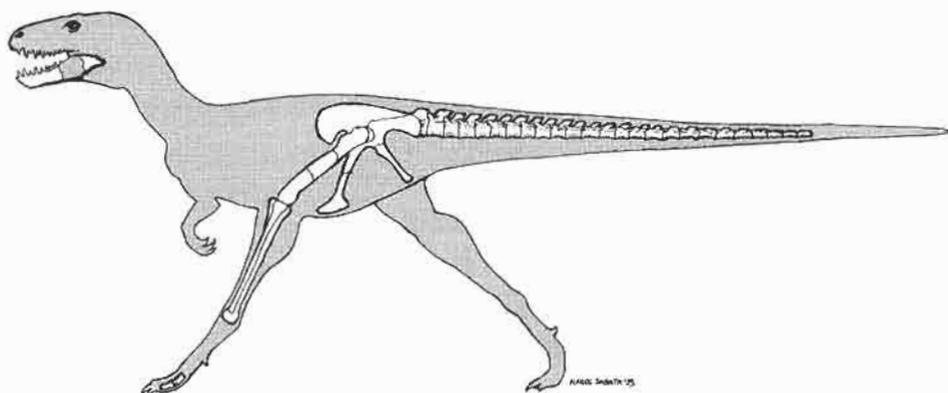
Fig. 1. Reconstruction of *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation of Nemegt. Mongolia.

By dinosaur standards, *B. ostromi* was a moderate sized theropod. It had a strong, toothed mandible somewhat resembling that of some 'carnosaurs', a relatively rigid tail, strong hips and slender hind limbs (Fig. 1).

B. ostromi is the twelfth theropod species detected thus far in the Nemegt Formation, the other species determined thus far being: *Therizinosaurus cheloniformis* Maleev 1954, *Tarbosaurus bataar* (Maleev 1955), *Maleevosaurus novojilovi* (Maleev 1955), *Deinocheirus mirificus* Osmólska & Roniewicz 1970, *Gallimimus bullatus* Osmólska *et al.* 1972, *Avimimus portentosus* Kurzanov 1981 (referred to as 'theropod gen. et sp. indet.' in Osmólska 1981), *Elmisaurus rarus* Osmólska 1981, *Oviraptor mongoliensis* Barsbold 1986, *Borogovia gracilicrus* Osmólska 1987, *Tochisaurus nemegtensis* Kurzanov & Osmólska 1991, and another theropod species from the Nemegt Formation, which is presently under study (Osmólska in preparation). This supports the present author's earlier conclusions (Osmólska 1980) about the strong diversity of theropods and the approximately equal proportions of herbivores to carnivores biological productivity during the Nemegt Formation sedimentation times. The latter would invalidate the predator/prey ratio as a means to evaluate the metabolic rates of dinosaurs.

Material

Only the holotype (ZPAL MgD-I/108) is known. The specimen was found by Zofia Kielan-Jaworowska in the sand layer of the lower portion of the Nemegt Formation, in the eastern part of the Northern Sayr at Nemegt (Gradziński & Jerzykiewicz 1972: fig. 1; specimen referred to as 'coeluroid dinosaur'). The specimen is represented by an incomplete skeleton, including: left mandible lacking its mid-section and tooth crowns; 1 sacral spine, 25 caudal vertebrae, 21 of which constitute a series; several

chevrons and fragments of chevrons, a few in articulation with caudals; damaged postacetabular processes of left and right ilium; proximal half of left pubis articulated with acetabular part of ischium; proximal and distal part of left femur, complete left tibia, fibula, astragalocalcaneum (ascending process fragmentary), left pedal phalanges II-2 and IV-1; measurements are given on Tab. 1.

The specimen, as found in the field, had all bones anterior to the pelvis strongly weathered and represented only by scraps. The mandible, however, judging by its position and the arrangement of the weathered postcranial skeletal fragments, certainly belonged to the same individual as the hind quarters and tail.

Taxonomic nomenclature

Theropoda Marsh 1881
Tetanurae Gauthier 1986
Genus *Bagaraatan* gen. n.
Type species: *Bagaraatan ostromi* sp. n.
Derivation of the name: Mongolian *baga* — small, *araatan* — predator.

Diagnosis. — Genus monotypic; diagnosis, stratigraphic and geographic range as for the type species.

Bagaraatan ostromi sp. n.
Figs 1–13.
Holotype: ZPAL MgD-I/108, including mandible and fragmentary postcranium.
Type horizon: Nemegt Formation, ?mid-Maastrichtian.
Type locality: Northern Sayr, Nemegt, Omnogov, Mongolia.
Derivation of the name: *ostromi* — in honor of Dr. John H. Ostrom.

Diagnosis. — Mandible with two surangular foramina, articular with oblique posterior surface and short retroarticular process; caudals with hollow, very thin-walled centra; hyposphene — hypantrum articulation stout, present in at least sixteen proximal caudals; prezygapophyses in proximal caudals with ridges on lateral surfaces; ilium with two deep depressions and a crestlike projection present on lateral surface of postacetabular process; femur with anterior crest below lesser trochanter; tibia and fibula fused distally with each other and with coalesced astragalocalcaneum.

Mandible

The mandible of *B. ostromi* is preserved in two parts and lacks its mid-section, including the posterior extremities of the dentary and splenial and the anterior portion of the adductor region (Figs 2–3). Based on the proportions of the dromaeosaurid mandible, which resembles the man-

Tab. 1. *Bagaraatan ostromi* gen. et sp. n.; measurements of ZPAL MgD-I/108 (in mm).

Left mandible		Pelvis	
preserved length of posterior part	63	right & left ilium:	
depth 20 mm in front of suran-		length of postacetabular process	155
gular foramen	41	depth of postacetabular process	70*
depth caudal to glenoid	23	length of acetabulum	50*
maximum labiolingual width		width of brevis fossa	40*
caudal to glenoid	23	right ischium:	
preserved length of dentary		length of pubic process	35
(teeth 1st–10th)	105	anteroposterior length of iliac process	25
depth of dentary	28	mediolateral width of iliac process	31
labiolingual width of dentary		external depth of iliac process	31
at symphysis	16	right pubis:	
labiolingual depth of dentary		anteroposterior length of shaft 45 mm	
at 10th tooth	11	below contact with ilium	45
		anteroposterior length of shaft 110 mm	
		below contact with ilium	17
Vertebrae		**Left hind limb**	
depth of sacral spine	48	femur:	
basal length of sacral spine	34	preserved length of proximal part	125
dorsal length of sacral spine	60	anteroposterior width across trochanters	58
1st preserved caudal:		mediolateral width across femoral head	58
overall depth	80	preserved length of distal part	105
length of centrum	44	mediolateral shaft diameter above	
depth of spine	25	ectepicondyle	27*
anterior width of centrum	35*	anteroposterior shaft diameter above	
anterior depth of centrum	45*	ectepicondyle	30*
8th preserved caudal:		mediolateral width across condyles	63
overall depth	65	anteroposterior width across tibiofibular	
length of centrum	45	crest	55
depth of spine	17	tibia:	
anterior width of centrum	27	length	365
anterior depth of centrum	30	length with astragalus	380
15th preserved caudal:		circumference at mid-length	93
overall depth	44	anteroposterior width of proximal end	68*
length of centrum	49	lateromedial width of proximal end	47*
depth of spine	9	mediolateral width of astragalocalcaneum	63
anterior width of centrum	26	anteroposterior length of calcaneum	35
anterior depth of centrum	23	height of ascending process	36*
20th preserved caudal:		fibula:	
overall depth	37*	length	350*
length of centrum	50	anteroposterior width of proximal end	47
anterior width of centrum	23	diameter at mid-length	7
anterior depth of centrum	23	phalanx II-2:	
		length	37
		proximal width	18
* — estimated		distal width	15
		phalanx IV-1:	
		length	34
		proximal width	23
		distal width	19

dible in *B. ostromi*, the approximate length of the lower jaw may be estimated as about 230–240 mm. The ventral margin in both preserved fragments of the jaw is thick and rounded. In the posterior fragment, the ventral margin is mostly formed of the prearticular, the angular and surangular reaching the ventral border only laterally. Behind the posterior margin of the angular, the ventral border of mandible is concave. Interdental plates are well developed, and the presence of the supradentary and 'antarticular' is probable.

Comparisons with mandibles of some other theropods, allow the inference that *B. ostromi* had a moderately shallow, parallel-sided dentigerous part and at least moderately deep adductor portion.

Dentary. – The preserved dentary fragment is shallow, parallel-sided, and slightly curved upwards anterior to the 6th tooth. All tooth crowns are broken off. Approximately 5–6 mm of the anterior tip of the dentary is lacking; the region of contact with postdentary bones is also not preserved. The fragment contains ten alveoli with preserved roots of teeth. Except for the first two alveoli which are round, the remaining ones are elongated mesiodistally and slightly narrowed in their mid-lengths, B-shaped, due to a medial indenting of the labial sheet of the dentary. The anterior part of the dentary, along the third to fifth tooth positions, is thick labiolingually and becomes somewhat compressed towards the rear. This is evidently linked with the oblique placement of alveoli of three respective teeth, the long axes of which are directed rather anterolabially – posterolingually than axially, as well as with the presence of an enlarged fifth tooth. The anterior margin of the dentary is sharp, straight, obliquely truncated, meeting the ventral margin at an angle. There is a narrow, rough zone along the anterior margin of the dentary which represents the zone of ligamental binding between mandibular rami; these were thus able to move independently. Most of the preserved length of the dentary shows a disparity in the depth of the labial (deeper) and lingual wall of the alveolar groove, equaling 4–5 mm. This disparity is, however, much smaller – to almost none – along the first four tooth positions.

Labial surface of the anterior portion of the preserved dentary fragment is uneven, mainly due to irregularly scattered foramina. Anteriorly, the labial surface is angularly bent which results in a short, oblique crest, dividing the anterior end of the dentary into two parts, the dorsal of which is vertical and the ventral slants ventromedially towards the anterior margin. Parallel to the alveolar margin runs a shallow and rather uneven groove, which anteriorly starts below the fourth/fifth tooth position. The groove contains a row of a few irregularly spaced foramina. Another, but less distinct row of foramina is present close to the ventral margin. Along the alveolar margin, the labial wall medially produces septal projections. These seem to be continuous with the interdental septa and contact (at least in the anterior septa) the respective septal projections of the interdental plates.

The lingual sheet of the dentary is thick and convex medially. The Meckelian groove is deep and runs over a distance between the sixth and fourth tooth positions, dividing rostrally the lingual surface of the dentary into two medially convex parts. Posterior to the groove, the dorsal and ventral parts are separated by the long wedge of the splenial. The thick ventral edge of the dorsal limb of the dentary overhangs the splenial, and it roofs a sulcus, which posteriorly prolonges the Meckelian groove. In the region close to the Meckelian groove the ventral limb medially overlaps the splenial. The ventral limb narrows posteriorly and below the 9th tooth position its thick, rounded ventral margin underlies the splenial (Fig. 3F).

Dentition. — Judging by preserved bases of crowns, the teeth were rather strong, with flattened crowns, except those of the first two teeth, which were rounded. In the posterior direction, crowns become gradually more compressed labiolingually. Judging by the measurements of the base of the fifth tooth crown (5.2×9 mm *versus* 4.5×7.8 mm in the fourth, and 4.5×7 mm in the sixth tooth) it was the strongest tooth in the jaw; the first tooth was weak (about 2.5 mm across the base) and placed at the very tip of the mandible. The pulp cavities are clearly visible and, as preserved, filled with crystallized matrix.

Interdental plates. — These are unfused, triangular and their apices curve laterally and meet the septal projections of the labial sheet of the dentary. The boundary between the plates and the lingual sheet of the dentary is very distinct. Bases of the interdental plates, starting with that between the fourth and the sixth tooth, are covered by a thin layer of dark matter, which probably corresponds to the supradentary. In places where this layer is damaged, the lingual sheet of the dentary displays a narrow shelf underneath.

Splenial. — Only the long, wedgelike anterior process of the splenial is preserved. It is thick and lies in the depression between the dorsal and ventral limbs of the lingual lamina of the dentary (Figs 2B, 3B, F). Differently than in other theropods in which the splenial is an element medial to the dentary, here its anterior process is tightly embraced by the dorsal and ventral limbs of the dentary, and anteriorly it seems even to be medially overlapped by the dentary, as mentioned above.

Angular. — Only a posterior process of the angular is preserved. It is a thin sheet of bone, covering slightly less than the lower half of the labial mandibular wall. It overlaps the surangular and ends somewhat behind the surangular foramina. It does not wrap around the ventral border of the mandible, but contacts the prearticular along this border.

Surangular. — The dorsal part of this bone is strongly thickened. In front of the glenoid region, the dorsal margin of the surangular distinctly rises forwards. On the labial side the surangular continues to the very end of the mandible and its oblique posterior margin adheres, along its entire

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Fig. 2. Mandible in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–C. Left dentary in lateral, medial, and dorsal views.
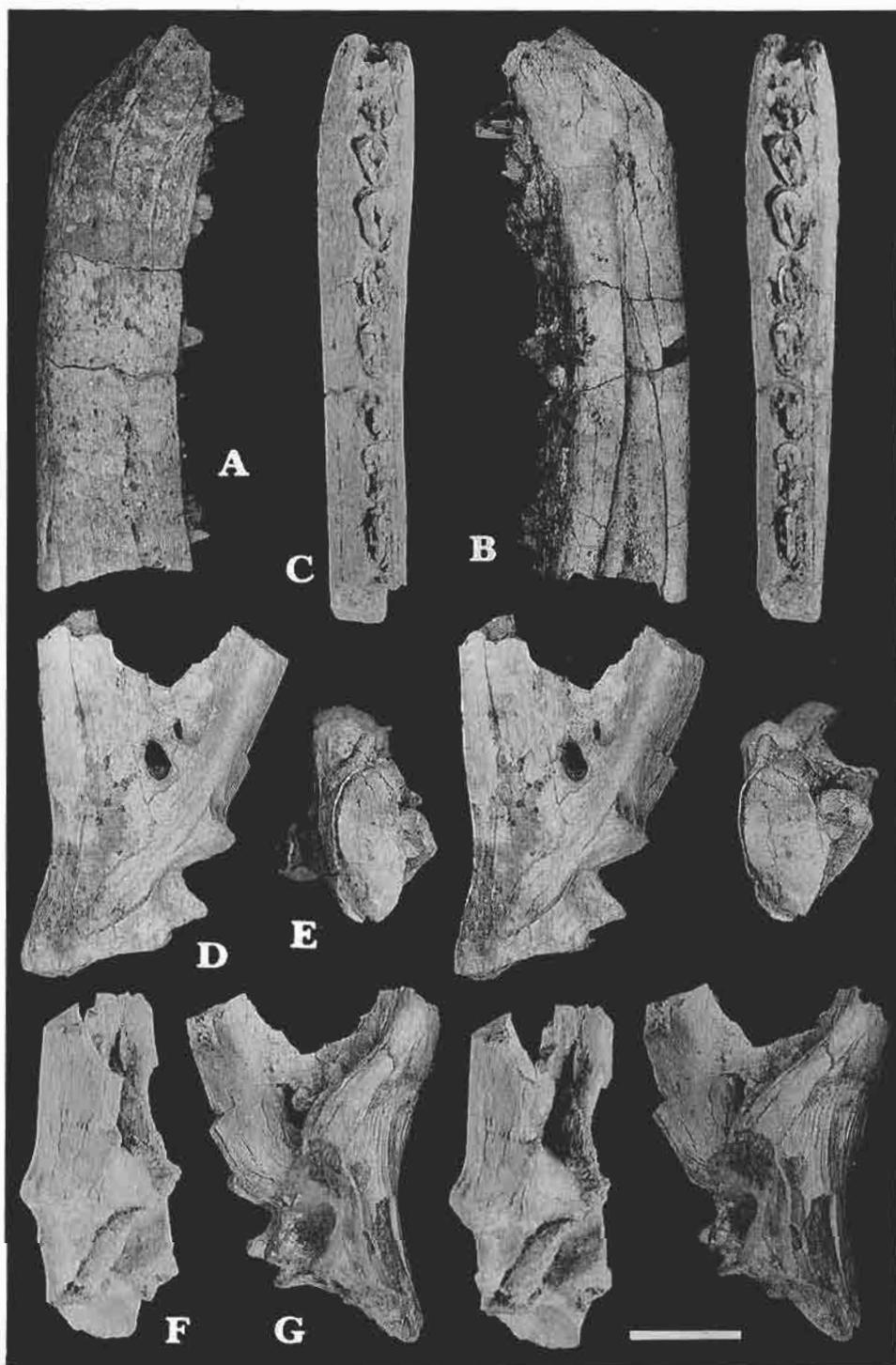
D–G. Posterior part of left mandible, stereophotographs, in lateral, posterior, dorsal, and medial views. Scale bar — 2 cm.
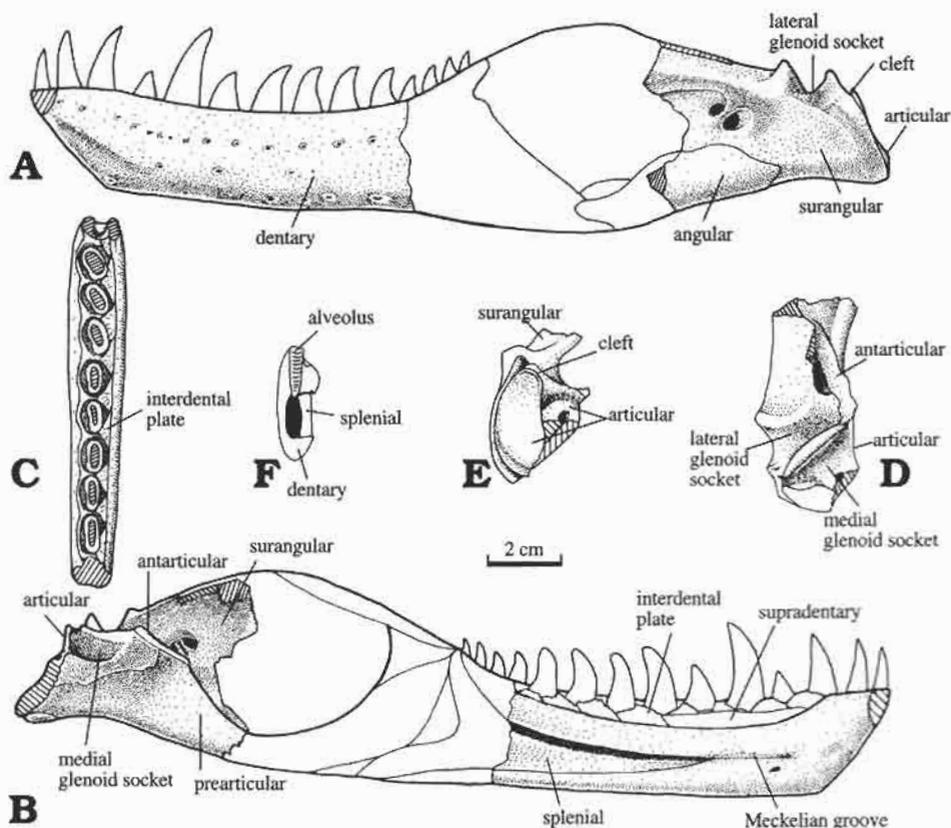
Fig. 3. Mandible in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–B. Reconstruction on left mandible in lateral and medial views. C. Left dentary in dorsal view. D–E. Posterior part of left mandible in dorsal and posterior views. F. Cross-section through dentary at the end of preserved fragment.

length, to the lateral margin of the articular. The posteroventral tip of the surangular is thickened and it ventrally underlies the articular, participating in formation of the retroarticular process. More anteriorly, a thin ventral portion of the surangular is sandwiched between the angular and prearticular. The posterodorsal part of the surangular is very stout. The dorsal margin is flattened to form a broad shelf, which slants laterally. The medial edge of this shelf is damaged. The shelf ends posteriorly in a strong, labiolingually extended, prominent boss, the preglenoid process. The boss forms the anterolateral boundary to the deep lateral socket of the glenoid fossa (Figs 2F, 3D). Posterolaterally, the surangular portion of the glenoid (the lateral socket) is delimited by a conspicuous, but less massive, conelike process. This postglenoid process is placed just at the dorsoposterior contact with the articular. The dorsomedial contact with the articular is well defined and the suture traverses posterolaterally–anteromedially the glenoidal region. The lateral glenoid socket is shallower than the

medial (on the articular). A stout medial process of the surangular but-tresses the prearticular and partly the articular, just anterior to the articular part of the glenoid (the medial socket). As in *Allosaurus fragilis* Marsh 1877 (Madsen 1976: p. 31), there is a sesamoidlike accessory ossification along the contact of the medial process of the surangular, the posterodorsal extremity of the prearticular and the medial surface of the articular (Fig. 3B, D). Its platelike shape is, however, different from the subrectangular 'antarticular' (a term applied by Madsen 1976) in *A. fragilis*.

The surangular crest is strong, but rounded externally rather than sharp. Below the crest, and above the contact with the angular, the bone is strongly depressed laterally. There are two relatively large surangular foramina separated by a flat, ventrally descending process.

Prearticular. — The preserved part of the prearticular forms the ven-trolingual part of the mandibular margin. Along the middle of the margin, there is a sharp contact with the angular laterally, which is replaced by the contact with the surangular more posteriorly. In the bottom of the adductor fossa, a thick prearticular shaft contacts laterally the surangu-lar. Further posteriorly, close to the region facing the surangular fenestrae, the antarticular overlies laterally the prearticular. The posterior part of the prearticular is thin and greatly expanded dorsoventrally. The dorsal extent of the prearticular on the articular is not known. As preserved, the posterior lamina does not cover the entire medial surface of the articular, being broken off 6–10 mm below the dorsomedial margin of the latter bone.

Articular. — The articular is damaged posteriorly along its posterome-dial margin. But, comparing the isolated articular YPM 5232 of *Deinony-chus antirrhopus* Ostrom 1969 with that in *B. ostromi*, one can conclude that in the latter species a presence of the medial, ascending process, similar to that in the dromaeosaurids, is probable. The dorsal surface of the articular has a triangular outline and is entirely occupied by the medial glenoid socket (Figs 2F, 3D). The anterior apex of the triangle contacts the medial process of the surangular laterally, the antarticular anteromedially and probably the prearticular medially. Along the surangular — articular dorsal contact, the articular bears a prominent, rounded ridge, which starts at the postglenoid process of the surangular and runs to the lingual extremity of the medial process of the surangular. This ridge separates the lateral (surangular) glenoid socket from the medial (articular) one. The latter is troughlike, deeper and narrower than the former, and extends obliquely anteromedially–posterolaterally. The posterior surface of the articular dips about 45° posteroventrally–anterodorsally, which causes that the articular extends ventroposteriorly forming a short retroarticular process. The posterior tip of this process is rough, and it provided space for insertion of the m. depressor mandibulae. Most probably, this attach-ment facet also extended somewhat medially. The posterior surface of the articular is covered by smooth, well finished bone. This surface is some-what concave, oval, its longer axis being the ventrodorsal one. Dorsally,

there is a deep cleft separating the main body of the articular from its posterior surface (Fig. 3A, E). It suggests that the most posterior part of the articular might have been formed from a separate ossification centre. Immediately posterior to the medial glenoid socket, there is an opening of a channel penetrating the bone. The opening leading into the sinus chamber is placed in approximately the same position in *Tyrannosaurus rex* Osborn 1905 (Molnar 1991).

Vertebral column

The vertebral column is represented by a sacral neural spine and 25 caudals, 21 of which constitute a continuous proximal series measuring 1020 mm.

The neural spine of the sacral (Fig. 12A) is preserved with fragments of vertebral arch. It is deep, platelike, very long anteroposteriorly, slightly narrowing towards its base due to the oblique posterior margin. The dorsal margin of the spine is very weakly arched. A groove runs along the anterior and posterior margin of the spine. On each side of the base of the spine there are still preserved proximal portions of transverse processes. The lateral surface of the spine is uneven, covered by short, vertical striae. Other remnants of the sacrum are the distal ends of sacral ribs fused to iliac blades, and they probably represent the third through the fifth rib on the right side, and the fifth on the left side (see description of the ilium below).

Caudal vertebrae. — The exact count of the caudals is unknown, the end of tail, as well as an unknown number of the most anterior caudals not being preserved (Figs 4–7). With the first completely preserved caudal, the posterior portion of the arch of the preceding vertebra (postzygapophyses, hyposphene and a part of the neural spine) is articulated. This fragmentary vertebra may represent the last sacral or one of the most proximal caudals (?the first). The latter assumption is more probable, judging by the expanded posterior margin of the spine, which is very much like that in other proximal caudals; this margin is much thinner in the preserved sacral spine. On the ventroposterior margin of the centrum of the first complete caudal found, there is a pair of articulating facets for a chevron, which also indicates that it was not the first caudal. However, the ventroanterior edge of the centrum of this caudal lacks chevron facets, thus most probably there was no chevron between the first complete caudal found and the preceding fragmentary one. In the description that follows, numbering of vertebrae starts with the first complete caudal preserved.

In the fourteen most proximal caudals found, the neural arches are not fused with centra and the suture is distinct in all fourteen proximal caudals, but becomes invisible from the 15th caudal backwards. Caudal centra are thin-walled and hollow (Fig. 6K); they are filled with crystallized
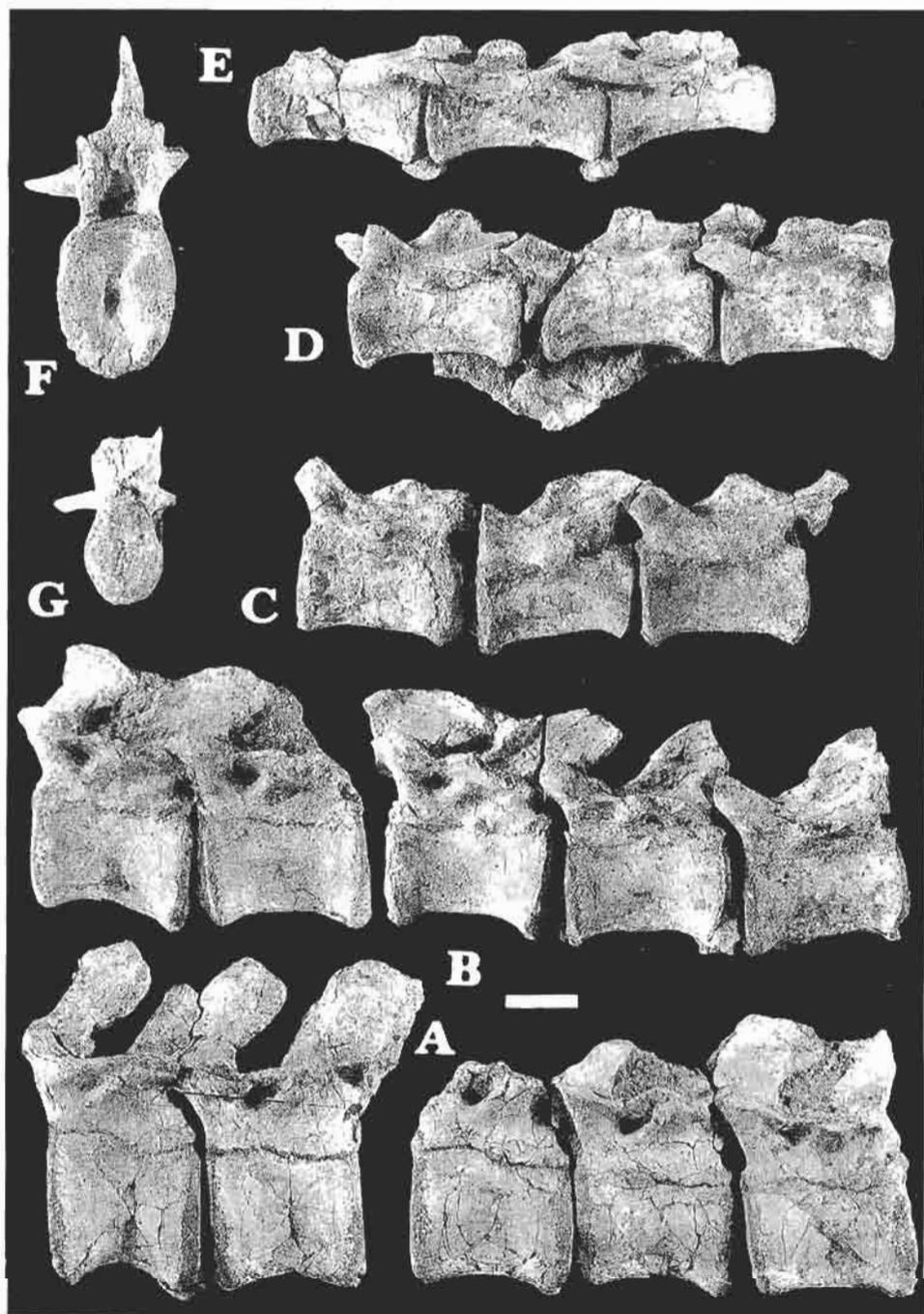
Fig. 4. Caudal vertebrae in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–E. Preserved caudals 1st–13th (A–C) and 15th–20th (D, E) in lateral view. F. Anterior view of 1st preserved caudal with articulated part of spine of preceding caudal. G. Anterior view of 11th preserved caudal. Scale bar — 2 cm.

matrix. Several tiny openings are visible on external surfaces of centra, leading to the chambers. Because of the hollow nature of most centra, their sides collapsed, especially in the first fourteen preserved caudals; the degree of deformation decreases posteriorly, and centra posterior to the 14th caudal are not deformed at all, their walls being relatively thicker. In contrast to the centra, the neural arches in all caudals found did not suffer deformation. The length of the centra is practically the same throughout first eleven preserved caudals; it slightly increases with the 12th through 19th caudals, then becoming gradually shorter towards the end. As usual in theropods, the caudal centra are spool-like, and they become gradually shallower backwards. There are no pleurocoels. The ventral surfaces of the centra are narrow, but because of the lateral crushing no details are visible in the thirteen most proximal caudals. In the more distal centra the ventral surface is flat or bears a faint groove. The more proximal centra (1st–11th) are procoelous but become amphiplatyan distally. In posterior view, the centra of the thirteen proximal caudals are vertically oval, but this surface becomes subquadrangular in more distal centra.

Transverse processes are present in the fourteen proximal caudals found, thus (assuming that there was at least one more vertebra included in the unpreserved anteriormost portion of the tail), they were present at least in the fifteen proximal caudals. The processes are horizontal and relatively wide anteroposteriorly. The pair preserved in the 1st caudal is lateroposteriorly directed, and those preserved in the caudals 6th through 14th are laterally directed. The transverse processes gradually shorten in the posterior direction and become displaced ventrally towards the suture between the arch and centrum.

More or less complete neural spines are preserved in most caudals. In the ten proximal caudals they are inclined backwards, long anteroposteriorly and moderately deep. The neural spines in these caudals have the anterior margin oblique, inclined dorsoposteriorly, smoothly passing upwards into the arched dorsal margin. The distal halves of these spines have rough lateral surfaces, and are extended posteriorly overhanging the anterior part of the succeeding caudals. The dorsal margins of spines preserved in the caudals 13th through 15th are depressed in the middle, and the depression divides the spine into two parts, the anterior and the posterior (Figs 4C–D, 7G–F). Distances between the extremities of the successive spines are short and the spine in the caudal 19th almost contacts the spine of the caudal 20th by its posterior projection, which extends beyond the posterior margin of the postzygapophysis. The result is an almost continuous septum formed along the dorsal side of the distal caudal series. In the majority of preserved caudals, the anterior and posterior margins of the neural spines are thickened at their bases which evidences a strong ligamental union between the vertebrae; in at least fifteen proximal caudals, a groove runs along the anterior margin of the spine.
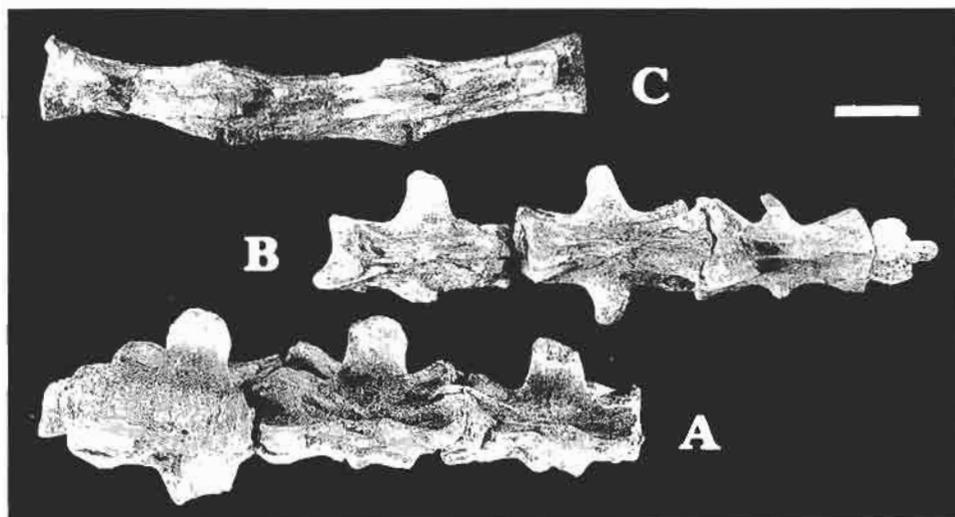
Fig. 5. Caudal vertebrae in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–B. Dorsal views of preserved caudals 8th–13th. C. Dorsal views of preserved caudals 18th–20th. Scale bar — 2 cm.

Prezygapophyses of the ten proximal caudals are massive, almost vertically directed (Figs 4A, 6B, E) while in most theropods they are anteriorly, or slightly anterodorsally directed. The length of these prezygapophyses measured from the floor of the neural canal, equals approximately two thirds of the depth of the respective centrum. Because of the vertical orientation of the prezygapophyses, their tips do not extend beyond the anterior margins of their respective centra in the five proximal caudals, and they only slightly extend beyond this margin in the next five caudals. Prezygapophyses of the more distal caudals gradually become elongated anteroposteriorly and in the most distal preserved caudals (21st–24th) they extend over about a third of the length of the preceding centrum. In the ten or eleven proximal caudals preserved, the lateral surfaces of the prezygapophyses have angular shapes due to longitudinal ridges, which run parallel to the dorsal margin of each (Fig. 6E–J). The ridges gradually 'migrate' downward and are situated more ventrally in the more posterior caudals of the proximal series. As a result, the portion of the prezygapophysis dorsal to the ridge becomes gradually deeper. Although it is not clearly visible in any caudal, it seems that only the dorsal portion of the prezygapophysis bears the articular facet for the postzygapophysis, while its ventroposterior portion forms the hypantrum. The articular facets are steeply inclined in the four most proximal caudals, and they become vertical in the more distal caudals.

Postzygapophyses extend far beyond the centra in all caudals preserved, which is correlated with the above mentioned moderate forward extent of the prezygapophyses.
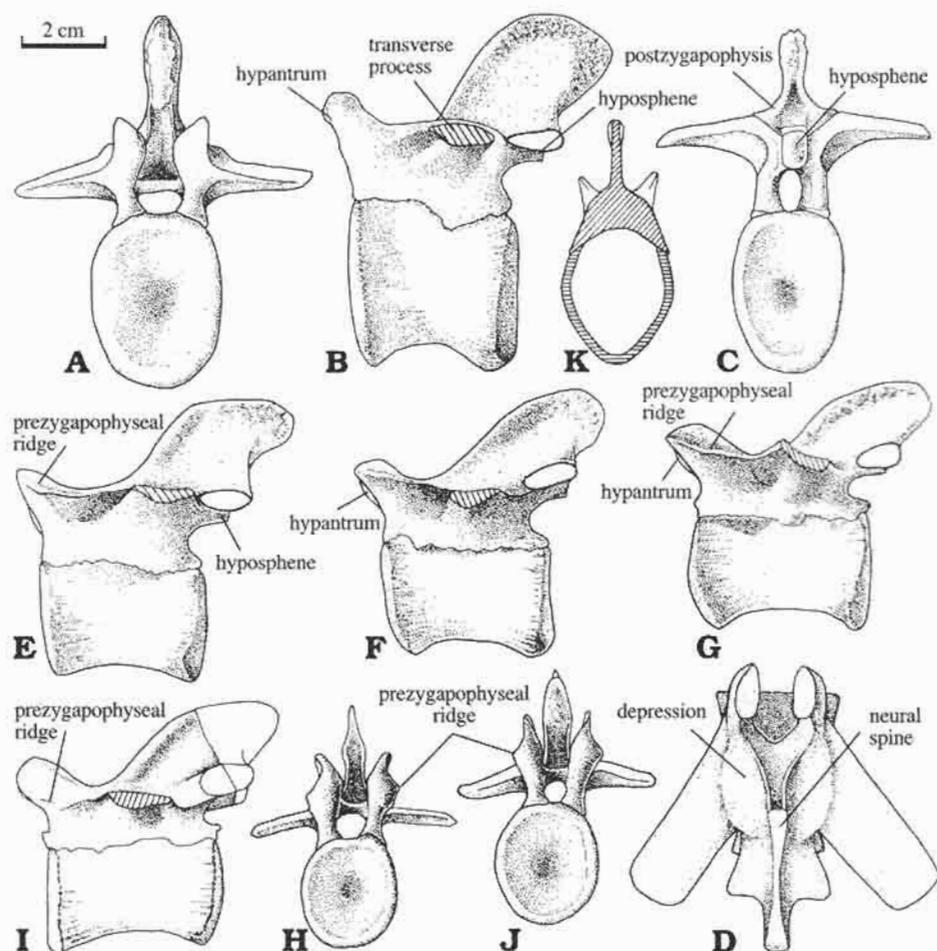
Fig. 6. Reconstructions of caudal vertebrae in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–D. First preserved caudal in anterior, lateral, posterior, and dorsal views, respectively. E–G, I. Lateral views of 5th, 7th, 8th and 9th preserved caudals. J–H. Anterior views of 8th and 9th preserved caudals. K. Cross-section through centrum of 14th preserved caudal, showing thinness of its walls.

Neural arches of the sixteen proximal caudals are very tightly connected between each other by the hyposphene — hypantrum articulations. As preserved, the arches are broken in the plane passing between the centra and the postzygapophyseal part of the arch of the preceding caudal is preserved in articulation with the prezygapophyses of the succeeding caudal. As the broken surfaces of the vertebrae 9th through 16th reveal, at least in these vertebrae there is a medial pneumatic chamber between the hyposphene and the base of the neural spine. These chambers are relatively small, being largest in the caudals 9th through 13th, in which they occupy the medial third of the arch width. In the cross-section the
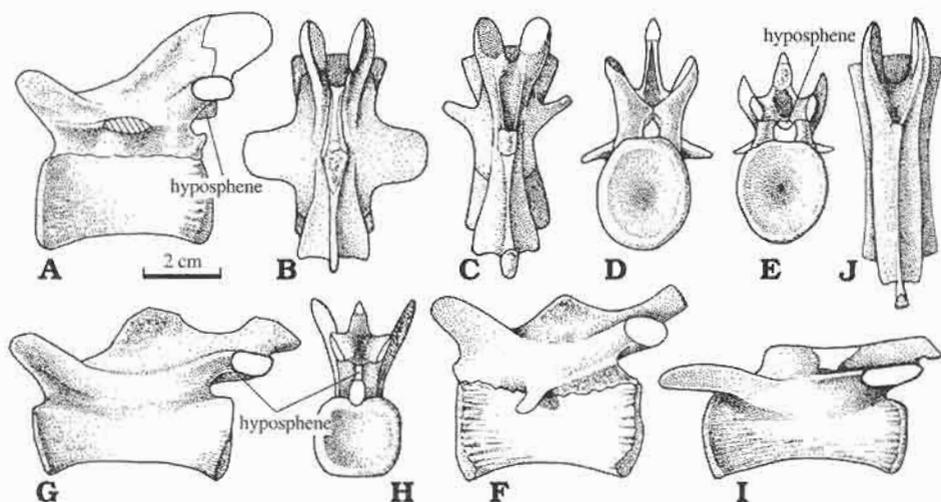
Fig. 7. Reconstructions of caudal vertebrae in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–B. Tenth preserved caudal in lateral and dorsal views. C–F. Thirteenth preserved caudal in dorsal, anterior, posterior, and lateral views. G–H. Fifteenth preserved caudal in lateral and posterior views. I–J. Nineteenth preserved caudal in lateral and dorsal views.

chambers have the shape of upturned drops. Their walls are thick and solid. It seems that the chambers are present only along the postzygapophyseal parts of the arches. The arches of the more proximal caudals are solid. The hyposphenes are very stout and very extensive in ten proximal caudals preserved, becoming gradually shallower and shorter distally. Hypantra are limited to narrow articular facets placed ventroposteriorly to the postzygapophyseal articular facets (see above).

Medially to the transverse process, at the base of the spine, the dorsal surface of the arch bears on each side a depression with a rough bottom (Fig. 6D). These depressions become narrower and shallower in the more distal caudals and they practically disappear in the 9th caudal.

Only a few chevrons, mostly incomplete and separated from the respective caudals, were found. It is evident that they did not bear extensions resembling those found in the dromaeosaurids. The chevron between the 14th and 15th caudal is almost complete and preserved *in situ*. In addition, basal portions of several more distal chevrons still articulated with caudals (18th–20th) were found as well as a few loose chevrons, which, judging by their shape, articulated with more proximal caudals. The preserved proximal chevrons have the form typical for many theropods: they are deeper than long and have flattened, short, somewhat anteroposteriorly extended distal ends. Along their anterior and posterior edges all chevrons bear a groove. The above mentioned chevron preserved *in situ* has a hatchetlike shape, with elongate distal extremity, the posterior portion of which is much longer than the anterior.

Pelvis

The pelvis is propubic and was strongly united with the sacrum. Remains of sacral ribs, probably representing the 3rd through the 5th, are fused with the iliac blades.

Ilium. — In addition to the postacetabular processes of the right and left ilium which are quite well preserved (Figs 8, 9A–B, E, 12B), there are also two indeterminable fragments, presumably of the preacetabular process (Fig. 9F–G). This inadequate material does not give information about the exact shape of the ilium, and allows only a rough estimation of the length of this bone. Hence, assuming that the length of the preacetabular process (measured from the center of the acetabulum) might be about equal or somewhat shorter to that of the postacetabular process, the total length of the ilium might reach 300–320 mm.

The postacetabular process is relatively shallow and is almost three times as long as the acetabulum. The partly preserved posterodorsal margin of the postacetabular blade indicates that it curved gently ventrally in lateral view and distally it was rounded rather than narrowed or truncated. The brevis shelf is wide, slightly arched and the brevis fossa well developed, widening posteriorly. Its ventrolateral margin is thickened (Figs 8D, 9B). In contrast to the massive structure of the ventral portion, the preserved part of the dorsal iliac margin is very thin. The medial and lateral surfaces of the postacetabular process are covered by distinct, oblique, subparallel striae, reflecting impressions of the muscle attachments. The right postacetabular process has a damaged ischiadic process, but a large portion of the dorsal acetabular border is preserved; most of the dorsal margin of the blade, as well as its ventroposterior tip, are broken off. The complete ischiadic process is preserved with the left ilium and was found in articulation with the ischium. Most of the acetabular portion, as well as the end of the postacetabular process are lacking in the left ilium and the dorsal margin is damaged along its medial section.

The dorsal margin of the acetabulum (right ilium) is somewhat extended medially, forming a medial supracetabular crest (Figs 8B, 9E). The lateromedial width of the dorsal acetabular border equals 20 mm; however it was wider, at least about another 5 mm, because the lateral supracetabular crest, which was probably also present, is broken off. The posterior wall of the dorsal half of the acetabulum is flat and lateromedially very wide. Just above the centre of the medial supracetabular crest a remnant of a sacral rib is fused to the medial surface of the iliac blade (Figs 8B, 9E). It is arbitrarily accepted here as the distal end of the 3rd sacral rib, because in the great number of advanced theropods the sacral rib attaching to the ilium above the acetabulum is the third one. A remnant of the 4th sacral rib is fused to the postacetabular blade just above the ischiadic peduncle. This rib is much broader anteroposteriorly than the former, but about as deep. The 5th sacral rib is very strongly expanded. The central, massive portion of this appendage (which may, in fact correspond to the sacral
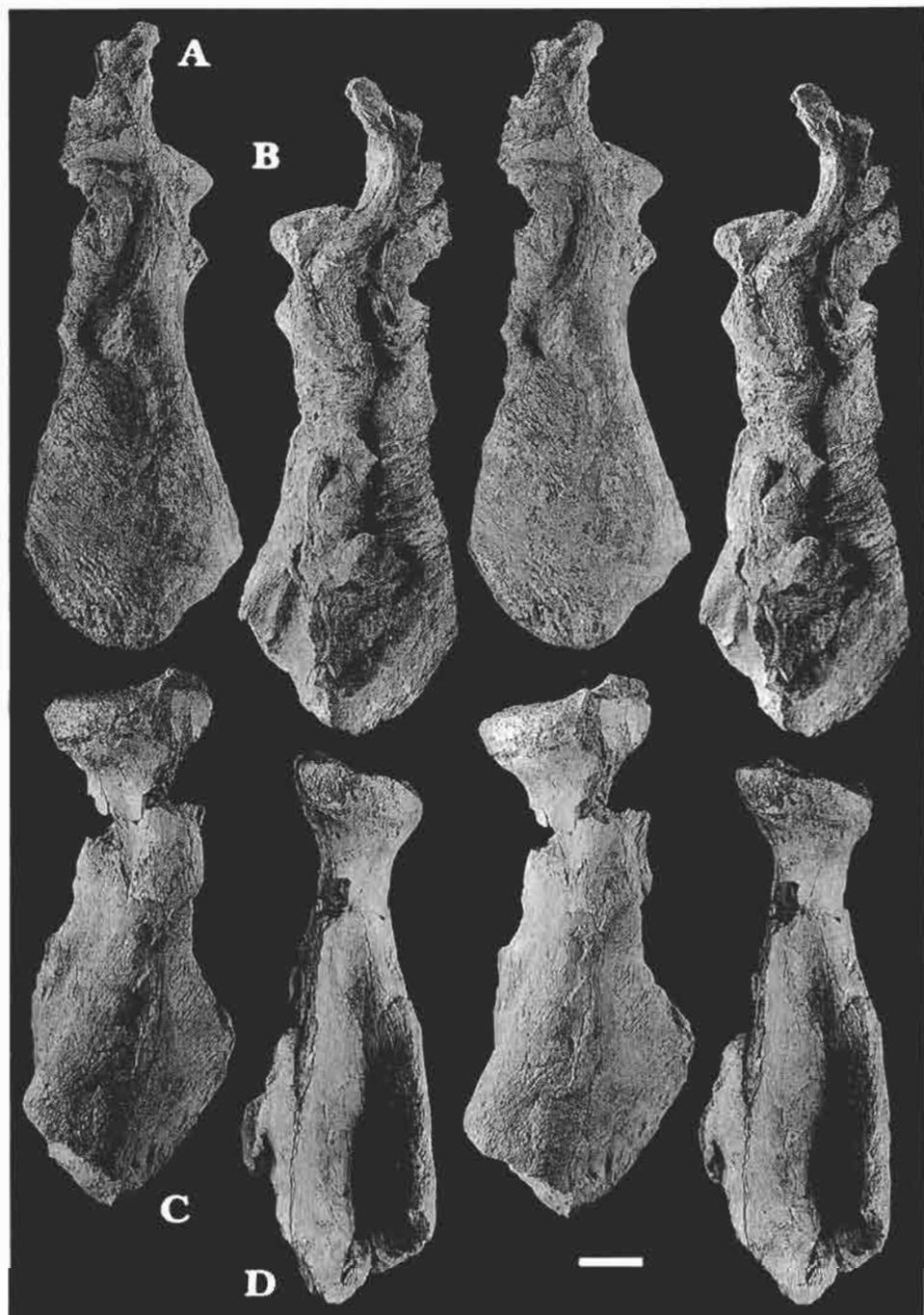
Fig. 8. Ilium in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–B. Stereophotographs of right postacetabular process in lateral and medial views. C–D. Stereophotographs of left postacetabular process in lateral and ventral views. Scale bar — 2 cm.
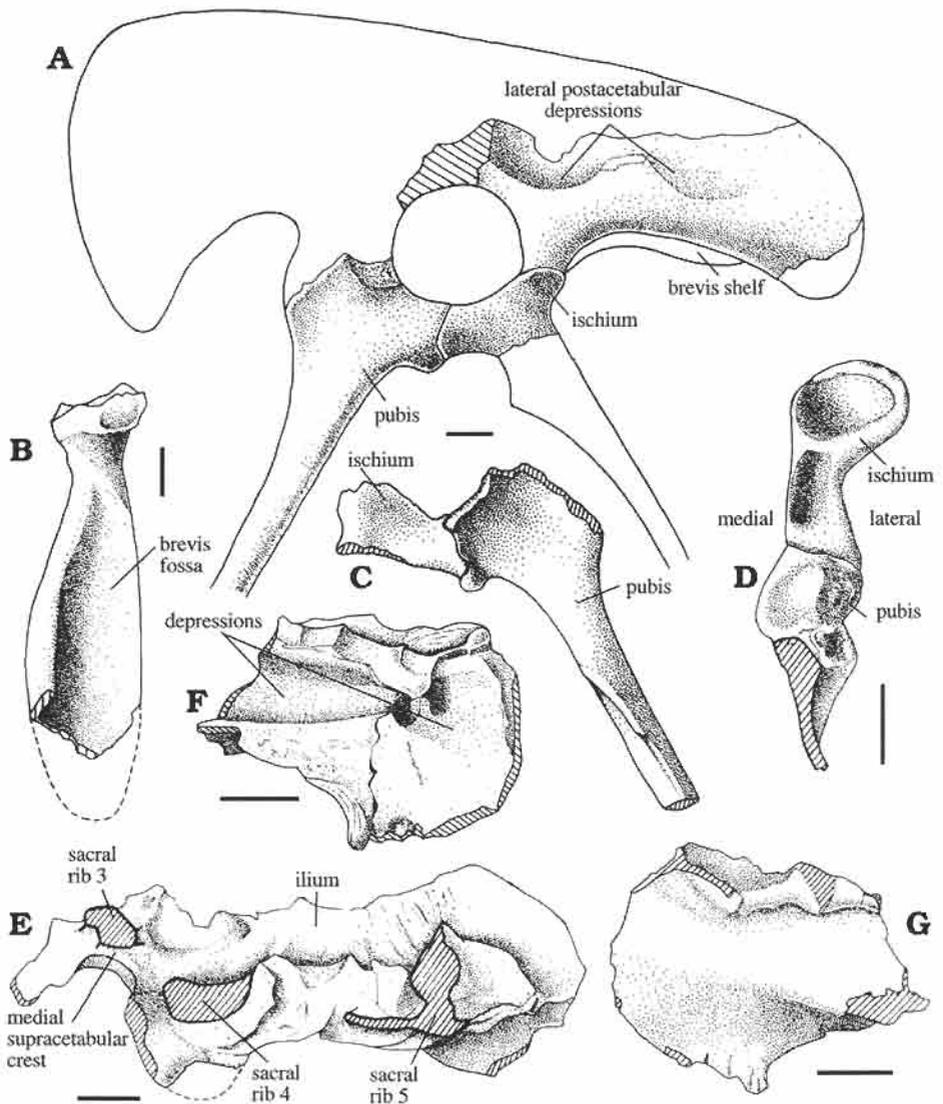
Fig. 9. Pelvis in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A. Reconstruction of pelvis in lateral view. B. Reconstruction of right postacetabular process of ilium in ventral view. C–D. Fragment of left pubis + ischium in medial and dorsal views. E. Right postacetabular process of ilium in medial view. F–G. Fragment of supposed right preacetabular process of ilium in ?lateral and ?medial views. Scale bars — 2 cm.

transverse process) extends anteromedially and posteromedially into relatively thin plates, which fuse with the dorsal surface of the medial iliac blade (= brevis fossa roof). The long line of contact between the 5th rib and the medial blade is visible along the medial margin of this blade and it ends close to the posterior margin of the ilium.

Fig. 10. Femur in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A–B, E. Stereophotographs of proximal end of left femur in medial, anterior and posterior views. C–D, F. Stereophotographs of distal end of left femur in medial, anterior, and posterior views. Scale bar – 2 cm.

The lateral surface of the postacetabular process of the ilium bears two depressions and a short, horizontal, thickened ridge, which separates these depressions and is placed somewhat caudally to the ischiadic peduncle (Figs 8A, C, 9A). One of the depressions is located just above the ischiadic peduncle. Its preserved ventral boundary is strongly thickened and semicircular. The second, more posterior, depression is located approximately 60 mm from the posterior edge of the iliac blade. It is somewhat shallower than the former and has a longitudinally oval (about 35 × 20 mm) shape. Some distance below the dorsal margin of the

postacetabular process, a deep, narrow through joins both postacetabular depressions. The ventral boundary of this trough is formed by the above mentioned strong, thickened ridge. The lateral surface of the postacetabular process, including the posterior depression, is covered by distinct, subparallel, posteroventrally–anterodorsally extended striae; but close to the posterior margin the course of these striae is deflected to become horizontal. Within the more anterior depression, the surface of the ilium seems smoother, at least anteriorly, while the bottom of the trough joining the depressions is very rough.

Two pieces of bone were found lying a short distance from the pelvis of *B. ostromi* and they also seem to belong to the ilium. One of them is thin, with a natural, even dorsal margin. It evidently represents the dorsal portion of the iliac blade, and comes, most probably, from its medial or anterior section. On the medial side, this fragment bears relatively dense, subparallel striae, which run almost perpendicular to the dorsal margin. The other fragment, the exact orientation of which is uncertain, may represent a portion of the preacetabular process of the ilium (Fig. 9F–G). Only one of its margins is natural (?the ventral). One (?medial) surface of the fragment bears a broad, elongate shelf, which narrows and finally disappears at the (?anterior) margin. The other (?lateral) surface bears two deep depressions. One of them (?the anterior) is smaller and shallower than the other (?the posterior), which is elongated and deepens towards the margin of the fragment. This depression results in the above mentioned horizontal shelf on the opposite side. The naturally preserved margin of this fragment is at first parallel to this shelf, then it curves off, somewhat resembling the ventral edge of the preacetabular process of the theropod ilium.

Pubis. — The preserved fragment of the left pubis measures 175 mm (Figs 9A, C–D, 12C–D). The distal end of the pubis and most of the iliac peduncle are broken off. The proximal part of the pubis is thin lateromedially. Of the iliac peduncle only the outer portion is preserved, which is slightly laterally extended and displays a dorsolaterally inclined surface for the contact with the pubic peduncle of the ilium. The anterodorsal border of the pubis is not preserved. There is no obturator foramen. The ischiadic process is massive but short; its acetabular portion is extended medially and relatively narrow, forming a medial lip. The sutural surface for the ischium is very extensive; the ischiadic peduncle of the pubis is extended posteroventrally, ventrally underlying the pubic peduncle of the ischium and fusing here with the later. The preserved proximal portion of the pubic shaft is slender, straight in anterior view and very weakly concave anteriorly in lateral view. Fifty mm below the ventral contact with the ischium, the posteromedial margin of the shaft slightly extends medially, over a distance of about 70 mm. The extended margin is very narrow and bears medially a rough surface (Figs 9C, 12D). Taking into account that the pubis shaft is not bowed towards the mid-line proximally and the medial extension is very small and bears the corrugated surface, connec-
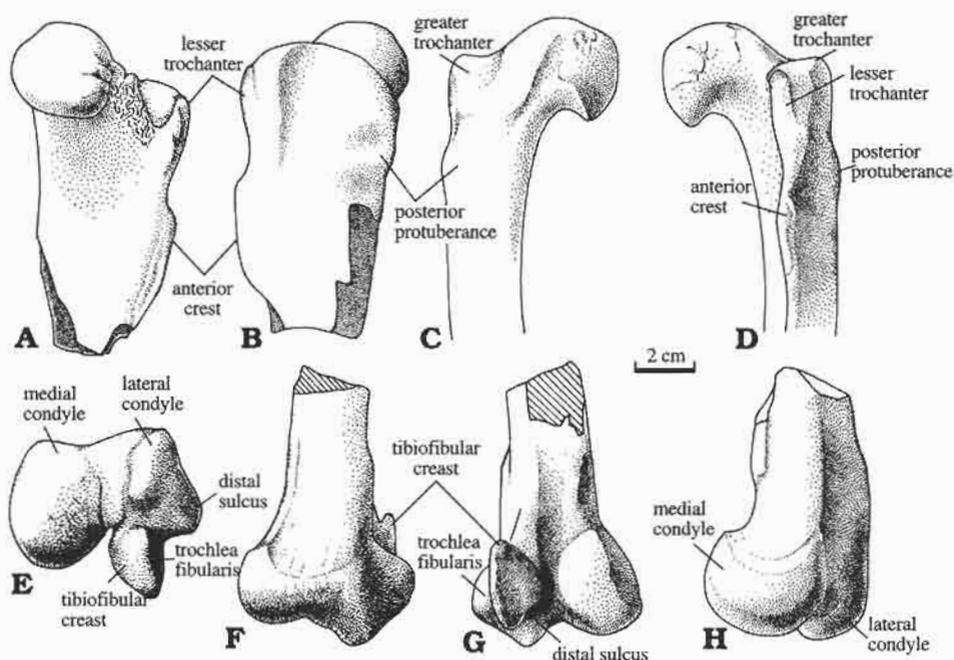
Fig. 11. Femur in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt. Mongolia. A–D. Proximal end of left femur in medial, lateral, posterior, and anterior views. E–H. Distal end of left femur in distal, anterior, posterior, and medial views.

tion with the opposite pubis was not direct but rather ligamentous. Ventral to this extension, the medial edge of the pubic shaft is smooth, rounded. Thus, there was no bony pubic 'apron' joining both pubes, and the interpubic contact might have been rather flexible.

Ischium. – Only the most proximal fragment of the left ischium is preserved which is articulated with the pubis (Figs 9A, C–D, 12C–D). The pubic process is long and shallow, forming slightly more than a half of the ventral acetabular rim. Its articular surface for the contact with the ischiadic process of the pubis is slightly oblique dorsoposteriorly–ventroanteriorly. The acetabular surface of the pubic process bears an elongate concavity, which is bounded medially by a low, thin wall. The iliac process is strong. Its proximal surface is oval, laterally elongated and bears a deep, funnel-shaped concavity for the contact with the ischiadic peduncle of the ilium. A broken off ventral portion of the latter peduncle is still preserved fused to the sutural surface on the iliac process.

Hind limb

Only the femur and crus are known in *B. ostromi*, the metatarsus is lacking completely and the pes is represented by but two phalanges.

As the femur lacks the mid-shaft, the femur/tibia ratio cannot be determined without doubt. However, judging by the considerable length and slenderness of the tibia, it is probable that this ratio was rather below 1.0, and a reasonable estimate is 0.80–0.90.

Femur. — Only the proximal and distal portions of the left femur are preserved (Figs 10–11). The circumferences of the distal end of the proximal portion and of the proximal end of the distal portion are almost the same and equal about 105 mm. Thus, it is reasonable to accept that the mid-shaft circumference of the femur was not larger. The combined length of both femur fragments equals about 230 mm. Taking into account the evident slenderness of the shaft, it is rather improbable that the femur in *B. ostromi* was longer than, or even equal to, the tibia (365 mm). The length of the lacking fragment of the shaft may be estimated at about 80–90 mm, thus a reasonable estimate of the femoral length would be about 310–320 mm.

The femoral head is convex, subspherical. The ventral margin of the head is well set off and there is a short, constricted neck, the axis of which projects dorsomedially at about 115° to the shaft. The posterior surface of the head is marked with a deep, vertical groove for the capital ligament. The greater trochanter is massive, separated from the head by a broad, very shallow depression and is lower than the head. Anterior to the head the greater trochanter is significantly extended and its medial surface is very rugose. The lesser trochanter is narrow, finger-shaped, almost as high as the greater; it is not separated from the latter but rather delimited by a faint furrow on the medial and lateral surfaces of the femur. Below the lesser trochanter, the anterior border of the shaft extends over 50 mm distance forming a crest (Figs 10A–B, 11A–B, D). The anterior margin of this crest is corrugated. Such an anterior crest is not developed in any known archosaur. The medial surface of the proximal end of the femur, anterior and distal to the head, is slightly concave. The lateral surface bears posteriorly a low protuberance placed some distance below the dorsal margin of the greater trochanter (Figs 10E, 11B–C). The region of the fourth trochanter is not preserved.

The lateral condyle is narrower than the medial. Its distal surface has the form of a conspicuous protuberance. A striking feature of the distal end of the femur is a distinctive, elongated and mediolaterally thick, lenticular tibiofibular crest, which is laterally and distally separated from the rest of the lateral condyle by a deep sulcus (Figs 10F, 11E, G). The medial condyle has a rounded, well finished articular surface. The condyles are distally separated by a broad and relatively shallow groove. The popliteal fossa is very deep and joins with the intercondylar groove by a deep and very narrow trough separating the tibiofibular crest from the medial condyle (Fig. 11E). Above the lateral condyle, the shaft is somewhat expanded laterally forming a sharp ectepicondyle (Fig. 11F–G). The entepicondyle, if developed, has not been preserved. The extensor groove is very shallow and placed close to the medial margin. Just above the distal articular end, the cross-section of the femoral shaft is subquadrangular:
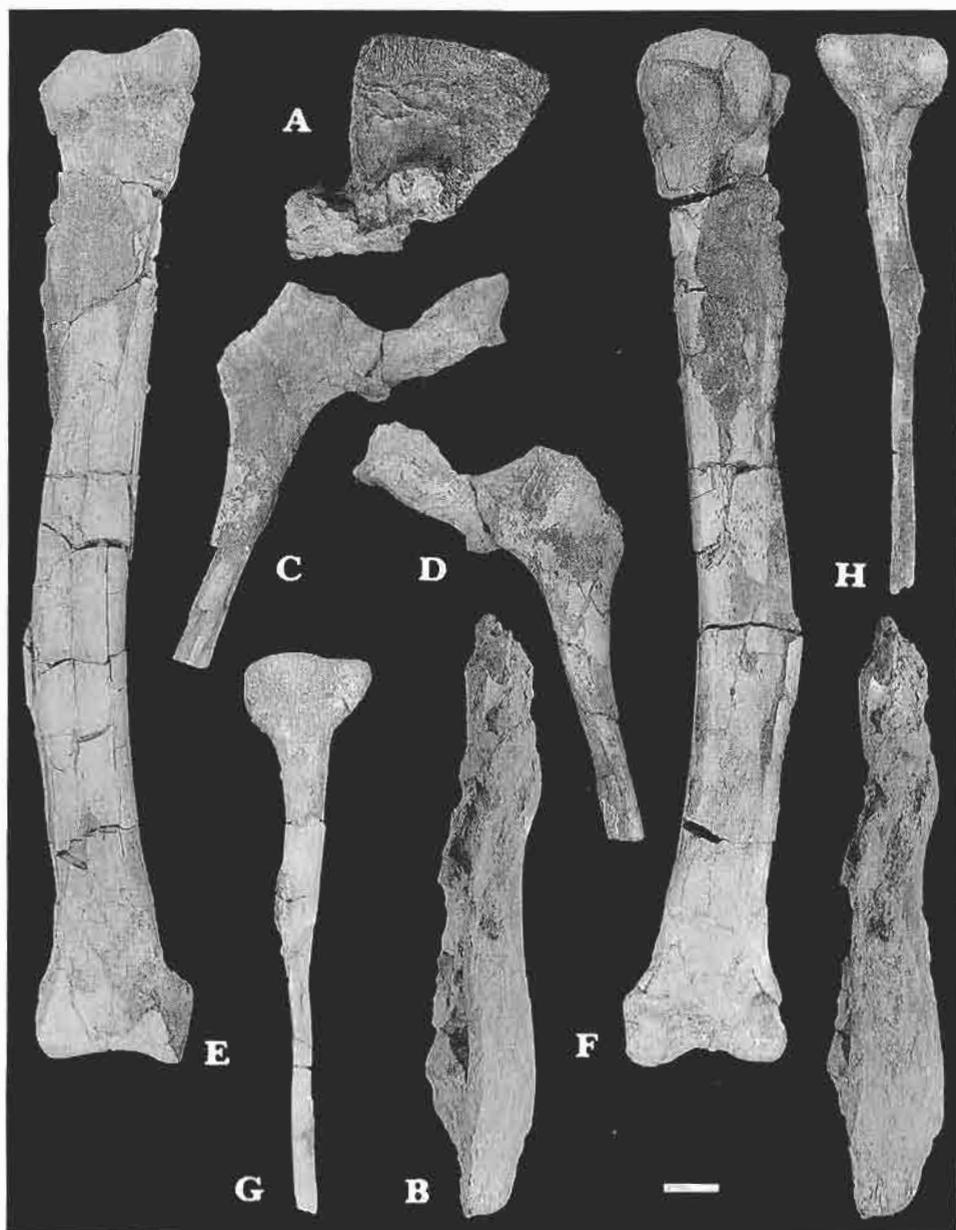
Fig. 12. *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt, Mongolia. A. Fragment of sacral vertebra. B. Stereophotograph of postacetabular process of right ilium in dorsal view. C–D. Left pubis in lateral and medial views. E–F. Left tibiotarsus with distal fragment of fibula in posterior and anterior views. G–H. Proximal fragment of left fibula in lateral and medial views. Scale bar — 2 cm.

the medial and lateral sides of the shaft are flat and meet the posterior and anterior surfaces at angles.

Tibiotarsus and fibula. — The tibia is distally fused with fibula and both these bones fuse with the coalesced astragalocalcaneum (Figs 12E–H, 13). The fusion is so complete, especially between the astragalus and calcaneum, that boundaries between bones are indiscernible.

The tibia is complete, although its shaft is broken in several places and somewhat flattened anteroposteriorly. The shaft is slender and slightly bowed, concave medially. The proximal end is subrectangular in top view rather than subtriangular as in other theropods (Fig. 13C). As in the allosaurids and tyrannosaurids, a projection is present on the proximal end of the tibia, which extends parallelly to the fibular head (Molnar *et al.* 1990: fig. 6.23). It resembles very much the lateral cnemial crest of birds, in which two cnemial crests are present separated by a deep anterolaterally facing intercnemial sulcus (Baumel & Witmer 1993). When the tibia is viewed from the lateral side, the cranial (medial) cnemial crest faces laterally, not anteriorly or anterolaterally, which, however, may be the result of a deformation. Compared with cnemial crests in the majority of theropods, the cranial crest in *B. ostromi* is relatively short and shallow, diminishing abruptly downwards over about one ninth of the tibial length. But it is larger and deeper than the lateral cnemial crest, which is parallel to the cranial crest. The lateral crest bears externally a small, concave facet for a contact with the anterior portion of the fibular head. Ventrally from this crest extends a sharp lateral edge which, further downwards, transforms into a very weak fibular crest. The posterior cleft in the proximal articular surface of the tibia, which is usually deep in most theropods, is shallow in *B. ostromi.*

Little can be said about the distal end of the tibia because of its almost traceless fusion with the astragalus and calcaneum. Only medially is a faint line between the medial condyle of tibia and the astragalus marked (Fig. 13D). The posterior surface of the distal end is very concave.

The fibula was found articulated with the tibia. It is complete although its proximal half has been slightly deformed *post mortem*. The proximal head of the fibula is anteroposteriorly short. The distal extremity of the fibula is somewhat deflected laterally. Except proximally, the fibular shaft adheres to the tibia over most of its length. Below the rough scar representing the attachment site of the m. iliofibularis, the fibula narrows, and becomes very thin. Its cross-section is triangular here, and the slightly concave medial wall adheres to the tibial shaft. Along its ventral quarter the fibula is fused with the tibia and with the ascending process of the astragalus, but it does not cover the latter as it does in ceratosaurians. Fusion of the fibula with the calcaneum is complete and the distal end of the fibula is marked only by a rounded knob close to the lateral surface of the calcaneum. The lateral edge of the fibular shaft extends somewhat beyond the lateral margin of the tibia, thus in posterior view the boundary between these two bones is distinct down to the distal end (Figs 12E, 13B).

The proximal tarsals are completely fused with each other and with the tibia and fibula producing the condyles of the distal end of the tibiotarsus.
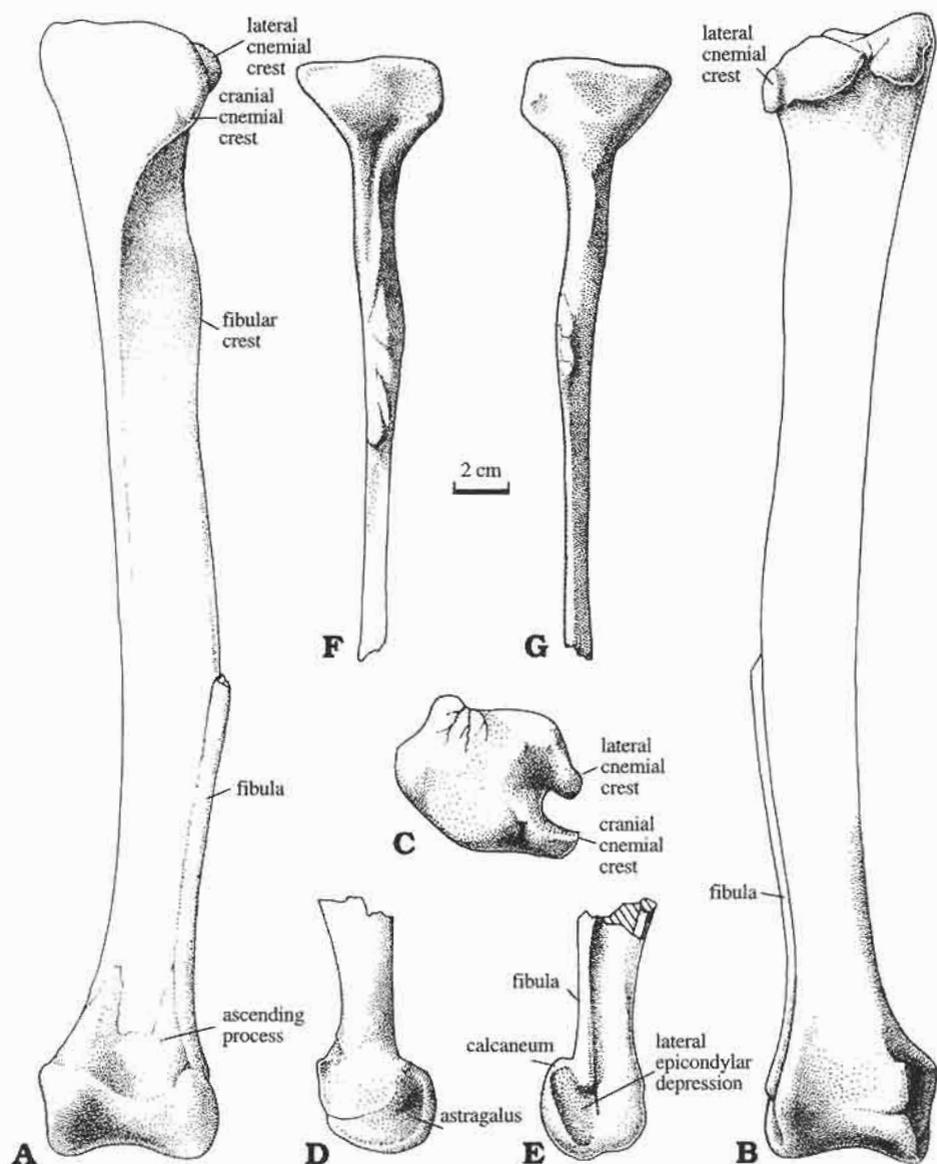
Fig. 13. Shin bones in *Bagaraatan ostromi* gen. et sp. n. from the ?mid-Maastrichtian Nemegt Formation at Nemegt. Mongolia. A–B. Left tibiotarsus + distal part of fibula in anterior and posterior views. C. Tibia in proximal view. D–E. Distal end of tibiotarsus + fibula in medial and lateral views. F–G. Proximal part of left fibula in medial and lateral views.

Except for its fusion with the adjoining bones, the astragalus seems similar to astragali of most Tetanurae. Its ascending process is damaged centrally, but it has a wide base and was rather symmetrical (Figs 12F, 13A).

The lateral side of the calcaneum is occupied by a deep, vertically elongated depression (= lateral epicondylar depression) (Fig. 13E). Ante-

riorly, the strongly convex calcaneal condyle extends upwards covering the anterior surface of the knoblike distal end of the fibula. This is the only place where faint lines, marking boundaries between these bones, are visible.

Pes. — Two phalanges of the left pes have been found. One of them is IV-1 while another most probably represents phalanx II-2. Phalanx IV-1 is short and stout with a subquadrate, concave proximal articular surface. Its distal end bears a shallow, broad intercondylar groove; the lateral condyle is larger than the medial. Collateral fossae are about equally deep. The extensor surface bears a deep depression at the distal articular surface.

The other phalanx, supposedly representing phalanx II-2, is about as long as phalanx IV-1 but much more slender; such proportions are often found in the second pedal digit of 'carnosaurs'. The proximal end of the phalanx is deep and narrow, the ridge on the articular surface is very low, indistinct and divides the surface almost symmetrically. On the extensor surface, the proximal end is thickened in the middle and significantly extended posteriorly. The distal articular end is narrower dorsally than ventrally, and is widely and very shallowly grooved. Collateral fossae are about equally deep.

Comparisons

Mandible. — The preserved mandibular parts in *Bagaraatan ostromi* are close in size to those in specimens YPM 5232 (dentary and articular) and YPM 5234 (surangular) of *Deinonychus antirrhopus* (Ostrom 1969). However, comparing these two species one notices that the mandible in *B. ostromi*, although similar in the depth of its dentary, is much more robust and thicker labiolingually and its adductor portion is deeper, the dorsal and ventral margins of the postdentary portion diverging distinctly forwards in front of the glenoid region. Unlike most other theropods, there are two surangular foramina in *B. ostromi*. The retroarticular process is short and and bears dorsally an oblique, posteroventrally slanting surface. Although short, the process is somewhat better developed than in *Dromaeosaurus albertensis* (Currie 1995) and in other avetheropodans, except the avimimids and oviraptorids. The similarly shaped retroarticular process is present in the ceratosaurian *Dilophosaurus wetherilli* Welles 1984.

The shallow, parallel-sided dentary of *B. ostromi* resembles in its proportions the dentary in the dromaeosaurids (Ostrom 1969; Colbert & Russell 1969; Sues 1977; Currie 1995, Barsbold & Osmólska in preparation). However, the dromaeosaurid mandible is thin, never expanded labiolingually along its dentigerous portion, straight rather than curved upwards, and the teeth are more compressed. All dentary teeth are about equal in size in the dromaeosaurids, while in *B. ostromi* the fifth one was probably larger (?fanglike). In the dromaeosaurids, the anterior margin of

the mandible is usually rounded rather than sharply and obliquely cut off as is the case in *B. ostromi*. The Meckelian groove (anterior to the contact with the splenial) is deep and runs almost medially in *B. ostromi*, over a distance not longer than three successive teeth, while it runs close to the ventral mandibular border and along at least five teeth in all adequately known dromaeosaurids.

Robustness of the dentary in *B. ostromi* and its oblique anterior end much resemble larger dentaries in some tyrannosaurids, e.g. in *Maleevosaurus novojilovi*, a specimen considered by Rozhdestvensky (1965) as a juvenile of *Tarbosaurus bataar*. The anterior extremity of the dentary is also somewhat thickened labiolingually in *T. bataar*, although in relation to its much larger size this thickening is not so large as in *B. ostromi*. The anterior dentary — dentary juncture was stronger in tyrannosaurids.

The recently described new Asian theropod, *Sinraptor dongi* Currie & Zhao 1993, has a similarly low dentary with poorly defined interdentary symphysis (Currie & Zhao 1993). However, its anterior margin is less angular than that in *B. ostromi* and it lacks the sharp, oblique labial ridge on the anteriormost part of the dentary, which seems to be a unique character of *B. ostromi*.

Interdental plates in *B. ostromi* are like those described and illustrated by Currie (1987: fig. 3D–E) in the dentary fragment assigned to *Dromaeosaurus albertensis* Matthew & Brown 1922, except that in the Mongolian species, the interdentary plates are entirely distinct elements. In this respect they are like interdental plates in the tyrannosaurids and allosaurids.

As in *B. ostromi*, the angular does not wrap around the ventral mandibular border in the tyrannosaurids (Russell 1970), allosaurids (Madsen 1976) and ceratosaurians (Welles 1984). In some dromaeosaurids (*Dromaeosaurus albertensis*: Colbert & Russell 1969; Currie 1995; *Velociraptor mongoliensis*: personal observation) the posterior process of the angular participates to a lesser extent in formation of the labial mandibular wall and it excludes the prearticular from most of the ventral margin of the lower jaw. However, inspecting casts of the respective bones of *D. antirrhopus*, I noticed that the posterior process of the angular is very similarly shaped as that in *B. ostromi* and it probably did not invade the lingual wall of the jaw, contrary to Ostrom's reconstruction (1969: fig. 16).

The presence of two prominent glenoid processes on the surangular is a very striking feature of *B. ostromi*. There is only one process in the dromaeosaurids (*Deinonychus*: Ostrom 1969; *Dromaeosaurus*: Colbert & Russel 1969; *Velociraptor*: personal observation), which conforms to the postglenoid process in *B. ostromi*, the lateral socket of the glenoid being bounded anteriorly by a very indistinct thickening on the dorsal margin of the surangular. The surangular in most ceratosaurians shows the well developed postglenoid process and a very weak preglenoid elevation (*Ceratosaurus*: Gilmore 1920; *Dilophosaurus*: Welles 1984), which corresponds to the preglenoid process. On the other hand, both processes seem to be

present in the surangular of *Syntarsus* (Rowe 1989). Construction of the surangular glenoid region in *B. ostromi* resembles that in the tyrannosaurids and allosaurids: two glenoid processes were illustrated in *Tyrannosaurus* (Osborn 1912; Molnar 1991), *Tarbosaurus* (Maleev 1974: fig. 18), *Albertosaurus*, *Daspletosaurus* (Russell 1970) and *Allosaurus* (Madsen 1976) and the preglenoid process is placed in these species close behind the surangular foramen, as in *B. ostromi*. However, it seems that the relative depth of the surangular is smaller in the latter. Two surangular foramina are present also in *S. dongi*, they are, however, not comparable because of their smaller size and different position. Two foramina were also mentioned by Norell & Clark (1992) in an undescribed dromaeosaurid from Mongolia.

Due to its deep, vertically expanded posterior lamina, the prearticular in *B. ostromi* is very different from that known in other theropods. This part of the prearticular is shallow in dromaeosaurids (Ostrom 1969; Currie 1995; Osmólska personal observation); it is also not expanded in *Dilophosaurus* (Welles 1984). The prearticulars is deep posteriorly in *Allosaurus* (Madsen 1976), but there is an embayment in its posterior margin, which seems to lack in *B. ostromi*. The most similar prearticular occurs in *Tyrannosaurus* (Molnar 1991).

The articular in *B. ostromi* is very similar to that in *D. antirrhopus*, although the latter species lacks the rollerlike separation of the glenoidal sockets, and the medial of these sockets is wider and extended mediolaterally rather than oblique. The posterior surface of the articular is relatively narrower and more concave in *D. antirrhopus*, and the tip of the retroarticular process is ventrally more strongly thickened, rounded. The retroarticular process is relatively long in *S. dongi*, however it is differently oriented than in *B. ostromi*. The structure of the articular and of the entire glenoid region are distinctly different in both these species. The retroarticular process is similar in size in *D. wetherilli*, and there is also the oblique dip of the posterior surface of the articular in this species.

Vertebral column. — The thin-walled, hollow caudal centra in *B. ostromi* are very striking. Although hollow centra are not exceptional in theropods, being considered as one of theropod synapomorphies (Sereno *et al.* 1993), the wall thinness in the caudal centra in *B. ostromi* (e.g. as compared with very hollow centra in ornithomimids) seems unusual. Bonaparte (1986) described a system of pneumatic cavities in the presacral vertebrae of *Piatnitzkysaurus floresi* Bonaparte 1986, which is especially extensive in the arch but less so in the centrum. He did not mention any pneumaticity in caudals. In caudals of *B. ostromi*, there seems to be only one central cavity in the arch; on the contrary, the hollow which pervades almost the entire caudal centrum is not comparable to the rather limited pneumaticity of the centra in *P. floresi*.

The proximal caudals in *B. ostromi* differ from those in most other theropods in several features. First, the shape and direction of the proximal caudal prezygapophyses, which are sturdy but short and subvertically

oriented (they do not almost extend beyond the centrum margin) and have a peculiar angular lateral surface. Prezygapophyses in *D. antirrhopus*, although also steeply dorsally directed in proximal caudals, are quite different, being slender and much longer relative to the centrum size; they do not display any ridge on their lateral surface, which gives the characteristic, angular appearance to the prezygapophyses in *B. ostromi*. This peculiar appearance is also absent in the Mongolian dromaeosaurid, *V. mongoliensis* (personal observation). Besides, in the latter species the prezygapophyses of the most proximal caudals are more slender and more anteriorly, than vertically, directed.

The neural spines in the proximal caudals in *T. bataar* (comp. Maleev 1974: fig. 26) have a slightly similar shape, also exposing a posteriorly extended distal portion, comparable to that in *B. ostromi*. The spines are, however, not rounded dorsally but angular, and not inclined posteriorly in *T. bataar*. There is a similarity between both these species in the very long and shallow neural spines of distal caudals. However, spines in *B. ostromi* are distinctly longer, overhanging about a quarter of the succeeding caudal, while in *T. bataar* they protrude only slightly beyond the posterior boundary of their own centra.

Zhao & Currie (1993: fig. 3) illustrate proximal caudals in *Monolophosaurus jiangi* Zhao & Currie 1993, which display short prezygapophyses, similarly shaped to these in *B. ostromi*, although it seems that their lateral surface do not bear any ridge.

The hyposphene–hypantrum articulation so far has been rarely reported in theropod caudals. Exceptions are *D. wetherilli* (Welles 1970), in which it is present at least in 6 proximal caudals (Welles 1984), *M. jiangi*, in which it is found 'at the base of the tail' (Zhao & Currie 1993: p. 2033) and *S. dongi* in which this articulation is 'not found in mid or distal caudals' (Currie & Zhao 1993: p. 2064); according to Currie & Zhao (1993: p. 2063) 'hyposphenes do not presist into the tail of *Allosaurus* as they do in more primitive forms like *Monolophosaurus* and *Sinraptor*'. In *B. ostromi*, hyposphenes seem more stout than in any of these species; most probably they occurred also in a longer series (at least 16) of the proximal caudals. Maleev (1974) mentions presence of supplementary articulations only between dorsals in *T. bataar*, although it occurs also in caudals (personal observation).

Chevrons in *B. ostromi* generally resemble chevrons in many theropods, e.g. the ornithomimids, tyrannosaurids and allosaurids. However, the anterior and posterior grooves seem to be more extended distally than they are in *Gallimimus bullatus* or *A. fragilis* (Madsen 1976: pl. 37). In the latter species, the vertically elongated chevrons seem to occur over the longer division of the proximal caudal series, the 20th chevron being still long (Madsen 1976).

Appendicular skeleton. — The ilium in *B. ostromi* is distinctive among theropods, because of peculiar depressions present on its lateral surface. A similar, but single, deep fossa marking the site of origin of the m.

iliofemoralis, was reported in some ceratosaurians (*Coelophysis, Syntarsus:* Row & Gauthier 1990). Depressions on the lateral surface of the ilium, one on the preacetabular and the other on the postacetabular process, were reported in some Jurassic theropods: *Stokesosaurus clevelandi* Madsen 1974, *Iliosuchus incognitus* Huene 1932 (Galton 1976) and *P. floresi.* In these cases depressions are separated by a vertical ridge running between the acetabular and dorsal margins of the iliac blade. Traces of a similar ridge are also present in *Tyrannosaurus* (Romer 1923) and were interpreted by Russell (1972) as a boundary between origins of two heads of the m. iliofemoralis. If a similar ridge were present in *B. ostromi* (this region is not adequately preserved in this species), the postacetabular depression would conform to two depressions present on the postacetabular blade in *B. ostromi.* The postacetabular portion of the ilium is much shorter and deeper in both compared species than in *B. ostromi.* A similar, long postacetabular process of the ilium and well developed, although much broader, brevis fossa is found in the ornithomimids (Osmólska *et al.* 1972). In this group, the medial blade on the preacetabular process is also similarly strong as in the species described here. The ornithomimid ilium is, however truncated posteriorly, not rounded (Barsbold & Osmólska 1990) as it probably was in *B. ostromi.*

The ilium in the opisthopubic pelvis of the dromaeosaurids also displays the relatively long postacetabular process, but this process seems to be relatively deeper and longer in *D. antirrhopus* and *V. mongoliensis,* although not in *Adasaurus mongoliensis* Barsbold 1983.

The pubis in *B. ostromi* generally resembles that in most propubic theropods, except for the lack of the bony 'apron'. As far as it can be compared, the greatest resemblance is to the ornithomimid pubis. From the pubis of the allosaurids (*A. fragilis*) and tyrannosaurids (*T. bataar*), this in *B. ostromi* differs mainly in being much more slender, and less concave anteriorly in lateral view, which is probably due to the smaller size of the animal. The ischiadic process is relatively shorter in *B. ostromi* than in these two species.

In spite of limited possibilities in comparing the ischium of *B. ostromi* with that in other theropods, some unique features may be observed. To my knowledge no other advanced theropod has the low, medial wall on the pubic process, which to a slight degree medially bounds the acetabulum. The deeply concave sutural surface of the iliac process displayed by the ischium in *B. ostromi* seems also to be a feature rarely observed; however, Maleev (1974: p. 170) mentions a deeply concave surface for the ischiadic peduncle of the ilium in *T. bataar.*

Although the femur in *B. ostromi* was most probably relatively shorter and certainly more slender than that in *T. bataar*, the articular ends of these femora are roughly similar in both species, although the anterior extension of the greater trochanter is much stronger in *B. ostromi*, incomparable to any other theropod. In both species the lesser trochanter is almost as high as the greater trochanter; that in *T. bataar* is, however

aliform, not finger-shaped as in *B. ostromi*. The dorsomedial inclination of the femoral head in respect to the long axis of the shaft is also similar in both species. The distinctive tibiofibular crest is also present in *T. bataar*, being especially distinct in smaller individuals of the latter species. This crest is, however, much thicker lateromedially and delimited distally by the sulcus in *B. ostromi* and its distance from the medial condyle is much smaller than in *T. bataar* and, to my knowledge, any other theropod.

The femur of *B. ostromi* might have had similar proportions to that in *D. antirrhopus*. The lesser trochanter in the latter species is also as high as the greater trochanter, finger-shaped, and not separated from the greater trochanter. In the American species both trochanters are placed on the same level with the femoral head, while they are somewhat below the head in the Mongolian species, due to the mediodorsal inclination of the femoral neck. In *B. ostromi*, the protuberance placed posteriorly on the lateral surface of the femur, below the greater trochanter, seems homologous to the element described by Ostrom (1976) as the 'posterior trochanter'. The latter was interpreted by Ostrom as a possible insertion of the m. ischiotrochantericus. The separate tibiofibular crest lacks in *D. antirrhopus*.

There is a great resemblance between the femur in *B. ostromi* and the femur PIN 2549-100 determined by Kurzanov (1987: fig. 36) as belonging to the 'avimimid from the late Cretaceous locality Iren Nor (China)'. Both femora have similarly shaped proximal and distal ends, although the femur was probably relatively shorter in *B. ostromi*. The similarity is apparent in the well pronounced articular heads and femoral necks, the poorly delimited lesser trochanters, which are as high as the greater, and in the presence of the protuberances on the lateral surface. Contrary to Ostrom (1976), Kurzanov (1987) considers this protuberance as the insertion of the m. iliotrochantericus. As mentioned by Ostrom (1976), the trochanteric protuberance occurs on many other theropod femora. The distal ends of femora are also similarly shaped in both compared forms. They have distinctive tibiofibular crests ('condylus lateralis' in Kurzanov 1987), although that in *B. ostromi* is larger, and laterally extended posterior parts of the lateral condyles ('condylus accessorius' in Kurzanov 1987), the extension being smaller in *B. ostromi*. Due to the thicker tibiofibular crest, the popliteal fossa is much narrower in the latter species. Although the distal end of the femur is generally similar (but without the distinctive tibiofibular crest) also in *A. portentosus* (Kurzanov 1987: fig. 19), its proximal end is incomparable, mainly due to the well separated lesser trochanter and the relatively well developed trochanteric shelf in the latter species. The distal articular end of the femur in *Mononykus olecranus* Perle *et al.* 1993 is slightly resemblant to that in *B. ostromi*, especially in the narrowness of the popliteal fossa (Perle *et al.* 1994: fig. 16E). However, the articular surface for the fibular head is less deep, and the 'ectcondylar tuber' (the structure considered by Chiappe in

Perle *et al.* 1994 as the precursor of the tibiofibular crest) less distinctive and differently shaped in *M. olecranus.*

Some ceratosaurians (*Syntarsus, Ceratosaurus, Dilophosaurus*) have the well developed tibiofibular crest, the base of which is laterally and distally delimited by a deep sulcus. In *B. ostromi,* the crest and the sulcus are similar as in *Ceratosaurus* (Gilmore 1920: pl. 4); the crest is even better developed in the Mongolian species and the distance separating it from the medial condyle is much shorter. The anterior crest present below the lesser trochanter in *B. ostromi* is a peculiar feature of this species, which, to my knowledge, does not occur in other theropods.

The slenderness of the crus is very striking in *B. ostromi.* The incompleteness of the skeleton makes it difficult to evaluate the relative length of the tibia. Nevertheless the latter seems to be exceptionally long: the length of the tibiotarsus almost equals almost the combined lengths of 9 proximal caudals. Similar proportions are found in the skeleton of the young individual of the ornithomimid *G. bullatus* (ZPAL MgD-I/94: tibiotarsus length 306 mm; comp. Osmólska *et al.* 1972). In the young individual of *T. bataar* (ZPAL MgD-I/3) this length (560 mm) equals to that of only 6 proximal caudals (K. Sabath, personal information). The bowing of tibia is, to my knowledge, an exceptional feature of *B. ostromi.*

The proportions of both shin bones are, to some extent, similar in the dromaeosaurids (*D. antirrhopus* — Ostrom 1969: figs 66, 67). As compared with the tibia of *D. antirrhopus* specimen AMNH 4371 (Ostrom 1976), that in *B. ostromi* is 15% longer but narrower across the distal end. The proximal articular surface of the tibia is similarly shallowly incised posteriorly in *D. antirrhopus,* but the lateral cnemial crest is not distinguished in the latter species, while the cranial crest is extended in the more anterior direction than in *B. ostromi.* The distal end of fibula is not deflected laterally in *D. antirrhopus* and *M. novojilovi* but it is in *T. bataar* (Maleev 1974: fig. 42). The proximal articular end is similar in *M. novojilovi* (Maleev 1974: fig. 61A) and, to some extent, also in *A. fragilis* (Madsen 1976: pl. 52D), because there are two cnemial crests in these species (Molnar *et al.* 1990: fig. 6.23), although the lateral crest is much less distinct in *A. fragilis.*

The fibula is similar to that in most other theropods, and especially to the fibula in *D. antirrhopus.* The only significant differences concern the proximal end which expands more rapidly upwards, and the triangular (*versus* rounded in *D. antirrhopus*) cross section of the distal portion of the fibula in *B. ostromi.* The proximal half of the shaft is also relatively more massive in the latter species than in *D. antirrhopus.*

As a rule, the tibia and fibula are not fused in theropods, except in ceratosaurians. However, according to the drawing in Maleev's (1974: fig. 61B) paper, the astragalus and calcaneum seem fused in *M. novojilovi;* it should also be mentioned that the tibia is 10% longer than femur in this species. Rowe (1989) and Rowe & Gauthier (1990) considered fusion of tibia, proximal tarsals and fibula as one of synapomorphies of the Cerato-

sauria. In the latter group, however, the same astragalar process is overlapped by the expanded distal end of the fibula, which is not the case in *B. ostromi*.

Relationships

A large part of the specimen here described is represented by the tail. However, detailed descriptions or illustrations of caudals are rare in theropod literature, and comparisons of *B. ostromi* with other theropods are limited in this respect. Examination of the caudals of some Late Cretaceous Mongolian theropods available to me (*T. bataar*, *V. mongoliensis*, *G. bullatus*, and *Ingenia yanshini* Barsbold 1981) shows that caudals in *Bagaraatan* are in many details extraordinary. The extremely thin-walled centra, the massiveness and extensive persistence of the hyposphene — hypantrum articulation, the laterally angled prezygapophyses, the rough and expanded neural spines, the dorsal depressions at the bases of proximal transverse processes form a suite of features autapomorphic to this taxon.

There is a number of features in *Bagaraatan* which are found also among the Ceratosauria. These are: the presence of one enlarged tooth in the mandible, the slightly elongated retroarticular process, the week fibular crest, the fibula fused distally with the tibiotarsus, the coossified astragalocalcaneum and the sulcus laterally separating the base of the tibiofibular crest from the fibular condyle. However, the above mentioned characters of the mandible do not have much significance for evaluating phylogenetic relationships, as they are theropod plesiomorphies. The same is true for the crural features: the first of them is evidently plesiomorphic for theropods, while the two others are found sporadically in different theropods and may be homoplasies. The only character common to the Ceratosauria and *Bagaraatan*, which might be considered as a synapomorphy, is the unique condition of the tibiofibular crest, but it seems more parsimonious to consider it as a homoplasy.

Among the less obvious similarities between *Bagaraatan* and the ceratosaurians one can mention the depressions on the postacetabular part of ilium in *Bagaraatan*, which might correspond to the lateral fossa on the iliac blade in *Syntarsus* and *Coelophysis* (Rath 1969: fig. 4B; Rowe & Gauthier 1990). However, the homology of these two structures looks doubtful. Strong fusion of sacral ribs with ilia, as well as the partial fusion of pubis and ischium in *Bagaraatan* might be also considered as cerato-saurian features; the fusion between particular pelvic bones and between the pelvis and sacrum is considered (Rowe & Gauthier 1990) as a synapomorphy of the Ceratosauria. However, the lack of anterior bowing of the pubis, and of the obturator foramen, characters occurring in the cerato-saurians, make the pelvis in *Bagaraatan* as a whole quite distinct from that in the ceratosaurians.

To sum up, most characters which *Bagaraatan* has in common with the Ceratosauria seem to represent either symplesiomorphies or homoplasies, hence it is more reasonable to consider this 'stiff-tailed' theropod as a tetanuran rather than a ceratosaurian. Unfortunately, most of the tetanuran synapomorphies, as indicated by Gauthier (1986) and revised by Holtz (1994), could not be determined in *B. ostromi*, because of incompletness of its skeleton. The astragalus bears the horizontal groove on its anterior face as in the Tetanurae, but the fibular crest on the tibia is very weak.

Provisionally it can be assumed that *Bagaraatan* is a member of the Avetheropoda Paul 1988 (*sensu* Holtz 1994), because it displays some synapomorphies of that grouping: the loss of the obturator foramen, the lesser trochanter proximally placed, the position of the cnemial crest. Any more precise assignment of *Bagaraatan* within the Avetheropoda is at the moment difficult and must wait until more complete material is found. It should be emphasized here that although some features of the mandible and the general shape of the long and slender shin bones of *Bagaraatan* resemble those of the dromaeosaurids, the propubic pelvis and the structure of the caudals, as well as the lack of ossified caudal tendons, render any close relationship of *Bagaraatan* with the Dromaeosauridae improbable. As was demonstrated above, *Bagaraatan* was primitive in many respects and it would be tentatively better understood as a sister taxon to the Allosauridae + Coelurosauria (both *sensu* Holtz 1994).

Some functional aspects of the skeleton

Bagaraatan ostromi (Fig. 1) was a theropod of moderate size by dinosaurian standards and its total length has been approximated 3.0–3.5 m, and its height at the hips less than 1 m. Judging by the size of the mandible, the skull was relatively small, hence the neck was probably rather slender. These arbitrary estimations depict *B. ostromi* as a theropod comparable in size to large *D. antirrhopus* specimens. In spite of its moderate size, the skeleton described in the present paper must have belonged to an adult, maybe even an old animal, as evidenced by the strong fusion between sacral ribs and ilium and the coossification of shin bones with proximal tarsals; the probable presence of the antarticular in the mandible also speaks in favor of the maturity of this individual.

The powerful, although relatively slender, mandible with strong teeth and the long, slim tibiotarsus indicate that *B. ostromi* might have been a long-legged, rather agile predator (?scavenger), even though the tibia/femur ratio cannot be presently determined with confidence.

The tail had to be relatively rigid along most of its length. Its structure is highly specialized and in its proximal section not comparable to other theropods. The long, thick hyposphenes, tightly fitted between the hypantra and persisting in the prolonged series of proximal caudals, most probably prevented dislocation of the proximal caudals and at the same

time permitted only a much limited degree of flexion, both in the horizontal and the vertical plane. Therefore, if there was any possibility of more significant lateral and vertical flexion of the tail, it had to take place between the tail and sacrum or close to the sacrum, within the missing portion of the caudal series. Rough and thickened posterior and anterior margins of the neural spines evidence very strong interspinal ligaments. Ridges on the lateral surface of prezygapophyses may represent sites of attachment of tendons possibly derived from parts of the epaxial musculature (e.g.: mm. spinoarticularis and articulospinalis). Tendons of the spinoarticular muscle might originate at the prezygapophyseal ridges and insert into the rough sides of the neural spines, those of the articulospinal muscle *vice versa* (Slijper 1946). The strongly posteriorly inclined spines make it highly probable that the articulospinal muscle was better developed in this region than the spinoarticular muscle (Slijper 1946). In relation to the adaptations present in the proximal series of caudals rendering the tail relatively rigid, it is more probable that fascicles of these muscles were transformed into tendons, paralleling the ossified tendons present in some ornithopods (Galton 1974; Norman 1980).

The more distal caudals have somewhat elongated zygapophyses and chevrons and this region of the tail resembles that in many other tetanurans with a relatively rigid distal part of tail, e.g. the tyrannosaurids.

The function of the peculiar tail structure in B. *ostromi* is difficult to explain. Nothing indicates that the presacral part of the body was especially heavy; the low ilium and slender legs speak rather in favor of a relatively gracile thorax. Thus, it seem unlikely that the tail served exclusively as a counter-balance, although it probably was massive and muscular. More likely its rigidity was a modification for speed (comp. Molnar & Farlow 1990).

Other functional dilemmas are the evidently overgrown musculature on the ilium, at least on its postacetabular portion, and the anteroproximal crest on the femur, below the lesser trochanter, which bears the distinct scar for muscular or ligamental attachment and is absent in other dinosaurs. It seems most reasonable to relate this scar with an insertion of a muscle which abducted and protracted the femur. Hence, the m. puboischiofemoralis (pars dorsalis) is the most probable choice, because a roughly similar location (cranial and dorsal) of the insertion area of this muscle is found in crocodilian femora (Rowe 1986). However, neither in crocodilians nor in other theropods has the insertion site a crestlike form.

Comparison with other reptiles shows that the two depressions present on the postacetabular process of the ilium most probably served as origin sites of two separate heads of the m. iliofemoralis or, the anterior of the two served as origin of the m. iliotrochantericus. The dorsomedially inclined femoral head shows that the femur was probably directed laterodistally. Unfortunately, deficiency of preservation of the acetabulum does not allow one to fit the femoral head in the hip socket, which would provide better information about the femur position. It cannot be stated whether

the femur was bowed. However, the medially concave tibiotarsus deserves attention, as this curvature brought the pes close to the sagittal plane, hence beneath the center of gravity of the animal. This would compensate the assumed laterodistal deviation of the femur from the sagittal plane.

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Streszczenie

W pracy opisano nowego mięsożernego dinozaura *Bagaraatan ostromi* gen. et sp. n. (Theropoda). Okaz obejmujący żuchwę, serię 25 kręgów ogonowych, fragmenty kości miednicy oraz kończyny tylnej, został znaleziony w osadach formacji Nemegt (?środkowy mastrycht) Kotliny Nemegt (Pustynia Gobi, Mongolia) przez Polsko-Mongolską Ekspedycję Paleontologiczną, w 1970 roku. Zachowane szczątki świadczą, że *B. ostromi* był teropodem ok. 3.0–3.5 m długim, o smukłych kończynach tylnych i usztywnionym ogonie. Długość żuchwy wskazuje, że czaszka była stosunkowo niewielka. Żuchwa jest masywna i zaopatrzona była w silne zęby, z których zachowały się tylko korzenie i podstawy koron. Jej część tylna jest dość wysoka i przypomina żuchwy teropodów zaliczanych do polifiletycznej grupy „Carnosauria", różni się jednak od nich bardziej wydłużonym wyrostkiem pozastawowym i dwoma, zamiast jednego, otworami w kości nadkątowej. W odróżnieniu od większości znanych teropodów, u których najwyżej tylko kilka przednich kręgów ogonowych wykazuje obecność dodatkowych wyrostków (hyposfenów) wzmacniających połączenia międzykręgowe, u *B. ostromi* wyrostki te występują miedzy kilkunastoma proksymalnymi kręgami ogonowymi, co ograniczało ruchomość ogona także w tym odcinku. Kość biodrowa *B. ostromi* wyróżnia się obecnością dwóch zagłębień na bocznej stronie wyrostka zapanewkowego, zapewne dla przyczepu bardzo silnego mięśnia biodrowo-udowego. Takie zagłębienia nie są znane u żadnych innych dinozaurów. W budowie podudzia zwraca uwagę częściowy zrost kości piszczelowej i strzałkowej ze sobą oraz z proksymalnym rzędem kości stępu. Zrost tych kości spotykany jest tylko w jednej, prymitywnej grupie teropodów, Ceratosauria, od której jednak *B. ostromi* różni się szeregiem zaawansowanych cech. Fragmentaryczność materiału, a zwłaszcza brak czaszki i kończyn przednich, sprawiają trudność w zaliczeniu *Bagaraatan* do jednej ze znanych jednostek taksonomicznych w obrębie Theropoda. Jednak pewne cechy diagnostyczne wskazują, że rodzaj ten jest przedstawicielem Tetanurae Gauthier 1986 i jest najbliżej spokrewniony z Avetheropoda Paul 1988, aczkolwiek jest od nich prymitywniejszy.