

THE UNIVERSITY of EDINBURGH

Edinburgh Research Explorer

Reassessment of the enigmatic Late Cretaceous theropod dinosaur, Bagaraatan ostromi

Citation for published version:

Slowiak-Morkovina, J, Brusatte, S & Szczygielski, T 2024, 'Reassessment of the enigmatic Late Cretaceous theropod dinosaur, Bagaraatan ostromi', *Zoological Journal of the Linnean Society*. https://doi.org/10.1093/zoolinnean/zlad169

Digital Object Identifier (DOI):

10.1093/zoolinnean/zlad169

Link:

Link to publication record in Edinburgh Research Explorer

Document Version: Peer reviewed version

Published In: Zoological Journal of the Linnean Society

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Reassessment of the enigmatic Late Cretaceous theropod dinosaur, *Bagaraatan ostromi*.

3	
4	Justyna Słowiak-Morkovina ¹ *, Stephen L. Brusatte ² , Tomasz Szczygielski ¹
5	
6	¹ Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.
7	² School of GeoSciences, University of Edinburgh, Edinburgh, United Kingdom.
8	
9	* Corresponding author: Justyna Słowiak-Morkovina ¹
10	Twarda 51/55, Warsaw, 00-818, Poland
11	Email address: justyna.slowiak@twarda.pan.pl
12	
13	Short running title: Reassessment of Bagaraatan ostromi.
14	FUNDING
16	This work was supported by the National Science Centre, Poland, grant no. 2019/35/B/NZ8/02292.
17	SLB's work on Nemegt theropods stems from his PhD at Columbia University and the American
18	Museum of Natural History, supervised by Mark Norell, whom he thanks for his friendship and
19	mentorship over the years. SLB was supported by a National Science Foundation Graduation
20	Research Fellowship, National Science Foundation Doctoral Dissertation Improvement Grant
21	(DEB 1110357), Columbia University, and American Museum of Natural History.
22	
23	AUTHORS' CONTRIBUTIONS
24	JSM conceived the study, wrote the initial manuscript, prepared the 3D models and figures; SLB
25	performed the phylogenetics analyses, revised the manuscript; TS helped in the taxonomical
26	interpretation of the data, photographed the specimens, revised the manuscript. All authors
27	discussed the results and contributed to the final manuscript.
28	
29	ACKNOWLEDGEMENTS
30	The presented material was collected during the Polish-Mongolian Paleontological Expeditions
31	organized by the Mongolian and Polish academies of sciences in the late 1960s and early 1970s.
32	This research was possible thanks to the work of all members of the expeditions, whom we would
33	like to acknowledge. We are grateful to Khishigjav Tsogtbaatar for the possibility to work on the
34	Tarbosaurus material housed in the Institute of Paleontology of the Mongolian Academy of
35	Sciences. JSM thanks Sanjaadash Ulziitseren, Damidansuren Idersaikhan, Zorig Enkhtaivan,
36	Chagnaadorj Bayardorj, and Bat-Erdene Erdenekhuyag for all their help during the research visit.
37	The manuscript benefited from input by Greg Funston and one anonymous reviewer. We thank
38	the Editor for processing the manuscript. We would like to thank Krzysztof Owocki for sharing
39	the thin section taken from the femur of ZPAL MgD-I/108 and Katarzyna Przestrzelska for the
40	accurate preparation of the caenagnathid vertebra. We also thank Boris Morkovin and Andrey

Podlesnov for sharing the photographs of *Avimimus portentosus* PIN 3907/1 and 3907/6. SLB thanks Peter Makovicky for the discussion on *Bagaraatan* while doing his PhD work, and acknowledges that he also independently came to the conclusion that the material represented a chimera of multiple theropods. SLB also thanks Grzegorz Niedźwiedzki, Tomasz Sulej, Jerzy Dzik, Magdalena Borsuk-Białynicka, and Zofia Kielan-Jaworowska for hosting him at the ZPAL collections over the years, and for their friendship and hospitality. We thank Jakub Zalewski, who prepared the life reconstruction of *Bagaraatan ostromi*.

51

52

53 54

Reassessment of the enigmatic Late Cretaceous theropod dinosaur, *Bagaraatan ostromi*.

ABSTRACT

The Late Cretaceous Bagaraatan ostromi, described by Osmólska in 1996, is one of the most 55 enigmatic theropod dinosaurs. The holotype possesses a peculiar combination of features, which 56 57 Osmólska suggested were indicative of a primitive position among theropods that could not be 58 further resolved. Other researchers have argued point to affinities with either derived bird-like 59 coelurosaurs or tyrannosaurids. We here reanalyze all material collected by Osmólska, which 60 reveals it to be a chimaera of multiple theropod taxa. The femur, tibiotarsus, one pedal phalanx, 61 and most of the bones undescribed in Osmólska's paper are identified as Caenagnathidae indet. 62 The mandible, cervical vertebrae, pelvis, tail, and one pedal phalanx-which we consider the 63 holotype of *B. ostromi*—show tyrannosaurid affinities, which are here supported by phylogenetic 64 analyses. We find only two potentially unique diagnostic features of the *Bagaraatan* holotype: double surangular foramina and a horizontal ridge on the lateral surface of the postacetabular 65 process of the ilium. Both, however, may be ontogenetically or intraspecifically variable, and thus 66 67 we conclude that the holotype of *B. ostromi* represents an indeterminate tyrannosaurid. The small 68 size of the holotype, and its possession of many features known to characterize juvenile 69 Tyrannosaurus rex, indicate that the skeleton belongs to a juvenile, which is one of the smallest juvenile tyrannosaurids currently known. 70

71

KEYWORDS ontogeny, Tyrannosauridae, juvenile, revision, holotype designation, genus revision73

ABBREVIATIONS: CMNH: Cleveland Museum of Natural History, Cleveland, Ohio, USA; LH:
Long Hao Institute of Geology and Paleontology in Hohhot, Inner Mongolia, China; MPC-D:
Mongolian Paleontological Center, Ulaanbaatar, Mongolia; PIN Paleontological Institute,
Moscow, Russia; ROM: Royal Ontario Museum, Toronto, Ontario, Canada; TMP: Royal Tyrell
Museum of Palaeontology, Drumheller, Canada; UALVP: University of Alberta Laboratory for
Vertebrate Paleontology, University of Alberta, Edmonton, Alberta; ZPAL Institute of
Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

81 82

INTRODUCTION

83 In 1996, Halszka Osmólska described and named a new species of a theropod dinosaur, Bagaraatan ostromi, based on a bone association collected in 1970 in the Nemegt Formation of 84 Mongolia by the Polish-Mongolian paleontological expeditions (ZPAL MgD-I/108). The 85 incomplete skeleton, estimated to belong to a moderately-sized carnivore that was 3.0-3.5 meters 86 87 long, included a partial mandible and the hind part of the body (pelvis, hind limb, and proximal tail), and was described by Osmólska (1996) as showing a mosaic of features that made it 88 89 impossible to determine its relationship with other theropods. She pointed out similarities with Dromaeosauridae (i.e., general structure of the mandible and slenderness of the hind limb), but 90 91 noticed that the presence of the propubic pelvis, short caudal prezygapophyses, and lack of ossified

92 caudal rods distinguishes it from dromaeosaurids. She also discussed affinity with tyrannosaurids,

93 due to the features of the mandible (i.e., shape and robustness of the anterior end, two glenoid

94 processes), but noted that the femoral trochanters are different in *B. ostromi* in contrast to

95 tyrannosaurids. Because of this unusual combination of features, Osmólska (1996) tentatively

96 considered *B. ostromi* to be a medium sized tetanuran with 'primitive' characteristics, and a 97 probable sister taxon to the Allosauridae and Coelurosauria. This placement, however, was not the

98 result of a phylogenetic analysis.

Later authors continued to be confused by the skeleton of *B. ostromi*. For example, Csiki and
 Grigorescu (1998) noticed similarities in the hind limb structure between *B. ostromi* and theropod

101 hind limb material from the Hateg Basin of Romania (*Bradycneme draculae* Harrison & Walker,

102 1975 and *Elopteryx nopcsai* Andrews, 1913), i.e., fusion of the tibia and proximal tarsals, presence

103 of a horizontal groove on the anterior surface of the astragalus, presence of a lateral tubercle on 104 the femoral lateral articular condyle, and the femoral head positioned above the greater and lesser

105 trochanter. *Br. draculae* and *E. nopcsai* were identified by Csiki and Grigorescu (1998) as a non-

106 coelurosaurian tetanuran and a maniraptoran, respectively. The authors proposed that those

107 species, together with *B. ostromi*, may represent a new clade of peculiar small theropods fairly

108 closely related to birds, also including the 'Iren Nor avimimid' PIN 2549/100 (Kurzanov, 1987;

109 Csiki & Grigorescu, 1998).

110 The idea that *B. ostromi* belonged to a clade of small, derived theropods was raised again with the

111 description of Xinjiangovenator parvus Rauhut & Xu, 2005, known from a partial articulated

112 hindlimb. This species was proposed as closely related to B. ostromi, forming a poorly known

113 Asian lineage of coelurosaurs (Rauhut & Xu, 2005). Subsequently, Br. draculae was identified as

an indeterminate representative of Maniraptora, E. nopcsai was recognized as a troodontid or a

- non-ornithuromorphan pygostylian bird (Naish & Dyke, 2004), the 'Iren Nor avimimid' was
- revealed to be a troodontid (Currie & Peng, 1993), and *X. parvus* was placed in a polytomy with

117 other basal Coelurosauria (Choiniere *et al.*, 2010). Indeed, the earliest phylogenetic analyses in

118 which *B. ostromi* was included placed it as a sister taxon to the derived coelurosaurian clade

- 119 Maniraptoriformes (Holtz, 1998), or even within the Maniraptora (Rauhut, 2000; Rauhut *et al.*,
- 120 2010), quite closely related to birds.

121 Some authors, however, noted striking similarities between *B. ostromi* and tyrannosaurids. Holtz

122 (2004) claimed that the prominent and laterally expanded surangular shelf, reduced and broadened

123 retroarticular process, and the presence of a ventral flange on the ischial peduncle of the pubis are

shared between *B. ostromi* and tyrannosaurids. However, he also pointed out that this comparison

should be treated with caution due to the fragmentary nature of the *B. ostromi* holotype. Later, *B.*

126 *ostromi* was recovered as a basal tyrannosauroid in two phylogenetic analyses (Carr & Williamson,

127 2010; Loewen *et al.*, 2013). In the first analysis, it was found in a polytomy, together with
128 *Iliosuchus incognitus* Huene 1932, *Stokesosaurus clevelandi* Madsen, 1974, *Eotvrannus lengi* Hutt

129 et al., 2001, Aviatyrannis jurassica Rauhut, 2003, and cf. Alectrosaurus sp. (see Carr &

130 Williamson, 2010). The second analysis (Loewen *et al.*, 2013) positioned *B. ostromi* together with

131 non-proceratosaurid tyrannosauroids closer to tyrannosaurids, i.e., *Dilong paradoxus* Xu et al.

132 2004, E. lengi, Raptorex kriegsteini Sereno et al., 2009, and Dryptosaurus aquilunguis (Cope,

133 1866). Thus, for the last two decades, *B. ostromi* has often been presumed to be a tyrannosauroid
134 (Currie, 2003a; Choiniere *et al.*, 2010; Alifanov, 2012; Bell *et al.*, 2012; Dalman, 2013).

135 Recently, however, B. ostromi has been considered a chimera of tyrannosaurid and non-

136 tyrannosaurid bones (Brusatte, 2013; Brusatte & Carr, 2016; Napoli et al., 2021), an intriguing

hypothesis that might explain the 'mosaic' of primitive and derived features noted by Osmólska
(1996). This idea has not yet been supported by careful description, comparisons, and
documentation of each bone of *B. ostromi*.

140 Here, we reassess the material of *B. ostromi* presented by Osmólska (1996). Although Osmólska

- 141 (1996) explicitly noted that there is no doubt that the bones of *B. ostromi* belonged to a single
- 142 individual, unpublished material catalogued under the same specimen number (ZPAL MgD-I/108)
- 143 indicates that the association was a multitaxic assemblage, thus putting the taxonomic identity of
- 144 individual bones into question. Thus, herein we redescribe, revise, and provide documentation of 145 all bones of the association, including the previously unpublished bones, and reassess the status of
- 146 *B. ostromi*. We indeed find that what Osmólska (1996) described as a single dinosaur skeleton is
- 147 actually a chimera of two taxa: an oviraptorosaur and bones belonging to a juvenile tyrannosaurid.

148 With this realization, we clarify the systematics of *B. ostromi* by designating an associated skeleton

in the assemblage as the holotype, discuss features that may support *B. ostromi* as a valid taxon,
but ultimately conclude that it mostly likely is an indeterminate tyrannosaurid due to its juvenile
status, thus removing a genus and species from the roster of Nemegt theropods. The holotype
specimen becomes one of the smallest juvenile tyrannosaurids known, providing valuable
information on tyrannosaurid growth and ontogeny.

- 154
- 155
- 156

MATERIALS AND METHODS

Material

The holotype of Bagaraatan ostromi, ZPAL MgD-I/108, was found in 1970 in Northern Sayr 157 (Nemegt Formation, Late Cretaceous) during the 7th Polish-Mongolian paleontological 158 159 expedition. The specimen was described as a partial skeleton including the mandible, incomplete 160 pelvis, incomplete left hindlimb, and proximal caudal vertebrae. According to Osmólska (1996), 161 the anterior part of the body of ZPAL MgD-I/108 was strongly weathered, thus not collected, but the position of the mandible in the field indicated that it belongs to the same individual as the back 162 163 part of the body. In the field, in the area where the holotype of *B. ostromi* was found, several bones 164 were collected and catalogued under the same specimen number: two cervical and one caudal 165 vertebrae, manus phalanx II-1 and ungual II-3, proximal end of a rib, and a few indeterminate 166 bones. Despite that, Osmólska excluded those bones from the description of B. ostromi (Osmólska's personal notes: 'Found together with B. ostromi but doubtful - not described' 167 [translation from Polish by the authors]). She preliminarily identified those bones as belonging to 168 indeterminate Oviraptorosauria. Unfortunately, no sketch or map of the arrangement of the bones 169 of *B. ostromi* was drafted and no photographs were taken before the excavation of the bones. Thus, 170 171 it is impossible to independently assess the position of the bones assigned to ZPAL MgD-I/108. 172 Herein, we assess all the bones found in the ZPAL MgD-I/108 assemblage, including the 173 undescribed fossils, some of which were used already in phylogenetic analyses (Loewen et al., 174 2013).

175 To account for the multitaxic character of that composite specimen, we redefine ZPAL MgD-I/108 176 as a catalogue number. The mandible, being the first specimen described in detail, figured, and 177 referred to B. ostromi by Osmólska (1996), as well as the most autapomorphic bone in the association, is here assigned the number ZPAL MgD-I/108. We also include the cervical and 178 179 caudal vertebrae and pelvis under this specimen number, as they were apparently found in continuity with the mandible in the field, linked by the eroded remains of the vertebral column 180 181 (Osmólska, 1996: p. 3). The size, preservation, and general phylogenetic affinities of these bones are also consistent with each other, and we consider them to belong to an associated skeleton, 182

which we refer as the holotype of the species *B. ostromi*. Two pedal phalanges were also found in
the assemblage; the size and taxonomic identity of the pedal phalanx IV-1 corresponds to ZPAL
MgD-I/108, and it is assigned to it. We exclude all the non-tyrannosaurid material from the
holotype of *B. ostromi* ZPAL MgD-I/108, and assign it the number ZPAL MgD-I/108/1.

187 188

Methods

189 The material was photographed using a Canon EOS M6 mark II camera. The fossils were also

190 digitalized using a Shining 3D EinScan Pro 2X 3D scanner fixed on a tripod with EinScan Pro 2X

191 Color Pack (texture scans), Ein-Turntable (alignment based on features), and EXScan Pro 3.2.0.2192 software.

193 The anteroposterior diameter of the surangular foramen and the skull length in 38 tyrannosauroid 194 specimens of various body sizes (list in the supplementary material) was measured based on 195 photographs and 3D models or published data in ImageJ 1.53e. The analysis includes ten 196 individuals of Tarbosaurus bataar (Maleev, 1955), Raptorex kriegsteini, ten of Gorgosaurus libratus Lambe, 1914, five of Tyrannosaurus rex Osborn, 1905, six of Daspletosaurus spp., and 197 one of Alioramus altai Brusatte et al., 2009, Qianzhousaurus sinensis Lu et al., 2014, 198 199 Bistahieversor sealeyi Carr & Williamson, 2010, Teratophoneus curriei Carr et al., 2011, and 200 Lythronax argestes Loewen et al., 2013, each. In the case of 'Shanshanosaurus huoyanshanensis' Dong, 1977 and Gorgosaurus libratus TMP 1994.12.155, the mandible length was taken instead 201 202 of the skull length due to lack of complete skulls. The mandible and skull length in T. bataar is 203 reported to be almost equal, ca. 1% of difference between in length between the lower jaw to the 204 length of the skull from premaxilla to occipital condyle (Maleev, 1974) and the skull and mandible in tyrannosaurids grow isometrically (Currie, 2003b). Therefore, we included those individuals 205 206 due to their importance, as they represent small juveniles. R. kriegsteini is not included here within 207 T. bataar; although it was proposed that Raptorex is a juvenile of the latter species (Fowler et al., 208 2023), recently it was once again suggested to be a valid taxon (Carr, 2023). R. kriegsteini still 209 requires a proper description in order to fully understand its affinities within the Tyrannosauroidea. Bagaraatan ostromi ZPAL MgD-I/108 is included, however; the length of the mandible is 210 211 estimated to 30 cm based on the similarly sized specimen of T. bataar MPC-D 107/7 (Tsuihiji et 212 al., 2011). Due to the presence of two surangular foramina in ZPAL MgD-I/108, that specimen is 213 represented on the plots by two points: one for the measurement of the posterior surangular 214 foramen alone, and the second for the measurement of the distance from the anterior margin of the 215 anterior surangular foramen to the posterior margin of the posterior surangular foramen. The 216 Pearson correlation coefficient was calculated in order to determine the linear dependence of the

skull length and the surangular foramen diameter. Then, a regression analysis was performed for 217 218 all tyrannosaurids and separately for the specimen groups of Tarbosaurus, Gorgosaurus, 219 Tyrannosaurus, and Daspletosaurus, to find the relationship between the size of the surangular foramen and the skull length in order to determine possible allometries and quantify the 220 221 classification of the surangular foramen into imprecise size categories ('small', 'medium', and 'enlarged'). Although it is accepted that the small or absent surangular foramen is present in basal 222 223 Tyrannosauroidea, and the enlarged fenestra (approximately 30% depth of the posterior end of the surangular; Carr and Williamson 2010:204; Sereno et al. 2009:52) is present in the 224 Tyrannosauridae, the imprecise and inconsistent 'small', 'medium', and 'enlarged' categories are 225 226 still applied in the literature concerning tyrannosaurids (e.g., Tsuihiji et al., 2011; Carr, 2020; Voris 227 et al., 2021). All statistical analyses were conducted in PAST 4.03.

228 The distal end of the femur was historically cross-sectioned above the condyles, but the resulting 229 histological thin sections were never published. The section was taken using standard procedures (Padian & Lamm, 2013) in the Institute of Paleobiology, Polish Academy of Sciences. The 100 230 231 and 50 µm ground sections were analyzed under normal and polarized light, including gypsum 232 wedge using a Nikon Eclipse LV100 POL polarizing microscope with a DS-Fil camera. The 233 pictures were combined together in NIS-Elements microscope imaging software. For the 234 description of bone histology we used standard terminology and definitions following Chinsamy-235 Turan (2005) and Padian & Lamm (2013).

236 The amended holotype of *B. ostromi* (ZPAL MgD-I/108) was scored by us in two phylogenetic 237 datasets to assess its position among coelurosaurian theropods broadly and tyrannosauroids in 238 particular. First, it was added to the Theropod Working Group (TWiG) phylogenetic analysis including a broad sample of 152 coelurosaurian theropods scored for 853 morphological characters 239 (Brusatte et al., 2014). We analyzed the dataset in TNT 1.5 (Goloboff et al., 2008) with Allosaurus 240 fragilis Marsh, 1877 as an outgroup. We began with a new technology search (with default 241 parameters for sectorial search, ratchet, tree drift, and tree fusion), which recovered a minimum 242 length tree in 10 replicates, in order to broadly sample tree space and identify major tree islands. 243 The returned most parsimonious trees were then subjected to a round of additional traditional 244 245 search (TBR) branch swapping, to more fully explore each tree island identified by the new 246 technology search. Second, to assess the position of the B. ostromi holotype among the 247 tyrannosauroids in particular, we scored it in a phylogenetic analysis including 31 tyrannosauroid species (and four outgroups) and 366 characters (the Nesbitt et al., 2019 version of the Brusatte & 248 249 Carr, 2016 dataset). The dataset was analyzed in TNT using the same parameters as above. For 250 both analyses, clade support was determined via Bremer supports and jackknife percentages.

251 252

SYSTEMATIC PALEONTOLOGY

DINOSAURIA OWEN, 1842; SAURISCHIA SEELEY, 1887; THEROPODA MARSH, 1881;
COELUROSAURIA HUENE, 1914; TYRANNOSAUROIDEA OSBORN, 1905; TYRANNOSAURIDAE
OSBORN, 1905; TYRANNOSAURIDAE INDET.

- 256
- 257 Bagaraatan ostromi Osmólska, 1996
- 258

 ZPAL MgD-I/108: incomplete right mandible (dentary, angular, surangular, prearticular, an articular), left and right incomplete ilia, nearly complete left pubis, partial right pubis, proxime end of left ischium, left pedal phalanx IV-1, 2 cervical vertebrae, 25 caudal vertebrae and 2 haem arches. Note on diagnostic characters We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the medi side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf; (6) convex anterior margin of the pubis; (7) cervical vertebrae with
 articular), left and right incomplete ilia, nearly complete left pubis, partial right pubis, proximend of left ischium, left pedal phalanx IV-1, 2 cervical vertebrae, 25 caudal vertebrae and 2 haemarches. arches. Note on diagnostic characters We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) present of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf; (6) convex anterior margin of the pubis; (7) cervical vertebrae with
 end of left ischium, left pedal phalanx IV-1, 2 cervical vertebrae, 25 caudal vertebrae and 2 haem arches. Note on diagnostic characters We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf; (6) convex anterior margin of the pubis; (7) cervical vertebrae with
 arches. arches. Note on diagnostic characters We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf; (6) convex anterior margin of the pubis; (7) cervical vertebrae with
 264 265 Note on diagnostic characters 266 We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> 267 series before untangling which different taxa they belong to. However, we note here that the 268 holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen 269 of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place 270 below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media 271 side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine 272 surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
Note on diagnostic characters We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
We provide a full diagnosis below, as we must first describe all of the bones of the <i>Bagaraata</i> series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
series before untangling which different taxa they belong to. However, we note here that the holotype individual can be referred to the Tyrannosauridae because of eight features: (1) presen of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the medi side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
 holotype individual can be referred to the Tyrannosauridae because of eight features: (1) present of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
of the dentary 'chin'; (2) transition between the anterior and ventral edges of the dentary place below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the medi side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis; (7) cervical vertebrae with
 below the fourth alveolus; (3) dorsoventrally narrow Meckelian groove deeply inset into the media side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis; (7) cervical vertebrae with
side of the dentary; (4) extremely reduced retroarticular process of the articular; (5) promine surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
272 surangular shelf: (6) convex anterior margin of the pubis: (7) cervical vertebrae with
273 hypapophysis; (8) thick posterior centrodiapophyseal laminae.
274
275 Locality and age
276 Northern Sayr, Nemegt, Ömnögov, Mongolia; Nemegt Formation.
277
278 Description
279 <i>Mandible</i>
280 Only two fragments of the left mandible are preserved: the anterior part of the dentary with poor
preserved supradentary, and a piece that includes articulated posterior parts of the surangula
angular, and prearticular, and the incomplete articular.
283 Dentary
The dentary is slender in general outline and shows an anterior expansion in comparison to the
midregion (28 mm deep at the third versus 25.5 mm deep at the ninth alveolus; Fig. 1–2), which is the third versus 25.5 mm deep at the ninth alveolus; Fig. 1–2), which is the third versus 25.5 mm deep at the ninth alveolus; Fig. 1–2), which is the ninth alveolus is $(28 \text{ mm deep at the third versus } 25.5 \text{ mm deep at the ninth alveolus; Fig. 1–2})$
is D-shaped in cross section. Also, the dentary is labiolingually expanded anteriorly: the anteri
end is wide labiolingually (measuring 16.3 mm) in comparison to the posterior part of the
preserved dentary (12.1 mm width; Fig. IC). The anterior tip of the dentary is missing; howev
clearly it was positioned higher than the level of the tooth row (its preserved base is already dors
relative to the rest of the bone; Fig. IA-B). The anteroventral margin is relatively straight and
strongly inclined posteroventrally, creating with the ventral margin of the dentary an angle of 1.
degrees. This creates a distinct chin ⁻ (i.e., slightly protruding region at the place where the
anteroventral and ventral margin meet) between the anterior and ventral surfaces, which
positioned underneath the third and fourth alveoli. The chin underneath the fourth alveoli
295 commonly seen in juvenile tyrannosaurines (Carr 2020: character 11/) and Alloramus all 206 (Drugette et al. 2012) but in adulte the 'chin' is placed cheed of the fourth cluschus li
²⁹⁰ (Diusaue <i>et al.</i> , 2012), but in adults the chin is placed ahead of the fourth alveolus, in 207 Tarbosaumus bataan (Fig. 2) and Turannosaumus yety (Drugatte and Corr. 2016, share-star 171)
251 <i>Turbosaurus balaar</i> (Fig. 5), and <i>Tyrannosaurus rex</i> (Brusalle and Carr, 2010: character 1/1).
299 tyrannosaurids with narrow jaws contrasting with the steeper rostroventral margin of deen-jaw

adult individuals, where the 'chin' migrates further anteriorly (Fig. 2-3; Carr & Williamson, 2004;

301 Carr, 2020).

302 The dorsal margin of the dentary is strongly concave in lateral view, even in the anterior part, a

303 feature of derived tyrannosaurids (Brusatte and Carr, 2016: character 177) that is also seen in

- juveniles and subadults (Currie & Dong, 2001; Tsuihiji *et al.*, 2011; Brusatte *et al.*, 2012; Funston
 et al., 2020b). The ventral margin of the dentary is only very slightly convex (Fig. 1A-C, 2E-F).
- 305 *et al.*, 2020b). The ventral margin of the dentary is only very slightly convex (Fig. IA-C, 2E-F).
 306 The lateral surface is smooth; the neurovascular foramina pierce the bone along an anteroposterior
 307 sulcus (i.e., dentary groove; Fig. 1A, 2E) 7.8 mm below the tooth row. The foramina are more
- numerous in the anterior part of the dentary, close to the symphysis (Fig. 1F, 2B). The dentary groove is an ontogenetically variable feature in tyrannosaurids, sharp and deep in juveniles and shallow in mature individuals (Fig. 3; Brusatte *et al.*, 2016; Carr, 2020). On the ventral side of the dentary, a second row of foramina, parallel to the ventral margin, is present. Anteriorly, those
- 312 foramina are larger and closely spaced; posteriorly, the foramina are smaller and widely spaced

313 (Fig. 1A, F, 2B, E).

The medial side of the dentary is smooth, with a deep and narrow groove that extends 314 315 anteroposteriorly between the interdental plates and the rest of the dentary (Fig. 1B, 2F). The interdental plates are poorly preserved, but their triangular shape is visible in medial view. The 316 symphysis is elongated, aligned anterodorsally, and has a nearly smooth surface (bearing only 317 minute, very subtle striations). A 'chin' is present, as in other tyrannosaurids (Brusatte and Carr, 318 2016: character 172), including small juveniles (Funston et al., 2020b) with the exception of 319 320 *Oianzhousaurus sinensis* (Lu *et al.*, 2014; Foster *et al.*, 2021). The ventral margin of the symphysis 321 ends below the fourth tooth alveolus, where a single anterior Meckelian foramen is present (Fig. 1B, 2F). The position is similar to that in T. bataar (e.g., ZPAL MgD-I/4, ZPAL MgD-I/175; Fig. 322 3) and other tyrannosaurids (Brusatte et al., 2010; Funston et al., 2020b), but in A. altai the foramen 323 is positioned further posteriorly, below the fifth tooth alveolus (Brusatte et al., 2012). The anterior 324 325 Meckelian foramen is located anterior to the anterior end of the Meckelian groove, which is 326 shallower anteriorly and cuts deeper into the dentary posteriorly. The deep and sharp inset of the 327 Meckelian groove is a characteristic of tyrannosaurids and close relatives (Brusatte and Carr, 2016: 328 character 178), and is seen in small juveniles of T. rex (Carr, 2020) and other juvenile 329 tyrannosaurids (Funston et al., 2020b). Anteriorly, the groove is positioned in the middle of the 330 medial surface of the dentary, but posteriorly, it is positioned in the upper third of the dorsoventral 331 height of the dentary. The distance between the Meckelian groove and the tooth row also shortens

332 posteriorly (from 13.25 mm anteriorly to 8 mm posteriorly). In dorsal view, the preserved part of

the dentary is straight (Fig. 1C, 2A), similar to A. altai (Brusatte et al., 2012) and juvenile T. bataar

334 (Tsuihiji *et al.*, 2011).

The dentary shows eleven tooth alveoli. Nine dentary teeth are broken off, but nine complete tooth alveoli are preserved, along with most of a tiny mesial-most alveolus at the front of the jaw, and the anterior end of the 11th alveolus at the back. The preserved part of the first alveolus is exceptionally small in comparison to other alveoli, whereas the second is larger than the first, but still smaller than the remaining teeth, and with a circular outline (Fig. 1F, 2B; Table 1). This

- indicates that the first two teeth in the jaw were smaller and more circular in cross section than the
- 341 remaining teeth, as is common in tyrannosauroids (Brusatte and Carr, 2016: character 175),

- 342 including small juveniles (Funston et al. 2020b). The alveoli posterior to the first two are elongated
- 343 mesiodistally, and have an eight-shaped outline in dorsal view (Fig. 1C, 2A). The labiolingual
- 344 width is the largest at the 3rd alveolar position and the anterior and posterior alveoli are narrower.
- 345 The anteroposterior length of the alveoli decreases anteriorly, so the 10th alveoli is the longest.
- 346 These alveoli indicate that the associated teeth are ziphodont, with labiolingual widths less than
- 347 60% mesiodisal lengths, as is the case in most theropods and juvenile tyrannosaurids, but differing
- from the labiolingually widened incrassate teeth of large adult tyrannosaurids (Brusatte and Carr,2016: character 201).
- 350
- 351 Supradentary

As correctly noted by Osmólska (1996), only a small, poorly preserved splinter of the supradentary is present in articulation, dorsal to the dentary and lingual to the interdental plates, at the level of the fifth to the seventh tooth (Fig. 1B, 2F). Some uninformative, miniscule scraps of bone are also present posteriorly. As preserved, the supradentary appears to be dorsoventrally narrow, covering less than one fifth of the mandible height.

- 357
- 358 Splenial

We could not confirm the presence of a triangular, slightly hooked anterodorsally anterior part of the splenial suggested by Osmólska (1996). The triangular element is most likely a cracked and inset ventral bar of the dentary.

- 362
- 363 Surangular

Only the posterior part of the left surangular is preserved (Fig. 1A-E, 4). The surangular is a 364 generally thin, plate-like bone which expands labiolingually at the dorsal margin. Lateroventrally, 365 the surangular is covered by the flat and mediolaterally thin angular (Fig. 1A, 4A). The angular 366 367 ends very close to (only 4 mm below) the surangular foramen. In ventral view, the connection between the surangular, articular, and prearticular is visible. The ventromedial edge of the 368 surangular contacts the prearticular. This contact is visible externally in the posterior part, but more 369 370 anteriorly the surangular is partly obscured by the angular – it continues only as a narrow splinter 371 along the posterior half of the preserved part of the angular. As preserved, the contacts between the bones in that area appear split as a result of compaction, so their precise layout may be 372 displaced, and thus it is possible that in vivo the surangular was either not exposed from under the 373 angular, or that the exposure was slightly larger but now is obscured and/or partly eroded. In any 374 375 case, the deformation most likely was not substantial. The angular tightly covers the surangular, 376 so the margin between those bones is barely visible laterally, but well-marked ventrally.

The most conspicuous aspect of the surangular is the presence of two surangular foramina: one smaller $(2.3 \times 1.5 \text{ mm})$ and positioned anterodorsally, and the second larger (diameter: 5.63 x 3.68 mm) and placed posteroventrally to the first one (Fig. 1A, 4A). Both are elongate, ovoid-shaped rather than circular, with the long axes directed posterodorsally. The bone is extremely thin between those foramina (Fig. 1E, 4F). This condition is different from most tyrannosaurids, where a single surangular foramen is enlarged, such that its dorsoventral depth is more than 30% of the depth of the surangular (Brusatte and Carr, 2016: character 179). This is the case in Nemegt 384 tyrannosaurids like alioramins (Brusatte et al., 2009, 2012; Lu et al., 2014), T. bataar (e.g., ZPAL 385 MgD-I/4, ZPAL MgD-I/31; Fig. 5), and the young juvenile Raptorex (Sereno et al., 2009). 386 However, in some other juvenile tyrannosaurids there is a single surangular foramen but it is small (Currie & Dong, 2001; Tsuihiji et al., 2011), and it has been determined that the size of the foramen 387 changes during the ontogeny of T. rex (Carr 2020: character 126). Both surangular foramina in B. 388 ostromi are located in a fossa below the lateral surangular shelf. There is no pneumatic pocket 389 390 posterodorsal to the surangular foramen, whereas nearly all other tyrannosaurids have one 391 (Brusatte and Carr, 2016: character 183), although it is absent in some specimens of T. bataar 392 (e.g., ZPAL MgD-I/4 ZPAL MgD-I/31; Fig. 5, and MPC-D 107/7, Tsuihiji et al., 2011). In B. 393 ostromi, the two foramina are separated by a laterally convex, lateroposterodorsally inclined, 394 dorsally thickening (up to about 5 mm), and gently posteroventrally bowed bar (Fig. 1A, 2A). The 395 bar buttresses the posterior part of the lateral surangular shelf.

396 There is a lateral surangular shelf above the foramina, close to the dorsal margin of the bone (Fig. 397 1A, E, 2A-B, F). Its lateral protrusion is not as prominent as in A. altai (Brusatte et al., 2012) or 398 T. bataar (e.g., ZPAL MgD-I/4, ZPAL MgD-I/5, ZPAL MgD-I/31; Fig. 5), but the lateral 399 protrusion of the surangular shelf is subtle, as in some juvenile tyrannosaurids (Currie & Dong, 400 2001; Tsuihiji et al., 2011; Foster et al., 2021). In lateral view, the shelf extends straight anteroposteriorly, paralleling the long axis of the mandible, as in tyrannosaurids, but differing from 401 402 the anteroventral or anterodorsal orientation in most other theropods (Brusatte and Carr, 2016: 403 character 182) The smooth surface of the adductor fossa dorsal to the shelf faces almost equally dorsally and laterally. This is similar to both species of Alioramus (Kurzanov, 1976; Brusatte et 404 405 al., 2012) and juvenile tyrannosaurids (Currie & Dong, 2001; Tsuihiji et al., 2011), but differs from the strongly laterally facing state in large adult tyrannosaurids (Brusatte and Carr, 2016: 406 407 character 184). In older T. bataar the fossa is just medial to the shelf, extends medioventrally, and 408 forms a depression (more pronounced in smaller specimens), but more medially the adductor fossa 409 curls up and faces strongly laterally (ZPAL MgD-I/31, ZPAL MgD-I/4, ZPAL MgD-I/5; Fig. 5). The dorsally pointing posterior edge of the adductor fossa is more pronounced than in A. altai 410 411 (Brusatte et al., 2012). There is a triangular fossa on the lateral surface of the surangular shelf 412 anteroventral to the glenoid, a distinguishing feature of derived tyrannosauroids (Brusatte and 413 Carr, 2016: character 185). The glenoid on the surangular (lateral glenoid socket of Osmólska, 414 1996) is a deep and anteroposteriorly narrow transverse concavity bound anteriorly and posteriorly by dorsally extended processes (the preglenoid process and conelike process, respectively; Fig. 1, 415 4). This is similar to A. altai (Brusatte et al., 2012) and juvenile T. bataar (Tsuihiji et al., 2011); 416 417 in larger T. bataar the glenoid is anteroposteriorly wider (ZPAL MgD-I/4, ZPAL MgD-I/5, ZPAL MgD-I/31; Fig. 5). Posteromedially to the glenoid fossa (lateral glenoid socket sensu Osmólska, 418 1996), in dorsal view, a deep and narrow fossa is present (medial glenoid socket sensu Osmólska, 419 420 1996). In T. bataar, the two glenoid fossae are not marked by the upraised lateral margin of the surangular. Two glenoid depressions are present in that species, but similar in depth and separated 421 422 by a gradual elevation (e.g., ZPAL MgD-I/4). In B. ostromi, the medial glenoid is much deeper 423 than the lateral glenoid. There is a fossa on the lateral surface of the surangular, ventral to the 424 glenoid, as is seen in derived tyrannosauroids (Brusatte and Carr, 2016: character 186). This fossa 425 is smooth as in A. altai (Brusatte et al., 2012), not rugose, as in in T. bataar (ZPAL MgD-I/4,

426 ZPAL MgD-I/5, ZPAL MgD-I/31). Distal to the glenoid, behind the posterior dorsal (conelike) 427 process, a second, groove-like concavity (cleft of Osmólska, 1996) is present bound posteriorly by 428 a small but well-defined dorsal projection, which continues medialy as a sharp, distinct ridge (Fig. 429 10^{-4} A). This feature occurs both in *A* altai and *T* bataar

- 429 1C, 4A). This feature occurs both in *A. altai* and *T. bataar*.
- The retroarticular process of the surangular is tiny, corresponding to the small corresponding
 process on the articular (Fig. 1A-B). This is a feature of tyrannosauroids (Brusatte et al., 2014:
- 432 character 76). This process is straight and slopes posteroventrally, similar to A. altai (Brusatte et
- 433 al., 2012) and Qianzhousaurus sinensis (Lu et al., 2014). In T. bataar (ZPAL MgD-I/4, ZPAL
- 434 MgD-I/5) it is oriented vertically. The medial hook process is nearly perpendicular to the
- prearticular axis of the surangular and constitutes almost 50% of the width of the surangular.
- 436
- 437 Angular
- 438 Only the left posterior part of the angular is preserved (Fig. 1D, 4A, C). It is plate-like, laterally
- convex, securely sutured, and tightly covers the surangular. Its margins are marked in the lateral
 view by a shallow groove historically marked with a pen, making the exact observation difficult
 (Fig. 1A, 4A). The dorsal margin of the posterior plate of the angular is convex below the anterior
 of the two surangular foramina and concave below the distal margin of the posterior foramen,
 where the dorsaloventral height of the angular decreases posteriorly. The distance between the
 dorsal margin of the angular and ventral margin of the posterior surangular foramen is short,
- 445 measures 4.2 mm The posterior margin is convex, pointing slightly upwards, and the ventral 446 margin is straight and contacts the surangular posteriorly and prearticular anteriorly. The posterior
- 447 tip of the angular is not complete. The preserved posterior end of the angular extends past the level
- 448 of the posterior margin of the posterior surangular foramen.
- 449
- 450 Prearticular
- 451 The posterior process of the left prearticular is preserved, and tightly articulated with articular posteriorly, angular ventrally, and surangular dorsally, laterally, and posteroventrally (Fig. 1B-E, 452 453 4C-D). The posteromedial tip of the prearticular is broken off. The preserved part of the 454 prearticular is medially concave in ventral view. The ventral margin between the prearticular, 455 angular (anteriorly), and surangular (posteriorly) runs sigmoidally in ventral view, and only posteriorly the margin between the bones curves medially (note that the bones are slightly split 456 along the ventral surface of the mandible, but that does not seem to distort their general layout). 457 458 The articular, surangular, and angular are tightly articulated with the prearticular. The prearticular 459 is not fused to the surangular and articular, similar to juvenile Tarbosaurus (Currie & Dong, 2001; 460 Tsuihiji et al., 2011) and A. altai (Brusatte et al., 2012) and in contrast to large T. bataar (ZPAL MgD-I/4, ZPAL MgD-I/5)The posteroventral margin of the prearticular is pointed downwards 461 462 (similar to A. altai), while in T. bataar it is oriented posteriorly. The distal concave margin
- 463 contacting the articular is shallower than in *T. bataar*.
- 464 465 Artic
 - 5 Articular
- 466 The articular is almost complete, lacking only the ventromedial part. It is tightly articulated with
- 467 the prearticular anteromedialy and contacts the surangular laterally. The posterior surface is

468 smooth, gently concave, and elliptic, over twice as tall as it is wide. The retroarticular process is 469 extremely reduced (Fig. 1, 4D-E), as in all Tyrannosauroidea, but differing from the much larger 470 processes in dromaeosaurids and other theropods (Brusatte *et al.*, 2014: character 76). The 471 attachment site for the jaw muscles on the articular is mediolaterally narrower than the glenoid 472 articular surface, and there is a very narrow non-articular region between the glenoid and the 473 muscle attachment. Both features are characteristic of most tyrannosauroids, but not other 474 theropods (Rauhut et al. 2010; Brusatte and Carr, 2016: characters 189, 190).

- 475
- 476 Antarticular

We could not confirm the presence of a separate antarticular suggested by Osmólska (1996). Aspreserved, the structure in question is a cracked medial edge of the surangular.

479 480

Postcranial skeleton

481 Cervical vertebrae

Two incomplete amphiplatyan cervical vertebrae are preserved (Fig. 6). They are similar in 482 483 structure and size: the anteroposterior length of the anterior cervical centrum (Fig. 6A-F) measures 484 35.8 mm, and the posterior cervical centrum (Fig. 6G-L) measures 36.5 mm. The articular surfaces of the centrum are oval, slightly concave, and shallow dorsoventrally. The heigh to width ratio of 485 the centra is 0.7 and 0.6 for the anterior and posterior cervical vertebra, respectively. The centra 486 are concave laterally, and thicken close to the parapophyses, which are oval in lateral view and 487 488 directed laterally (Fig. 6B, H). On the lateral sides of the centra, pleurocoels (lateral pneumatic 489 fossae) are present. Above the pleurocoels, the posterior centrodiapophyseal laminae are thick and laterally offset, and demarcate a deep infradiapophyseal fossa anteriorly, as in all tyrannosaurids, 490 491 but differing from the thinner laminae of more basal tyrannosauroids (Brusatte and Carr, 2016: 492 character 213). Sutures between the centra and neural arches are open. Small, eroded 493 hypapophyses on the anterior region of the ventral surface of the cervical vertebrae are present, as 494 in tyrannosaurids and close relatives (Brusatte and Carr, 2016: character 214), including juveniles 495 such as the A. altai holotype (Brusatte et al., 2013).

496 The cervical vertebrae are similar to the mid- or posterior cervical vertebrae of the juvenile 497 tyrannosaurid '*Shanshanosaurus huoyanshanensis*', as both exhibit flat ventral surfaces of the

498 centrum, which are also narrow-waisted, biconcave, and with a large, and single pleurocoel on the

- 499 lateral side (Currie & Dong, 2001).
- 500
- 501 Caudal vertebrae

502 Twenty-one caudal vertebrae were found in articulation (Fig. 7-14). Four distal caudal vertebrae 503 and two haemal arches were also found (Fig. 14-15), but cannot be fitted to the articulated tail. 504 The first preserved caudal is taller dorsoventrally than long (Fig. 7A-F; Table 2), whereas the 505 second is roughly equal in height and length (Fig. 7G-L), and all successive centra are longer than 506 tall (Fig. 8-14; Table 2). The transverse processes disappear starting from the 15th preserved caudal 507 (Fig. 12M-R). In *T. bataar* (ZPAL MgD-I/4, ZPAL MgD-I/175, and ZPAL MgD-I/177) the height 508 of the centrum is similar to its length in the 5th caudal vertebrae, and the transverse processes

509 disappear starting from the 18^{th} caudal vertebra. Thus, we estimate that the preserved articulated

- 510 part of the tail ZPAL MgD-I/108 represents the 4th to 24th caudal vertebrae. Moreover, in the first
- 511 preserved caudal, the transverse processes are oriented posteriorly (Fig. 7A-F), which is a typical 512 condition of the proximal caudal vertebrae of tyrannosaurids.
- 513 The neural arches of the caudal vertebrae in ZPAL MgD-I/108 are co-ossified with the centra in
- all bones, but the remnant of the suture is visible in the proximal centra, up to the 18th caudal (Fig.
- 515 12M-R). This suture is also present in the proximal caudal vertebrae of other tyrannosaurids,
- 516 including T. bataar, and also in some other theropods like ornithomimids (e.g., Gallimimus
- 517 *bullatus* Osmólska et al., 1972 ZPAL MgD-I/94).
- 518 The caudal centra are all amphicoelous; only the first preserved caudal of ZPAL MgD-I/108 is
- 519 somewhat concave anteriorly and flat posteriorly (Fig. 7A-F). In both *T. bataar* (ZPAL MgD-I/4, 520 ZPAL MgD-I/175, and ZPAL MgD-I/177) and *T. rex* (Brochu, 2003), the caudal vertebrae are
- amphicoelous, and the first four centra are somewhat concave anteriorly. This supports the
- 522 identification of the first preserved caudal of ZPAL MgD-I/108 as the 4th caudal vertebra (Fig. 7A-
- 523 F). The lateral surfaces of the centra do not have any pleurocoels or other pneumatic features, and
- 524 on the ventral surfaces there are no ridges (Fig. 7-14). The articular surfaces for the hemal arches
- are present at the posteroventral end of the centra; these are well-visible, and similar in shape as
- 526 in *T. bataar* (e.g., ZPAL MgD-I/175).
- The neural arches are generally incomplete. The robust and rectangular neural spines of the 527 528 proximal caudal vertebrae lack their dorsal ends, but even as preserved they project beyond the level of the posterior limit of the respective centra, as in most other tyrannosaurids (Brusatte and 529 530 Carr, 2016: character 229). The ontogenetic component to this character was noticed by Carr 531 (2020), in T. rex the spinous processes of the caudal vertebrae do not extend behind the level of the posterior edge of the centrum, as in juvenile *T. bataar* (Tsuihiji et al., 2011) and apparently the 532 533 Raptorex holotype (Sereno et al., 2009). In adult T. rex the spinous process of the caudal vertebrae 534 extend posterior to the centrum (Carr, 2020), as it is also in T. bataar (ZPAL MgD-I/3, ZPAL MgD-I/175). The neural spines of ZPAL MgD-I/108 are inclined posteriorly along the tail, similar 535 536 to A. altai (Brusatte et al., 2012) and Qianzhousaurus sinensis (Lu et al., 2014), and in contrast to 537 T. bataar, in which the neural spines project more vertically (ZPAL MgD-I/4, ZPAL MgD-I/175, 538 and ZPAL MgD-I/177). Further distally, the neural spines become stronger inclined posteriorly, 539 and from the 16th caudal vertebrae they become short dorsoventrally and elongated
- anteroposteriorly (Fig. 12-14). The dorsal expansion present on the posterodorsal end of the neural
 spine in other tyrannosaurids (Brusatte *et al.*, 2012) is not preserved in *B. ostromi*, and thus its
 presence cannot be confirmed.
- 543 The transverse processes are mostly incomplete in the caudal series of *B. ostromi*. Proximal caudal 544 vertebrae have anteroposteriorly long and dorsoventrally thin distally narrowing transverse processes. From the 9th caudal vertebra onwards, the transverse processes are still thin and flat, 545 and directed laterally. Then, the 15th caudal vertebra shows reduced transverse process, much 546 shorter and narrow anteroposteriorlyy. The 16th and 17th caudal vertebrae have minute transverse 547 processes, and the 18th and further caudal vertebrae lack the transverse processes (Fig. 12-14). On 548 549 the anteroventral surface of each transverse process, where the process meets the prezygapophysis, 550 there are two laminae that define a deep, triangular concavity. This is present in most other
- 551 tyrannosaurids, including juvenile specimens like the *A. altai* holotype (Brusatte et al., 2012), but

- absent in more basal tyrannosauroids and other theropods (Brusatte and Carr, 2016: character 231).
- 553 A triangular depression was noticed in A. altai (Brusatte et al., 2012) at the region where the
- transverse process meets the neural spine, but in *B. ostromi* it is proportionally wider and
- shallower. In *T. bataar*, the depression is rather broad and shallow, regardless of the animals' size
- 556 (ZPAL MgD-I/3, ZPAL MgD-I/4, ZPAL MgD-I/175); however, the depth and width of the
- 557 depression depend on the preservation: in the caudal vertebrae of *T. bataar* ZPAL MgD-I/3, the 558 depression is narrow and deep on the left side and shallow and wide on the right side. The depth
- and breadth of the fossa is best explained by taphonomic deformation, and thus its taxonomical
- 560 value is limited.
- 561 The prezygapophyses of the proximal caudal vertebrae are positioned more vertically than in T.
- 562 *bataar* (ZPAL MgD-I/3, ZPAL MgD-I/4, ZPAL MgD-I/175) and *A. altai* (Brusatte *et al.*, 2012).
- Further distally, the prezygapophyses point more anteriorly, and from the 17th caudal onwards,
 they are longer and project even more anteriorly (Fig. 12-14). The surface and shape of the articular
- surfaces of the prezygapophyses is not visible due to their tight articulation with the
 postzygapophyses or damage. The postzygapophyses are positioned behind the centrum and their
- articular surfaces face lateroventrally, more laterally than in *T. bataar* (ZPAL MgD-I/3, ZPAL
 MgD-I/4, ZPAL MgD-I/175) and *A. altai* (Brusatte *et al.*, 2012).
- 569 Due to the close articulation between the caudal vertebrae, the hypantrum between the 570 prezygapophyses is not visible. The hyposphene between the postzygapophyses is large and 571 rectangular in *B. ostromi*, similar to *T. bataar* (ZPAL MgD-I/3, ZPAL MgD-I/4, ZPAL MgD-
- 572 I/175), and in contrast to the delicate hyposphene found in *A. altai* (Brusatte *et al.*, 2012).
- 573
- 574 Ilia
- 575 The ilia are incomplete; the left and right ventral postacetabular processes, part of left proximal preacetabular process, and apparently two fragments of the dorsal edge of the left ilium blade are 576 577 preserved (Fig. 16). Osmólska (1996) mentioned (but did not illustrate) a thin bone fragment found 578 some distance from the remainder of the pelvis, with an even natural dorsal edge and dense, 579 perpendicular striations on one of the surfaces, which she interpreted as the dorsal edge of the 580 ilium. The material catalogued under ZPAL MgD-I/108 includes two fragments fitting that 581 description (Fig. 16K-N). Given the presence of other dinosaur species in the association and lack 582 of articulation with the remainder of the skeleton, their affinity to *B. ostromi* is uncertain, although 583 possible.
- The base of the preacetabular process was positioned above the pubic peduncle, as marked by the attachment site of the *M. iliofemoralis internus*, the cuppedicus fossa (Fig. 16A-B), characteristic
- 586 for tyrannosaurids and other tetanurans (Hutchinson, 2001; Carrano & Hutchinson, 2002).
- 587 Dorsally, the cuppedicus fossa is a wide and slightly concave area, which curls down laterally and 588 forms the ventral margin of the preacetabular process. The dorsal margin of the preserved element
- 589 of the preacetabular blade is crushed diagenetically. Above the ventral margin of the preacetabular
- 590 blade, a depression is present.
- Above the acetabulum, on the lateral surface of the right iliac blade (Fig. 16G-J) an eroded linear
- ridge is present (Fig. 16I). This structure is present in all tyrannosauroids, including the juvenile
- 593 MPC-D 107/7 (Tsuihiji et al. 2011), but excluding Raptorex kriegsteini and Qianzhousaurus

sinensis (Lu *et al.*, 2014; Brusatte and Carr, 2016: character 258). Possibly, the absence of this feature in the latter two may reflect an individual or growth variation.

596 The right postacetabular process is taphonomically compressed mediolaterally, and its pubic peduncle and the supraacetabular crest are eroded (Fig. 16C-F). The ischial peduncle is robust, and 597 the acetabular surface is flat. Distally, the ischial peduncle is laterally, ventrally, and medially 598 599 surrounded by a shallow depression. Further posteriorly from the ischial peduncle, ventrally, a 600 large and deep brevis fossa is present. It is concave, wide mediolaterally, and gradually widens 601 posteriorly: from 11 mm anteriorly to 28 mm distally. Such widening occurs also in A. altai 602 (Brusatte et al., 2012). There is no foramen at the base of this fossa, as in T. bataar (ZPAL MgD-603 I/4), but the foramen is present in A. altai (Brusatte et al., 2012). The medial and lateral walls of 604 the brevis fossa are formed by the medial and lateral flanges of the postacetabular process. The 605 lateral flange is thicker than the medial flange, as in T. bataar (ZPAL MgD-I/3) and A. altai 606 (Brusatte *et al.*, 2012). The brevis fossa is visible in lateral view only anteriorly; further posteriorly 607 it is concealed by the lateral flange of the postacetabular process. Above the beginning of the brevis 608 fossa, the lateral flange of the postacetabular process continues dorsally as a dorsal, ca. 24 mm 609 long crest described by Osmólska (1996), surrounded by anterior and posterior depressions.

610 On the medial surface of the right ilium of ZPAL MgD-I/108, parts of three sacral ribs are present: 611 one above the acetabulum, the second above the pubic peduncle, and the last positioned on the

medial flange (Fig. 16C-J). Due to the position of the sacral ribs, we agree with Osmólska (1996)
that they belong to the third to fifth sacral vertebra. If so, the laterally exposed brevis fossa
terminates posteriorly at the level of the anterior part of the fifth sacral vertebra.

615

616 Pubes

The left pubis (proximal part and shaft preserved) is more complete than the right (where only the 617 proximal part is preserved; Fig. 17). The articulation facet for the ilium is preserved in the left 618 619 pubis (Fig. 17A-E). The contact with the pubic peduncle of the ilium is clear: the lateral margin is laterally extended with a rugose surface. In dorsal view, the pubic portion of the acetabulum is 620 621 wider transversely, but shorter anteroposteriorly, than the ischial part. Below the acetabulum, the 622 pubis narrows medialolaterally and forms a thin plate. The pubic tuberosity is incomplete, but it is 623 present as a distinct convex structure as in many tyrannosauroids, including juveniles such as the 624 *Raptorex* holotype, but it does not have the highly rugose from of large subadult and adult 625 tyrannosaurids like T. bataar (ZPAL MgD-I/3, ZPAL MgD-I/5) (Brusatte and Carr, 2016: 626 character 270). In B. ostromi, the tubercle is essentially level with the obturator notch, as in 627 tyrannosaurids (Brusatte and Carr, 2016: character 271). Ventral to the pubic tuberosity and the 628 articulation surface with the ischium, the pubis narrows anteroposteriorly and slightly widens 629 transversely. Here, the main shaft of the pubis is anteriorly concave when seen in lateral view (Fig. 17A), as in tyrannosaurids generally, but differing from the straighter condition in the juvenile 630 Raptorex holotype (Brusatte and Carr, 2016: character 269). On the posteromedial surface of the 631 632 bone, the beginning of the pubic apron is preserved: a sigmoidal crest running along the medial 633 surface of the pubic shaft (Fig. 17B, D-E). Its shape is similar to T. bataar (ZPAL MgD-I/175). 634 The medial surface of the pubic apron is missing. The pubic shaft is circular in cross section, 635 starting from the region where the pubic apron appears, and remains circular until the end of the

636 preserved part of the pubis (although the lateral surface of the pubic shaft is missing). In distal 637 view, the proximal part of the pubis (above the shaft) is less bowed laterally than in T. bataar 638 (ZPAL MgD-I/3, ZPAL MgD-I/175). This, however, can be accounted for the twice larger size 639

(ca. 7 m in length) of these two subadult individuals of T. bataar than B. ostromi.

640

641 Ischium

642 Only the proximalmost left ischial plate including the peduncles is preserved (Fig. 17A-D). The articular surface of the pubic peduncle is tightly articulated with the ischial peduncle of the pubis. 643 The pubic peduncle is separated from the ischial peduncle by an elliptic concavity. In dorsal view, 644 645 the concavity is walled laterally by a wide and low margin (5 mm wide mediolaterally in the 646 narrowest place), which expands anteriorly and posteriorly until reaching the peduncle margins, 647 forming an hourglass-shaped margin (Fig. 17C). Medially, the concavity is walled by a straight, mediolaterally thin, and dorsally extended, lamina, which is also present in other tyrannosaurids. 648 The articular surface of the pubic peduncle is 26 mm tall proximodistally, and 20 mm wide 649 650 mediolaterally. The lateral surface of the preserved part of the proximal ischium is concave. 651 whereas the medial surface is only slightly concave. The articular surface of the iliac peduncle is 652 31 mm wide mediolaterally, and 23.5 long anteroposteriorly. The lateral margin of the iliac peduncle is strongly extended laterally. In dorsal view, it is elliptical, and has a concave articular 653 654 surface with the ischial peduncle of the ilium, similar to other tyrannosaurids (Brusatte, Carr & Norell, 2012). 655

656

657 Pedal phalanx

The left phalanx IV-1 is 33 mm long (Fig. 18), its length to width ratio is 1.5. The proximal articular 658 surface is wider (22 mm) than tall (19 mm; unlike in for T. bataar, where the proportions are 659 opposite: ZPAL MgD-I/29; ZPAL MgD-I/175; ZPAL MgD-I/206), however, the dorsal and 660 661 plantolateral margins of the phalanx are incomplete. The proximal articular surface is concave, in a similar manner to T. baatar individuals. The medial margin of the articular surface is slightly 662 663 concave, and the opposite lateral margin is convex. In the dorsal and planar view the phalanx IV-664 1 of ZPAL MgD-I/108 is rectangular, only slightly narrowed in the middle. In the lateral and 665 medial view, the phalanx is triangular in overall shape, clearly narrows (stronger on the lateral than medial side) just before the distal condyles. In dorsal view, a supracondylar basin is present, just 666 behind the slightly elevated margin of the distal articular surface. The supracondylar basin is only 667 668 slightly wider mediolaterally than long proximodistally (the length to width ratio is 0.8; in T. 669 *bataar* specimens the basin is much wider than long, the ratio is ca. 0.4) and in comparison to T. 670 bataar individuals the basin is shallower. The lateral condyle is smaller than the medial condyle, and the lateral ligament pit is shallower in comparison to the medial one as in all T. bataar 671 individuals studied (ZPAL MgD-I/3; ZPAL MgD-I/4; ZPAL MgD-I/5; ZPAL MgD-I/29; ZPAL 672 673 MgD-I/175; ZPAL MgD-I/206; ZPAL MgD-I/331). The distal margin of the medial condyle is 674 circular, its dorsal end do not form a pointed posteriorly tip, as young T. bataar (ZPAL MgD-I/29), 675 but in contrast to larger individuals (ZPAL MgD-I/3; ZPAL MgD-I/4; ZPAL MgD-I/5; ZPAL 676 MgD-I/175; ZPAL MgD-I/206; ZPAL MgD-I/331), where the tip is present. In dorsal view, the 677 distal margin of the medial condyle is pointing anteromedially. The medial condyle is higher

678	plantodorsally and wider medialolaterally than the lateral condyle. The distal condyles are
679	separated by a cleft (which is acute and narrower in comparison to <i>T. bataar</i> individuals) along
680	the entire articular surface. The rounded margin of the lateral condyle in lateral view is not
681	complete on the plantar side. On the dorsal side, the margin of the articulation surface is smooth,
682	only slightly lifted up. In larger individuals of <i>T. bataar</i> the dorsal end of the articular surface in
683	lateral view is clearly demarcated.
684	The pedal phalanx IV-1 of young T. bataar ZPAL MgD-I/29 shows the same length to width ratio
685	as ZPAL MgD-I/108. In subadults of T. bataar the ratio is 1.3 (e.g., ZPAL MgD-I/175), and in
686	adults it is 1.2 (e.g., ZPAL MgD-I/206). Despite the fact that the phalanx IV-1 of B. ostromi is
687	slender than in subadult and adult <i>T. bataar</i> , it is short and wide, as is typical for tyrannosaurids,
688	in contrast to elongated and slender pedal phalanges of ornithomimids (length to width ratio is 1.7
689	for G. bullatus ZPAL MgD-I/94), caenagnathids (length to width ratio is 2.1 for Elmisaurus rarus
690	ZPAL MgD-I/98), or troodontids (length to width ratio is 1.7 for Borogovia gracilicrus ZPAL
691	MgD-I/174).
692	
693	OVIRAPTOROSAURIA BARSBOLD 1976; CAENAGNATHOIDEA STENBERG, 1940; CAENAGNATHIDAE
694	STENBERG, 1940
695	
696	Referred material
697	ZPAL MgD-I/108/1: Left manus phalanx II-1, manus ungual I-2, proximal and distal ends of the
698	left femur, tibiotarsus, and rib.
699	
700	Note on diagnostic characters
701	We provide full details below, as we must first describe all of the bones of the <i>Bagaraatan</i> original
702	series before untangling which different taxa they belong to. However, we note here that this set
703	of bones can be referred to Caenagnathidae because of: (1) the presence of lateral pleurocoels in
704	the proximal caudal centra: (2) lesser and greater trochanters in contact: (3) clearly demarcated
705	accessory trochanter: (4) gracile and straight shape of the manual phalanx.
706	accessory accentation, (1) gracine and straight shape of the manual pharantic
707	Locality and age
708	Northern Savr Nemegt Ömnögov Mongolia: Nemegt Formation
709	rorment suyi, romege, onmogov, mongona, romeger onnanon.
710	Description
711	Caudal vertebrae
712	The centrum of one caudal vertebra is preserved (Fig. $19A_{-F}$). It is 28 mm long, 19.5 mm tall, and
712	23 mm wide (the heigh to width ratio of the centrum is 0.8). The centrum is oval, only slightly
71/	compressed dorsoventrally. Laterally, the centrum hears one pleurocoel (pneumatic foramen) on
715	each side. The presence of lateral pleurocoels in the caudal vertebrae is a synanomorphy of
716	Cooregratheides (Lamonne <i>et al.</i> 2014). The contrum is only slightly concernate laterally. Ventrally
717	two parallel ridges extend along the centrum as in <i>Elmingumus namus</i> (specimen MPC D 100/110
/ / 710	Womingia aphiansis' Barshold at al. 2000)
710	Nomingia goviensis Barsoola et al., 2000).
119	

720 Ribs

- 721 Only a proximal part of a dorsal rib is preserved; the rib is broken at the tuberculum (Fig. 19G-H).
- 722 The capitulum is bulbous. Behind the slightly convex articular surface no depression is present, in
- contrast to tyrannosaurids (*T. bataar* e.g., ZPAL MgD-I/3, ZPAL MgD-I/4, ZPAL MgD-I/175and
- A. altai see Brusatte et al., 2012). Also, in contrast to the latter, the tuberculum is enlarged. Because
- the capitulum and tuberculum are at a similar level, the rib likely comes from the posterior part of
- the ribcage. The overall shape of the preserved part of the rib corresponds to the morphology in
- 727 caenagnathids (e.g., Caenagnathidae indet. ZPAL MgD-I/99).
- 728
- 729 Manus phalanx II-1.
- 730 The left phalanx is straight and elongated, measuring 76.6 mm (Fig. 19O-T). The proximal
- articular surface is taller (18 mm) than wide (16 mm) and divided by a low ridge, which is narrow
- dorsally and wide ventrally. On both sides of the ridge, the articular surfaces are teardrop-shaped
- and strongly concave. The distal medial condyle (13.5 mm high) is smaller than the lateral one
- (15.4 mm high) and separated by a deep and narrow furrow. The medial ligament pit is shallower
- than the lateral ligament pit. The width of the distal end is 15 mm; the length to width ratio of thephalanx is 4.7.
- 730 phalanx is 4.7. 727 The encoded attraight share of the menus phalany II 1 of 7DAL McD 1/108
 - 737 The gracile and straight shape of the manus phalanx II-1 of ZPAL MgD-I/108/1 is the same as in 729 E arms ZPAL MgD I/08, although the shalaws of ZPAL MgD I/108/1 is leaven. The leavest of
 - *E. rarus* ZPAL MgD-I/98, although the phalanx of ZPAL MgD-I/108/1 is larger. The length of
 manus phalanx II-1 of ZPAL MgD-I/98 is 66 mm, the proximal width 14 mm, and the distal width
 - 740 12 mm (the length to width ratio is 4.7, same as for ZPAL MgD-I/108/1). The manus phalanx II-
 - 1 of ZPAL MgD-I/108/1 shares also with *E. rarus* slightly downturned distal condyle and
- 742 expanded articular surfaces of the distal condyles. Other theropods known from the Nemegt
- 743 Formation, i.e., tyrannosaurids (*T. bataar*, e.g., ZPAL MgD-I/3, ZPAL MgD-I/4), ornithomimids
- 744 (G.bullatus, cast of MPC-D 100/11; Deinocheirus mirificus Osmólska & Roniewicz, 1970, cast of
- 745 MPC-D 100/18), avimimids (alvarezsaurids (*Mononykus olecranus* (Perle *et al.*, 1994)), and
- oviraptorids (e.g., Oksoko avarsan (Funston et al., 2020a), Nemegtomaia barsboldi Lu et al., 2005
- 747 (Fanti *et al.*, 2012)) do not have manual phalanges that are so straight, slender, and elongated.
- 748
- 749 Manus ungual II-3
- 750 The ungual is elongated (54 mm in length), curved, and very narrow, and the proximal articular 751 surface is 13 mm wide (Fig. 19I-N). The ungual lacks only the distal tip. The proximal articular 752 surface is oval (longer dorsoventrally than mediolaterally). A vertical ridge, which is dorsally and 753 ventrally expanded but constricted in the middle section, extends across the middle of the articular 754 surface. The articular surfaces on both sides of the ridge are strongly concave. The dorsal edge of the articular surface forms a robust dorsal lip, surrounded by a depression. A ventral process is 755 present on the ventral edge of the articular surface. The articular surface is separated by a notch 756 757 from the ventrodistally located enlarged flexor tubercle. Laterally and medially, the collateral
- 758 groove extends along the entire ungual, starting from the area above the flexor tubercle.
- 759 The manus ungual II-3 is not known in *E. rarus*, however, the presence of the distinctive dorsal
- response of Caenagnathidae. Comparison
- with the manual unguals of an North American caenagnathid *Chirostenotes pergracillis* Gilmore,

762 1924, CMN 2367 (Funston, 2020) the ungual of ZPAL MgD-I/108/1 is less curved than the 763 phalanges I-2 and III-4, but more straight, similar to II-3. Moreover, the proximal articulation is 764 offset and the flexor tubercle is distally positioned and smaller in contrast to unguals I-2 and III-4, which further supports its identification as II-3 of a caenagnathid. Other theropods known from 765 the Nemegt Formation, i.e., tyrannosaurids (T. bataar, e.g., ZPAL MgD-I/3, ZPAL MgD-I/4), 766 ornithomimids (G. bullatus, cast of MPC-D 100/11; D. mirificus, cast of MPC-D 100/18), 767 768 alvarezsaurids (M. olecranus (Perle et al., 1994)), and oviraptorids (O. avarsan (Funston et al., 769 2020a), N. barsboldi (Fanti et al., 2012)) do not have such enlarged, curved, and transversely 770 narrow manual unguals with an enlarged flexor tubercle distinctly separated from the ventral 771 process and distinctive dorsal lip. 772

773 Femur

Two parts of the left femur are preserved: the proximal and distal end; most of the shaft is missing,

so the length of the femur is unknown (Fig. 20). The circumference of the shaft portions preserved
with the distal and proximal parts is 105 mm. Osmólska (1996) hypothesized that ca. 80–90 mm
of the shaft is missing, adding up to a total femur length of 310–320 mm.

778 The proximal part of the femur (Fig. 20A-E) is narrower lateromedially than longer 779 anteroposteriorly. In dorsal view, the femur is L-shaped. The posterior part of the greater trochanter 780 is connected to the femoral head that projects mediodistally, and the anterior part of the greater 781 trochanter is widened anteriorly. In anterior view, the femoral head is positioned higher than the 782 greater trochanter and they are separated by a broad, shallow depression. The surface of the 783 rounded femoral head is rugose. In posterior view, a wide groove for the capital ligament is present on the femoral head. In medial view, the femoral head is ovoid, and its posterodorsal margin is 784 wider than the anteroventral end. The neck is narrower anteroposteriorly than the head; and the 785 ventral margin of the head is directed downward before connecting to the neck. The neck extends 786 787 upward from the greater trochanter, which is wider lateromedially than the lesser trochanter. The 788 lesser trochanter is almond-shaped in anterior view. The dorsal margin of the femoral trochanters 789 in lateral view is arched; the small, anteriorly positioned lesser trochanter is separated by a shallow 790 groove from the much anteroposteriorly longer greater trochanter. On the lateral surface of the 791 proximal part of the femur, the separation between the lesser and greater trochanter is marked by 792 a shallow and short groove. Below the lesser trochanter, the accessory trochanter (anterior crest sensu Osmólska, 1996) is present. It is slightly expanded anteriorly and extends along the 793 preserved part of the proximal shaft. The accessory trochanter keeps a consistent lateromedial 794

795 width along the preserved proximal part of the shaft. A posterior tubercle is present below the 796 greater trochanter, well visible in anterior and posterior views.

797 The distal end of the femur is now longitudinally shorter than described by Osmólska (1996), 798 because it has since been thin sectioned. At that time, it measured 105 mm; now, only the 799 distalmost part of the femur including both condyles is present, measuring 52 mm (Fig. 20F-J). 800 The medial condyle is bigger than the lateral condyle, but the lateral condyle extends further 801 distally than the medial condyle. The condyles are distally separated by a deep but narrow notch 802 (the popliteal fossa). Anteriorly and distally, the condyles are separated by shallower and wider

803 depressions (the extensor grooves). The medial condyle is convex with a slightly rugose surface.

The lateral condyle bears an elevation on its distal surface. The tibiofibular crest extends posteromedially. In lateral view, the tibiofibular crest is axe-shaped, and projects further posteriorly than the medial condyle.

The accessory trochanter appeared in Tetanurae as a branch of the distal base of the lesser 807 trochanter and it was reduced in Eumaniraptora. The accessory trochanter is smaller in basal 808 Tetanurae, Carnosauria, basal Coelurosauria, Tyrannosauridae, and Ornithomimosauria, than in 809 810 Caudipteryx spp., Microvenator celer Ostrom, 1970, Caenagnathidae, and some Oviraptoridae 811 (Hutchinson, 2001). The accessory trochanter of the femur of ZPAL MgD-I/108/1 is clearly 812 demarcated from the lesser trochanter and forms a dorsoventral flange, comparable as seen in 813 Caenagnathidae, e.g., E. rarus ZPAL MgD-I/98, Anzu wyliei Lamanna et al., 2014, or Ch. 814 pergracilis (Currie & Russell, 1987). The lesser and greater trochanters are in contact as in all 815 Caenagnathoidea (Lamanna et al., 2014). The proximal end of the femur further resembles the 816 femur of E. rarus ZPAL MgD-I/98 in possessing a cylindrical head positioned higher than the greater trochanter and separated by a depression, which is wider in the larger (ontogenetically 817 818 older, as indicated by the difference in size between those specimens) ZPAL MgD-I/108/1. Such 819 an embayment is also present in other Caenagnathidae, e.g., A. wyliei (see Lamanna et al., 2014), 820 E. rarus (see Barsbold et al., 2000), or Ch. pergracilis (see Currie & Russell, 1987). A wide groove 821 on the posterior surface of the femoral head for the capital ligament is present in both E. rarus 822 ZPAL MgD-I/98 and MgD-I/108/1. Also, similar to Caenagnathidae, the lateral condyle of the 823 femur ZPAL MgD-I/108/1 is positioned more distally than the medial condyle, and the tibiofibular 824 crest is well demarcated (A. wyliei (see Lamanna et al., 2014), E. rarus (see Barsbold et al., 2000), 825 or Ch. Pergracilis (see Currie & Russell, 1987)). The extensor groove is distinct, but shallow, consistent with E. rarus (see Barsbold et al., 2000). The proximal and distal ends of the femur 826 ZPAL MgD-I/108/1 are of similar size to the measurements in E. rarus (see Barsbold et al., 2000), 827 828 so the probable length of the whole bone was similar, ca. 285 mm.

- 829
- 830 Bone microstructure of femur.

831 A histological section of the distal part of the shaft, above the condyles, shows a large marrow 832 cavity and thin (ca. 2 mm) cortex (Fig. 20K-L). The external part of the cortex (half of its thickness) 833 is built of parallel-fibered bone with scattered secondary osteons. The vascularization is laminar, 834 and growth marks are absent. In the section no definite primary osteons were seen, although the 835 external cortex is poorly preserved, possibly obscuring their presence. The inner cortex is sharply 836 demarcated from the external cortex and built of densely packed secondary osteons: up to 4 837 generations are present. Close to the marrow cavity, resorption cavities are present, surrounded by 838 a thick layer of lamellar bone (up to 0.3 mm). The marrow cavity is surrounded by a thinner layer of lamellar bone (0.15 mm) and filled by slender and elongated bony trabeculae. 839

- 840 The section shows features typical for the metaphyses of long bones: extensive secondary 841 remodeling, lack of growth marks, numerous resorption cavities. Thus, due to the lack of any 842 growth record in the section, it is not possible to estimate the growth ratio.
- 843 The bone microstructure of the femur in caenagnathids is unknown. Thus far, bone histology of
- the tibiae of cf. *Anzu wyliei* (ROM 65884) and Caenagnathidae indet. (UALVP 57349) have been
- described (Funston & Currie, 2018; Cullen et al., 2021). Both, however, represent young

846 individuals, as indicated by their predominant fibrolamellar bone, high vascularity, and limited

- secondary remodeling (none in UALVP 57349 and up to 30% of cortex in OMVP 65884). The
- 848 predominance of fibrolamellar bone and high vascularity are also seen in the cortices of the femora

and fibulae of the oviraptorid Oksoko avarsan, regardless of their ontogenetic age (Funston et al.,

850 2020). Even in the large-bodied cf. A. wyliei (ROM 65884), the section from the tibia revealed a

851 predominately primary tissue with generally high vascularity and limited secondary remodeling

852 (Cullen *et al.*, 2021). As can be noticed, the section taken from ZPAL MgD-I/108/1 is different

853 from the Caenagnathoidea described before, and it is explained as a result of its sectioning at the

- 854 metaphysis, and not diaphysis as it is usually done.
- 855

856 Tibiotarsus

The left tibiotarsus is complete and measures 380 mm (Fig. 21A-F). The bone is slender, slightly bowed laterally (possibly taphonomically exaggerated), and the distal fibula is fused to the distal tibia and calcaneum (Fig. 21A-C). The shaft is elliptical in cross section (circumference: 95 mm) and is compressed anteroposteriorly, possibly as an effect of taphonomical crushing. Proximally, the tibia expands anteriorly and slightly mediolaterally; its anteroposterior depth is 47.5 mm and mediolateral width is 59.2 mm. Distally, where the tibia is fused with the astragalocalcaneum distally and the fibula laterally, the tibia expands mediolaterally and measures 57.3 mm.

- 864 The cnemial crest condyle (cranial cnemial crest sensu Osmólska, 1996) is robust, laterally deflected, and short in anterior view, comprising only ca. 15% of the maximum proximodistal 865 tibiotarsus length. The fibular condyle (lateral cnemial crest sensu Osmólska, 1996) is also robust, 866 867 slightly curved anteriorly, and shorter mediolaterally and dorsoventrally than the cnemial crest. Between the cnemial crest and fibular condyle, a deep and posteriorly curved incisura tibialis is 868 present (Fig. 21A-E). The medial proximal condyle of the tibiotarsus is long anteroposteriorly; 869 anteriorly it is smoothly connected with the cnemial crest, and posteriorly it is separated from the 870 871 fibular condyle by a triangular cleft. The posteromedial edge of the medial proximal condyle of 872 the tibiotarsus is posteriorly extended. Below the fibular condyle, the fibular crest is present. It is 873 tall dorsoventrally, ca. 20% of the tibiotarsus length. The crest gets wider mediolaterally and 874 deflects anteriorly; however, the crest is not strongly pronounced. The distal end of the crest is
- 875 rectangular.

876 The fibula is fused to the lateral side of the distal end of the tibia, along the distal ca. 23% of the 877 tibiotarsus length (Fig. 21A-C). The distal end of the fibula is partly fused with the calcaneum. The outline of the distal part of the fibula is marked and distinguishable against the remaining 878 879 bones. The suture between the astragalocalcaneum and distal tibia are clearer in anterior than 880 posterior view; however, that may be a matter of preservation. No suture is visible between the astragalus and calcaneum. The calcaneum shows a lateral depression (lateral epicondylar 881 depression), below the suture with the fibula. The preserved, incomplete ascending process of the 882 astragalus extends along 7.5% of the of the tibiotarsus length. In anterior view, it has subtriangular 883 884 pointed medial and lateral processes, separated by a deep depression. At the base of the ascending 885 process, a shallow median depression is present, above which a low, mediolaterally extended ridge

is located (Fig. 21A).

887 A proper tibiotarsus—in which the tibia is fused to the proximal tarsals—is recognized in three 888 non-avian maniraptoran taxa: Alvarezsauridae, Troodontidae, and Avimimidae. Both 889 alvarezsaurids known from the Nemegt Formation (Mononykus olecranus Perle et al., 1993 and Nemegtonykus citus Lee et al., 2019) have a proximodistally short fibula, which does not reach 890 even the midshaft of the tibiotarsus (Perle et al., 1994; Lee et al., 2019). The presence of a 891 892 tibiotarsus in the troodontids know from the Nemegt Formation is variable. In the larger species 893 Zanabazar junior (Barsbold, 1974), the astagalocal caneum is not fused to the tibia (Norell et al., 894 2009), while in the smaller Borogovia gracilicrus Osmólska, 1987, a tibiotarsus is present 895 (Osmólska, 1987; Cau & Madzia, 2021). The hindlimb is unknown in the third troodontid from the Nemegt Formation, Tochisaurus nemegtensis Kurzanov & Osmólska, 1991. Only a fragment 896 of proximal right fibula of *Bo. gracilicrus* is preserved, but the distal end of the tibiotarsus does 897 898 not show any signs of fusion with the distal fibula, as in other Troodontidae e.g., Gao et al. (2012). 899 Oviraptoridae and Caenagnathidae show a fused astragalus and calcaneum, but not to the tibia (Currie et al., 2016). Finally, a fused tibiotarsus including the distal end of the fibula is an 900 901 autapomorphy of Aviminus spp. (Kurzanov, 1981; Funston et al., 2018).

902 However, ZPAL MgD-I/108/1 would be an exceptionally large representative of Avimimus; the 903 largest reported tibiotarsus of A. nemegtensis MPC-D 102/92 measures 282 mm (Funston et al., 2016), and in A. portentosus PIN 3907/1 it is 257 mm long (Kurzanov, 1981), whereas ZPAL 904 MgD-I/108/1 measures 380 mm, similar to E. rarus MPC-D 100/119 i.e., 355 mm. The 905 906 histological sections of the Iren Dabasu avimimids, revelated that the largest sectioned specimens were already adults (Funston et al., 2019). Moreover, three features of the tibia are shared for 907 908 ZPAL MgD-I/108/1 and E. rarus: (1) the medial proximal condyle is more protruded dorsally than in Avimimus spp.; (2) the fibular crest is longer and its distal end is rectangular, not arcuate as in 909 Avimimus spp.; and (3) the medial malleolus protrudes further medially than in Avimimus spp. 910

911

912 Fibula

913 The left fibula is complete, measuring 340 mm. The distal end is partially fused to the calcaneum, 914 and laterally fused to the tibia, along ca. 33% of the fibula's length. It is similar to Aviminus 915 portentosus, in which the fibula is fused to the tibia along 1/3 of its length (Kurzanov, 1981). The 916 proximal anteroposterior length of the fibula is 47.1 mm. The proximal end of the fibula is 917 triangular in the lateromedial aspect, only slightly concave medially in dorsal view (Fig. 21G-K), 918 similar to E. rarus (MPC-D 100/119; Barsbold et al., 2000), and in contrast to rectangular proximal 919 end in Avimimus spp. (Kurzanov, 1981; Funston et al., 2016). Distal to the expanded proximal 920 end, the fibula narrows anteroposteriorly. On the medial surface is a long (74.2 mm, about 22% of 921 total length) fusiform attachment for the fibular crest of the tibia. At this level, on the anterior surface of the fibula, an elliptical iliofibularis tubercle is present. Distally, the fibula strongly 922

923 narrows anteroposteriorly and has a triangular cross section along ca. 65% of its total length.

Despite the distal part of fibula fused with the tibia in a similar manner to *Avimimus* spp. the proximal end of the fibula is more triangular, as in MPC-D 100/119 (Barsbold *et al.*, 2000), than rectangular, as seen in *Avimimus* spp.

927

928 Pedal phalanx

929 The left phalanx II-2 is 35 mm long (Fig. 19U-A') and its length to width ratio is 2. The proximal 930 articular surface is triangular in posterior view, and can be divided into lateral and medial teardrop-931 shaped concave articular surfaces, separated from each other by a smooth ridge running in the 932 middle of the proximal articular surface. In the lateral and medial view the proximal articular 933 surface is strongly concave, the plantar margin extends backward, and the lip-shaped dorsal margin 934 (extensor turbecle) is elevated dorsally, and directed posteriorly. The distal articular surface is 935 composed of lateral condyle and slightly shorter plantodorsally medial condyle, which are separated by a concavity, which is shallow dorsally, but gets deeper along the articular surface to 936 its end on the plantar side. In anterior view, the lateral condyle extends downwards, than the medial 937 938 condyle. The ligament pits are well marked on the both sides of the phalanx, the lateral ligament 939 pit is elongated anteroposteriorly, and the medial ligament pit is circular.

940 The phalanx II-2 is similar to the corresponding phalanx of E. rarus (ZPAL MgD-I/98; length to width ratio: 2.1), especially in the structure of the proximal articular surface, i.e., two teardrop-941 shaped surfaces separated by a ridge, and the lip-like extensor tubercle. The phalanx II-2 in other 942 theropods from the Nemegt formation differs from the one of ZPAL MgD-I/108/1. This phalanx 943 in G. bullatus (ZPAL MgD-I/94) is compressed (the length to width ratio is 1.4), and the extensor 944 945 tubercle is less pronounced than in ZPAL MgD-I/108/1. The phalanx II-2 is even more compressed in *B. gracilicrus* (ZPAL MgD-I/174; the length to width ratio is 1.2). The proximal articular surface 946 947 in T. bataar (ZPAL MgD-I/3, ZPAL MgD-I/4, ZPAL MgD-I/29, ZPAL MgD-I/175) is wider than long, in contrast to E. rarus, G. bullatus, and ZPAL MgD-I/108/1. The length to width ratio of the 948 949 phalanx II-2 in *T. bataar* is 1.5-1.6, depending on the ontogenetical age.

950 951

SIZE OF THE SURANGULAR FORAMEN IN TYRANNOSAURIDS

952 The Pearson correlation coefficient for the measurements of the anteroposterior length of the 953 posterior surangular foramen and skull length is high and statistically significant (0.85653; 954 p=0.0001), indicating that the anteroposterior diameter of the surangular foramen is dependent on the skull length in tyrannosaurids (Fig. 22A). The regression analysis for all specimens and taxa 955 included shows a negative slope and a high correlation coefficient (slope: 1.32; R²=0.8; p=0.0001), 956 and the same is true even when juveniles are excluded (slope: 1.2; R²=0.68; p=0.001). The same 957 is true for Tarbosaurus bataar (slope: 0.04; R²=0.78; p=0.0005), Tyrannosaurus rex (slope: 0.03; 958 $R^2=0.94$; p<0.1), Gorgosaurus libratus (slope: 0.05; $R^2=0.76$; p<0.01), and Daspletosaurus spp. 959 (slope: 0.08; R²=0.88; p<0.01; Fig. 22B). This indicates a negative allometry, so the size of the 960 961 surangular foramen decreases during ontogeny in those tyrannosaurid species. This trend was 962 reported previously for T. rex (Carr, 2020). Our analysis does not find the surangular foramen of Bistahieversor sealevi, Daspletosaurus spp., Teratophoneus curriei, Qianzhousaurus sinensis, and 963 A. altai as enlarged in comparison to other tyrannosaurids. Also, the surangular foramen of T. 964 bataar is not smaller than in other tyrannosaurids as reported previously (Tsuihiji et al., 2011; 965 966 Voris et al., 2021).

- 967
- 968

PHYLOGENETIC ANALYSIS

The parsimony analysis of the larger, inclusive dataset of coelurosaurian phylogeny (based on Brusatte et al., 2014) resulted in 10 000 most parsimonious trees (the memory limit in TNT) of 971 3361 steps (CI=0.322, RI=0.777). The strict consensus tree (Fig. 23) places Bagaraatan ostromi 972 among tyrannosauroids, as the sister taxon to the clade Dryptosaurus aquilunguis + 973 Tyrannosauridae. B. ostromi shares seven synapomorphies with tyrannosauroids or major 974 inclusive clades: (1) extremely reduced retroarticular process of the articular; (2) pubic tubercle forming a convexity on the anterior margin of the pubis; (3) mediolateral width of the jaw muscle 975 976 attachment site of the articular equal to glenoid width (*Dilong paradoxus* + Tyrannosauridae); 977 surangular shelf (4) prominent and (5) not overhanging the surangular foramen, which abuts the 978 shelf (Eotyrannus lengi + Tyrannosauridae); (6) cervical vertebrae with hypapophysis (Xiongguanlong baimoensis Li et al., 2010 + Tyrannosauridae); and (7) thick laterally offset 979 980 posterior centrodiapophyseal laminae, which demarcates a deep infradiapophyseal fossa anteriorly 981 in the anterior-middle cervical vertebrae (B. ostromi + Tyrannosauridae). These results strongly 982 support the tyrannosauroid affinity of the B. ostromi holotype. The exact position of B. ostromi outside of Tyrannosauridae, however, may be an artefact of the immature status of the specimen. 983 Because of the robust tyrannosauroid affinities of the B. ostromi holotype, its more precise 984 985 relationships within Tyrannosauroidea are better tested with a phylogenetic dataset designed to 986 assess tyrannosauroid ingroup relationships. Thus, when we included it in the tyrannosauroid 987 dataset of Brusatte and Carr (2016), we found 40 most parsimonious trees (769 steps, CI=0.553, RI=0.812). The strict consensus tree (Fig. 24) places B. ostromi within a polytomy of derived 988 989 tyrannosauroids (with Bistahieversor sealeyi, Qianzhousaurus sinensis, Alioramus spp., and 990 Appalachiosaurus montgomeriensis, Albertosaurinae, and Tyrannosaurinae), which indicates that 991 it is either a member of Tyrannosauridae or a very close relative. Among the synapomorphies of 992 Tyrannosauroidea found also in *B. ostromi* are: (1) cervical vertebrae with hypapophysis; and (2) thin, sharp, and deeply inset Mackelian groove on the dentary. The synapomorphies of 993 994 Tyrannosauridae (or a slightly more inclusive clade, depending on the resolution of the polytomy) 995 present in B. ostromi are: (1) transitional point between the ventral and anterior margins of the 996 dentary positioned below the 4th alveolus; (2) the presence of a dentary 'chin'. Finally, the presence 997 of a small surangular foramen is found to be an autapomorphy of B. ostromi, a reversal from the enlarged condition in closely related taxa. 998

Because of the juvenile nature of the specimen (see below), we interpret these results as strong
support for the tyrannosaurid (or near-tyrannosaurid) affinities of *B. ostromi*, but do not put much
stock into its exact position on the tree, because juveniles often fall out more basally than adults
in phylogenetic analysis (Tschopp *et al.*, 2015).

1003 1004

1005

DISCUSSION

The Bagaraatan assemblage ZPAL MgD-I/108

1006 It will remain unknown why Osmólska (1996) refrained from even mentioning some of the 1007 remaining bones found together with what she considered to be *Bagaraatan ostromi*. Our complete 1008 reanalysis of the material collected and catalogued together revealed that ZPAL MgD-I/108 is not 1009 a single individual, but an assemblage of two different non-avian dinosaurs, in which only one 1010 individual was partly articulated. The presence of an oviraptorosaurian in the chimaera explains 1011 why some previous phylogenetic analyses found *B. ostromi* related with Maniraptora (Holtz, 1998; 1012 Rauhut, 2000; Rauhut *et al.*, 2010). 1013 Osmólska (1996) did remove most bones of the Caenagnathidae indet. found as part of ZPAL 1014 MgD-I/108 from what she considered to be *B. ostromi*, possibly due to the fact that 15 years earlier 1015 (Osmólska, 1981) she described a caenagnathid from the Nemegt Formation, *Elmisaurus rarus* with characteristic elongated manual phalanges. The caenagnathid bones from the assemblage 1016 which she did not exclude from the description of *B. ostromi* are: the femur, tibiotarsus, and pedal 1017 phalanx II-2 (ZPAL MgD-I/108/1). The femur of the holotype of *E. rarus* is incomplete—e.g., the 1018 1019 accessory trochanter is missing-and thus Osmólska possibly missed the similarities in the structure of the proximal end of the femur of E. rarus and the specimen she considered to be B. 1020 1021 ostromi. The femur of ZPAL MgD-I/108/1 definitely does not belong to a tyrannosaurid due to the 1022 presence of a: (1) clearly demarcated anterior trochanter, which is proximodistally long; (2) saddle-1023 like proximal margin of the femur; (3) lateral condyle positioned more distally than the medial 1024 condyle, and (4) tibiofibular crest well demarcated. Body size of the individual ZPAL MgD-1025 I/108/1 was similar to E. rarus (see Barsbold et al., 2000). The identification of the tibiotarsus is more problematic. The fusion of the astragalocalcaneum with the tibia and the fusion of the distal 1026 1027 end of fibula to the tibia should unambiguously indicate a representative of Avimimidae 1028 (Kurzanov, 1981; Funston et al., 2018). However, the large (for an avimimid) size of the 1029 tibiotarsus, and the morphological features of the tibia and fibula are more reminiscent of the Caenagnathidae. In the latter taxon, the fusion usually occurs between the astragalus and 1030 calcaneum and less often between the distal tarsals and metatarsals (as proposed by Currie et al., 1031 1032 2016 in mature individuals). There are two caenagnathids thus far known in which the astragalus 1033 fused with the tibia (Atkins-Weltman et al. in review). Therefore, given the large size of the 1034 individual, a caenagnathid-like general morphology of the tibia and fibula, and the general tendency towards the fusion of the bones among the heel joint in the Caenagnathoidae, we decided 1035 to recognize the tibiotarsus as belonging to an senile or/and atypical (in the terms of bone fusion) 1036 caenagnathid. The size of the tibiotarsus fits to the remaining bones of ZPAL MgD-I/108/1, thus 1037 1038 they likely belonged to a single individual. Finally, the pes phalanx II-2, as described above, matches the general morphology seen in the caenagnathids. Thus, the hind limb bones that 1039 1040 Osmólska (1996) originally considered a part of B. ostromi could not have been found in 1041 articulation with each other, nor with the tyrannosauroid skeleton that we designate as the amended 1042 holotype of B. ostromi. Two species of caenagnathids were known from the Nemegt Formation of Mongolia: E. rarus and 'N. gobiensis'; however, the validity of the latter was recently called into 1043 question (Funston et al., 2018, 2021), implying that only one caenagnathid lived in the Nemegt 1044 Formation: E. rarus, thus the specimen ZPAL MgD-I/108/1 is most likely a representative of that 1045 1046 species.

Finally, the mandible, axial skeleton, and pelvis of the B. ostromi material was found in 1047 articulation, as noted by Osmólska (1996; Fig. 25). This specimen, ZPAL MgD-I/108, is here 1048 designated as the holotype of *B. ostromi* and is referred to Tyrannosauridae indet. due to the 1049 presence of numerous diagnostic features, including a dentary 'chin' and the position of the 1050 transition between the anterior and ventral edges of the dentary below the fourth alveolus (Fig. 1). 1051 1052 Those features were considered synapomorphies of *Bistahieversor sealeyi* + *Appalachiosaurus* 1053 montgomeriensis + Tyrannosauridae (Brusatte et al., 2010; Brusatte and Carr, 2016) and appear 1054 early in the ontogeny of tyrannosaurids (Funston et al., 2020b). The dorsoventrally narrow

1055 Meckelian groove deeply inset into the medial side of the dentary is a tyrannosauroid 1056 synapomorphy, also present already in hatchlings (Funston et al., 2020b). The extremely reduced 1057 retroarticular process of the articular and prominent surangular shelf present in B. ostromi are also typical for tyrannosauroids (Brusatte et al., 2014). The features of the postcranial skeleton, such 1058 as the convexity on the anterior margin of the pubis (present in all Tyrannosauroidea), cervical 1059 vertebrae with a hypapophysis (present in *Xiongguanlong baimoensis* + Tyrannosauroidea) and 1060 1061 thick posterior centrodiapophyseal laminae (present in Dryptosaurus aquilunguis + Tyrannosauroidea) further support the close affinities of this associated holotype skeleton of B. 1062 ostromi with tyrannosaurids. 1063

Only three clearly valid tyrannosaurid species are currently known from the Nemegt Formation in 1064 Mongolia: the large-bodied, common *Tarbosaurus bataar*, and the much smaller and uncommon 1065 1066 long-snouted Alioramus remotus and Alioramus altai. Another potentially valid taxon, Raptorex kriegsteini (Sereno et al., 2009; Carr 2023), also most likely comes from the Nemegt Formation 1067 (Fowler et al. 2011), but as its holotype is a very small juvenile, its taxonomic status is difficult to 1068 1069 determine and awaits full description of the material. B. ostromi is much smaller than all of them 1070 (Raptorex notwithstanding), with an estimated body length not larger than 3 m, vs 10 m in T. bataar and 5-6 m in the known subadult skeletons of Alioramus spp., which admittedly may have 1071 been larger as adults (Brusatte et al., 2009, 2012). The size of Bagaratan's mandible is slightly 1072 larger than those of 'Shanshanosaurus huoyanshanensis', which was once considered a valid 1073 1074 species from the Chinese Subashi Formation (contemporary to the Nemegt Formation; Wan et al., 1075 2007), but is now regarded a juvenile tyrannosaurid (Currie and Dong, 2001). The B. ostromi mandible, however, is similar in size and general structure to the mandible of the juvenile T. bataar 1076 MPC-D 107/7 described by Tsuihiji et al., (2011). This raises a question: does B. ostromi represent 1077 a juvenile of one of the already known Nemegt tyrannosaurid species? 1078

1079 1080

Is Bagaraatan ostromi a valid taxon?

Osmólska (1996) listed eight diagnostic features for Bagaraatan ostromi: (1) two surangular 1081 1082 foramina (also considered by Holtz (2004) an autapomorphy of *B. ostromi*); (2) articular with an 1083 oblique posterior surface and a short retroarticular surface; (3) caudal vertebrae with thin-walled 1084 centra; (4) hyposphene-hypantrum articulations in at least the first 16 caudal vertebrae (also listed by Holtz (2004) as an autapomorphy of *B. ostromi*); (5) prezygapophyses in proximal caudal 1085 vertebrae with ridges on the lateral surfaces; (6) ilium with two deep depressions; (7) femur with 1086 1087 the anterior trochanter (anterior crest sensu Osmólska); and (8) tibia and fibula fused distally. The status of those features is shortly discussed below. Because we have now reidentified the hindlimb 1088 1089 bones as belonging to other non-tyrannosaurid taxa, those features regarding the hind limb were discussed above, so they will be omitted in this section. 1090

1091 The ilium with a distinct ridge on the lateral surface of the postacetabular process, demarcated 1092 anteriorly, medially, and posteriorly by depressions, is striking (Fig. 16). It occurs symmetrically 1093 on both ilia, and better preserved on the left, which is less compressed. Such ridges are not found 1094 in other theropods, to our knowledge, and are not present in juvenile *Tarbosaurus bataar* (MPC-1095 D 107/7) nor the other tyrannosaurid juvenile, *Raptorex kriegsteini* (Sereno *et al.*, 2009). 1096 Therefore, they may be a diagnostic feature of *B. ostromi*. 1097 The ridges on the lateral surfaces of the prezygapophyses are found also in the proximal caudal 1098 vertebrae of Tyrannosaurus rex, running from the anterior margin of the transverse process to the 1099 prezygapopysis (Brochu, 2003). Similar ridges on the prezygapophyses of anterior caudal vertebrae are also present in T. bataar (ZPAL MgD-I/176). Osmólska (1996) did not quantify how 1100 thin-walled the caudal vertebrae centra of B. ostromi are in comparison to other theropods. We do 1101 1102 not recognize any clear difference between the centrum thickness of B. ostromi and other 1103 theropods. The stout hyposphene-hypantrum articulations in at least the first 16 caudal vertebrae 1104 was considered an autapomorphy of B. ostromi by Osmólska (1996) and Holtz (2004). The presence of the hyposphene-hypantrum articulation is seen in many archosaurs, is strongly 1105 correlated with body size and is often present already at a young age, before the articulation is 1106 necessary to support the large mass of the fully-grown animal (Stefanic & Nesbitt, 2019). The 1107 1108 hyposphene-hypantrum articulations are common in theropods, and for instance, are present in the 1109 caudal vertebrae of medium-sized T. bataar (ZPAL MgD-I/176). The oblique posterior surface 1110 and short retroarticular surface of the articular, also listed by Osmólska (1996), are tyrannosauroid 1111 synapomorphies (Brusatte et al., 2014).

1112 The presence of two surangular foramina and the ridge on the lateral surface of the postacetabular process of ilium seem to be only two features listed by Osmólska (1996) which distinguish B. 1113 ostromi from other tyrannosaurids. The two surangular foramina were also later listed by Holtz 1114 (2004) as unique for *B. ostromi* in comparison to other theropods (Currie et al., 2003). There is 1115 1116 some confusion in the literature about the size of the surangular foramen in tyrannosauroids, and 1117 its phylogenetic significance and ontogenetic and individual variation. In their phylogenetic dataset of tyrannosauroids, Brusatte and Carr (2016) used a character which simply divided the 1118 size of the foramen into two states: those with a dorsoventral depth less than or greater than 30% 1119 of the depth of the posterior end of the surangular. This was based on earlier characters used by 1120 Sereno et al. (2009, Carr and Williamson (2010), and Brusatte et al. (2010). The enlarged condition 1121 1122 was found to be synapomorphic of a clade consisting of Dryptosaurus + Tyrannosauridae, whereas 1123 the primitive smaller foramen is seen in more basal tyrannosauroids like Suskityrannus,

- 1124 Eotyrannus, Dilong, and proceratosaurids.
- 1125 Other authors, however, have considered the foramen differently. The size of the surangular 1126 foramen in tyrannosaurids was divided into moderate (Gorgosaurus libratus, Albertosaurus
- 1127 sarcophagus Osborn, 1905, T. rex, and T. bataar) or enlarged (Bistahieversor sealevi, 1128 Daspletosaurus spp., Teratophoneus curriei, Thanatotheristes degrootorum Voris et al., 2020,
- Qianzhousaurus sinensis, and Alioramus altai) states by Voris et al., (2021). However, the 1129
- surangular foramen in T. rex and Albertosaurus sarcophagus used to be also classified as smaller 1130
- than in other tyrannosaurids (Carr & Williamson, 2004). Other authors reported that the surangular 1131
- foramen in T. bataar is smaller than in other tyrannosaurids and invariant during ontogeny 1132
- 1133 (Tsuihiji et al., 2011; Voris et al., 2021). Also, the surangular foramen in 'Shanshanosaurus 1134
- huoyanshanensis' was described as large (Currie & Dong, 2001), but later as small (Tsuihiji et al.,
- 2011). For T. rex, the size of the surangular foramen was first reported as increasing (Carr, 1999), 1135
- 1136 but later as decreasing in size, through ontogeny (Carr, 2020).
- 1137 Because of this confusion, we built a dataset to examine the size of foramina in a quantitative
- 1138 context. In tyrannosaurids the mandible, skull, and femur growth are isometric, and are related to

1139 the body size of the individual (Currie, 2003b). Thus, we assessed the relationship between the 1140 size of the surangular foramen and skull length (as a proxy for body size). Our results (Fig. 22) 1141 show that in all taxa the size of the surangular foramen decreases during ontogeny (negative allometry), and is strongly correlated with the length of the skull. Thus, e.g., A. altai (IGM 1142 100/1844) and the similarly sized G. libratus (TMP 1991.36.500) have surangular foramina of 1143 proportionally the same size. Although the surangular foramen-skull length correlation is 1144 1145 statistically significant, variability in surangular foramen size is also apparent, especially in G. 1146 *libratus* and *T. bataar*; for which the data are less fitted to the trend than for the other species (R²=0.76-0.78, vs. R²>0.88-0.94 in *Daspletosaurus* spp., and *T. rex*; Fig. 22). Indeed, although 1147 the surangular foramen is rather enlarged in *Tarbosaurus* individuals (as in other tyrannosaurids; 1148 Fig. 22) bigger than MPC-D 100/66 (skull length: 45 cm), few exceptions were found within the 1149 1150 hypodigm. The surangular foramen of the medium-sized specimen MPC-D 107/14 is exceptionally 1151 small in comparison to other T. bataar individuals of similar size (e.g., ZPAL MgD-I/3; MPC-D 107/5; Fig. 5). Moreover, a specimen larger than the listed above, MPC-D 100/60, shows 1152 1153 asymmetrical surangular foramina: the left one is smaller (anteroposterior length: 23 mm) and the 1154 right one is larger (anteroposterior length: 40 mm). The smaller surangular foramen of the left 1155 mandible can be noticed as an outlier in the Figure 22. So, apparently, there was some variability in the timing of the surangular foramen enlargement, at least in T. bataar. The size of the 1156 surangular foramen in *B. ostromi*, regardless if measured for the single (posterior only) or double 1157 (posterior + anterior) foramina, falls into the overall variability of surangular size in the 1158 1159 tyrannosaurids generally and T. bataar specifically. The position of the surangular foramen in 'Shanshanosaurus' and T. bataar MPC-D 107/7 is similar to the position of the posterior opening 1160 in the surangular of Bagaraatan and those individuals cluster together on the plot. In turn, if the 1161 length of the area of both surangular foramina was measured for B. ostromi, it clusters with 1162 Raptorex kriegsteni, the surangular foramen of which was previously reported as 'enlarged' 1163 1164 (Fowler *et al.*, 2011).

1165 What might explain the strange double set of foramina in Bagaraatan? The bone between the 1166 anterior and posterior surangular foramina in B. ostromi is very thin, and the relative position of 1167 this area and both foramina matches the surangular foramen of *Raptorex kriegsteni* and *T. bataar* 1168 (ZPAL MgD-I/31). The surangular in tyrannosaurids during the early years of life was invaded by a pneumatic diverticulum (Gold et al., 2013), which pneumatized the bone and formed the enlarged 1169 surangular foramen, bordered by a pneumatic pocket posterodorsal to it. Because more basal 1170 tyrannosauroids have a small foramen without a pneumatic pocket, it is not clear if there was any 1171 pneumatic diverticulum in this region in these species. Due to the fact that pneumatic diverticula 1172 induce bone resorption when they contact bone (Bremer, 1940; Witmer, 1997; Wedel, 2007), we 1173 propose that the mandible of *B. ostromi* exhibits local bone resorption induced by the pneumatic 1174 1175 diverticula, that would explain the extremely thin bone between the anterior and posterior foramen. We hypothesize that if the pneumatization process continued slightly longer, the two foramina 1176 might have merged into a single large foramen, which is the common condition in Dryptosaurus 1177 1178 + Tyrannosauridae (Brusatte and Carr, 2016). This proposal is supported by the fact that the 1179 posterior surangular foramen in *B. ostromi* is similar in length and positioned in a similar place as 1180 in the smaller 'Shanshanosaurus' and T. bataar MPC-D 107/7 (skull length about 29 cm) specimens. Furthermore, the area of the surangular containing the posterior and anterior surangular foramina, and the thinned bone between them, matches the length and position of the surangular foramen in *Raptorex* (skull length about 30 cm). Therefore, *B. ostromi* (also ca. 30 cm long skull) possibly captures the precise moment of ongoing bone resorption and perforation due to the pneumatic diverticulum. This process likely occurred early in ontogeny, in specimens 2–3 m long, which were probably 2–3 years old at the time of death (as indicated for *T. bataar* MPC-D 107/7 by Tsuihiji *et al.* (2011)). Apparently around this growth stage the pneumatic diverticulum invaded

- 1188 the bone, and thus variability in the size, shape, and even number of foramina is to be expected.
- 1189

1190

Juvenile Tyrannosauridae indet.

1191 Due to its small body size and similarity to other juvenile tyrannosaurid specimens from the 1192 Nemegt, it is likely that *Bagaraatan ostromi* is a juvenile tyrannosaurid. We tested this hypothesis

1193 further by determining if *B. ostromi* shows juvenile features that have been well documented in

1194 *Tyrannosaurus rex*, whose ontogenetic osteological changes have been chronicled in detail by Carr

1195 (2020). We recognized that *B. ostromi* shows 22 juvenile, and only 5 adult mandible features found

1196 in *T. rex* by Carr (2020). Four out of the 22 juvenile features were found only in early juveniles,

- and the remaining eighteen in late juveniles.
- The mandible characters recognized both in *B. ostromi* and juveniles of *T. rex* are: (1) increasing 1198 posteriorly size of the first three alveoli of the dentary; (2) shallow dentary in lateral view; (3) 1199 shallow coronoid region of the surangular; (4) no ridge delimiting the caudoventral fossa of the 1200 angular caudal process; (5) first two dentary alveoli much smaller than the latter alveoli; (6) 8th 1201 tooth is the mesiodistally longest in the dentary; (7) the alveoli decreasing posteriorly in 1202 mesiodistal length from the sixth to seventh alveolus; (8) single large pit median to the Meckelian 1203 fossa; (9) low angle of the 'chin'; (10) lightly textured 'chin' region; (11) distance of the 1204 ventralmost dentary foramen from the dorsal margin of the dentary to the total height of the bone 1205 1206 greater than 40%; (12) the lateral extension of the surangular shelf horizontal; (13) surangular shelf not slanted; (14) small surangular foramen; (15) caudal extent of the coronoid process declining 1207 1208 before it reaches the glenoid; (16) presence of an embayment on the caudal margin of the 1209 surangular foramen; (17) cleft between the caudal glenoid process dorsoventrally short and 1210 shallow; (18) caudal end of the surangular shelf fading below the glenoid region; (19) lateral scar on the surangular present; (20) caudal glenoid process as tall as the rostral process; (21) lateral 1211 1212 scar on the surangular rugose and shallow; (22) dorsal orientation of the anterior glenoid foramen (Carr, 2020). 1213
- 1214 The prevalence of features shared by *B. ostromi* with juvenile *T. rex* supports the identification of 1215 *B. ostromi* as a young tyrannosaurid. The less numerous adult *T. rex* features (Carr, 2020) found
- 1216 in *B. ostromi* are listed below, with comments regarding variability within *Tarbosaurus bataar*.
- 1217 (1) The second dentary tooth is more than 75% of the mesiodistal length of the third dentary tooth.
- 1218 The proportions between the first three dentary teeth in *T. bataar* seem to be variable. In the
- 1219 subadult ZPAL MgD-I/175, the second dentary tooth is less than 75% of the mesiodistal length of
- 1220 the third dentary tooth, and in the adults (ZPAL MgD-I/5) it is between 70–78%. (2) The combined
- 1221 mesiodistal lengths of the first two alveoli of the dentary are greater than the mesiodistal length of
- 1222 the third alveolus, as in all examined individuals of *T. bataar* (subadults ZPAL MgD-I/45, ZPAL

1223 MgD-I/46, ZPAL MgD-I/175; and adults ZPAL MgD-I/4, ZPAL MgD-I/5; Table 1). However, 1224 the difference in all T. bataar specimens is greater (ca. 4 cm) than in B. ostromi (1 cm). (3) Lack 1225 of the deviation in the 'chin' region, which is not recognized in any examined T. bataar specimen (ZPAL MgD-I/45, ZPAL MgD-I/46, ZPAL MgD-I/175, ZPAL MgD-I/4, ZPAL MgD-I/5), nor it 1226 has been described in juvenile T. bataar MPC-D 107/7 (Tsuihiji et al., 2011). (4) The caudal 1227 surangular foramen is positioned far anteriorly to the glenoid, as in all *T. bataar* individuals (ZPAL 1228 1229 MgD-I/4, ZPAL MgD-I/5, ZPAL MgD-I/31) including the juvenile MPC-D 107/7 (Tsuihiji et al., 1230 2011). (5) Short and deep glenoid fossa in adult T. rex and B. ostromi. A shallow and long glenoid fossa can be recognized in 'Shanshanosaurus huoyanshanensis' see (Currie & Dong, 2001), but 1231 already in the slightly larger MPC-D 107/7 and B. ostromi, as well as young and adult T. bataar 1232 (ZPAL MgD-I/4, ZPAL MgD-I/5 ZPAL MgD-I/31), it is narrow and deep. Those features possibly 1233 1234 indicate some species-dependent variability, similar to the proportion of the antorbital fenestra, which does not shorten as much during the ontogeny of T. bataar as it does in T. rex (Tsuihiji et 1235 1236 al., 2011).

1237 As it is clear that the *B. ostromi* holotype belongs to a juvenile tyrannosaurid, the question 1238 becomes: can we identify which species it belonged to? We can first make comparisons to the other Nemegt tyrannosaurids: T. bataar and Alioramus spp. The mandible of B. ostromi is 1239 generally similar to juvenile T. bataar or putative juveniles of that species like 'S. 1240 huovanshanensis' and Raptorex kriegsteni see (Currie & Dong, 2001; Sereno et al., 2009; Fowler 1241 1242 et al., 2011; Tsuihiji et al., 2011). The dentary is straight in the dorsal and ventral view, shallow, 1243 slender, thickens and tapers dorsally at the anterior end. B. ostromi, similarly to MPC-D 107/7, 1244 but in contrast to T. bataar specimens and A. altai, does not show any pneumatic pocket behind the surangular foramen (Tsuihiji et al., 2011; Brusatte et al., 2012). The cervical vertebrae of B. 1245 ostromi strongly resemble the middle or posterior cervical vertebrae of 'S. huoyanshanensis'. They 1246 share the posterodorsal rather than dorsal inclination of the neural spines, and less flexed centra 1247 than in adult, large tyrannosaurids (Currie & Zhiming, 2001). The fusion of some bones occurred 1248 1249 early in the ontogeny of tyrannosaurids, e.g., the juvenile T. bataar has already fused nasals 1250 (Tsuihiji et al., 2011). However, the articular remains unfused with the surangular in B. ostromi, 1251 similar to 'S. huoyanshanensis', juvenile T. bataar (MPC-D 107/7), and A. altai (see Brusatte et 1252 al.; 2012). In contrast, in *Raptorex* and larger *T. bataar* individuals the articular is fused to the 1253 surangular. Moreover, early in ontogeny partial fusion of the pelvis was reported in *Raptorex* (see 1254 Fowler et al., 2011), and young T. rex (BMR P2002.4.1, 'Jane'; Larson & Parrish, 2013). On the other hand, the pelvic bones are unfused in B. ostromi, juvenile T. bataar (MPC-D 107/7), and 1255 subadult A. altai (see Brusatte et al., 2012) However, an early fusion of the cranial sutures may 1256 not necessarily be associated with an early fusion of postcrania, since these functional units could 1257 be subjected to developmental plasticity or separate evolutionary pressure depending on the 1258 ecology and preferred or available diet. The coossification of postcranial sutures and fusion 1259 between bones among tyranosaurids require further study. However, due to their high variability, 1260 also in juveniles, we do not find them as a adequate indicator for growth stage in tyrannosaurids. 1261

We can more thoroughly compare *B. ostromi* to young juvenile *T. bataar*, because no young
juveniles of *Alioramus* spp. are known thus far. Due to the fact that both tyrannosaurids occur in
the Nemegt Formation and *B. ostromi* lacks diagnostic features of either *Alioramus* spp. (see

1265 Brusatte et al., 2012) or T. bataar (see Hurum & Sabath, 2003) which is mostly due to the 1266 fragmentary nature of the holotype skeleton, we cannot assign ZPAL MgD-108/1 to any particular 1267 species. Some subtle features suggest that B. ostromi may be a juvenile of T. bataar: e.g., (1) already strongly expanded anterior end of the dentary, (2) 'chin' well demarcated, (3) lack of the 1268 pneumatic pocket next to the surangular foramen. However, because those features may potentially 1269 be a result of intraspecific variability or be more widespread among juvenile tyrannosaurids than 1270 1271 currently suspected, we cannot clearly determine whether B. ostromi is a juvenile of T. bataar or 1272 Alioramus spp. Thus, we consider B. ostromi to be an indeterminate juvenile representative of the 1273 Tyrannosauridae. This assessment may be modified in the future, when more juvenile individuals 1274 of tyrannosaurid taxa are known (particularly young individuals of *Alioramus* spp.) and the growth series and variability at early life stages are better understood. 1275 1276

CONCLUSIONS

1278 The enigmatic theropod described by Osmólska (1996) from the Late Cretaceous Nemegt Formation of Mongolia, Bagaraatan ostromi, is a chimaera of two non-avian dinosaurs. First, the 1279 femur, tibiotarsus, and pedal phalanx II-2 together with several other bones not described by 1280 Osmólska but catalogued under the same specimen number (manus phalanges, caudal vertebrae, 1281 and rib) are referred here to the Caenagnathidae. Second, the mandible, axial skeleton, pelvis, and 1282 1283 pedal phalanx IV-1-which together form an associated skeleton-are considered here as the 1284 holotype of B. ostromi and identified as Tyrannosauridae indet. (Fig. 25). Due to the presence of 1285 numerous juvenile features, which are seen in young individuals of *Tyrannosaurus rex*, and many shared similarities with juvenile *Tarbosaurus bataar* and putative representative of that species 1286 1287 ('Shanshanosaurus') we propose that *B. ostromi* is a juvenile tyrannosaurid. There are two features distinguishing B. ostromi from other tyrannosaurids: the ridge separating two depressions on the 1288 lateral surface of the postacetabular process and the presence of a double surangular foramen. The 1289 1290 latter we interpret as a result of ongoing bone resorption due to the entrance of the pneumatic 1291 diverticulum into the surangular. Three (or four) previously known tyrannosaurids co-occur in the Nemegt Formation: T. bataar, Alioramus altai, and A. remotus (and maybe R. kriegsteni), and the 1292 morphology of the mandible suggest that B. ostromi is most similar to juvenile T. bataar. However, 1293 1294 due to the lack of diagnostic features in the preserved material, which would clearly indicate its 1295 taxonomic identity, and the confounding issues of individual and ontogenetic variation in 1296 tyrannosaurids, we simply conclude at the moment that *Bagaraatan* is a juvenile tyrannosaurid, of 1297 uncertain species placement. Yet, we do not elect to formally sink *B. ostromi* as a name, because 1298 we have identified some potentially diagnostic features at the species level, and because tyrannosaurid specimens are commonly found in the Nemegt Formation, meaning that future 1299 discoveries should help clarify this taxonomic issue. 1300

1302COMPETING INTERESTS1303The authors declare that they have no competing interests.13041305

1277

1301

1306	REFERENCES
1307	Alifanov VR. 2012. Suborder Theropoda. In: Kurochin EN, In: Lopatin A V., eds. Fossil
1308	vertebrates of Russia and adjacent countries. Part 2: Fossil reptiles and birds. Moscow: CEOS,
1309	169–240.
1310	Andrews CW. 1913. On some bird remains from the Upper Cretaceous of Transylvania.
1311	Geological Magazine 5: 193–196.
1312	Atkins-Weltman; K.L.; Simon; J.D.; Woodward; H.N.; Funston; G.F.; Snively; E.R.
1313	Accepted pending minor revisions. A new oviraptorosaur (Dinosauria: Theropoda) from the end-
1314	Maastrichtian Hell Creek Formation of North America. PLoS ONE manuscript no PONE-D-23-
1315	20976 [Resubmitted July 5; 2023].
1316	Barsbold R. 1974. Saurornithoididae, a new family of small theropod dinosaurs from Central
1317	Asia and North America. Palaeontologia Polonica 30: 5–22.
1318	Barsbold R, Osmólska H, Watabe M, Currte PJ, Tsogtbaatar K. 2000. A new oviraptorosaur
1319	(Dinosauria, Theropoda) from Mongolia: the first dinosaur with a pygostyle. Acta Geologica
1320	<i>Polonica</i> 45: 97–106.
1321	Bell P, Currie PJ, Lee YN. 2012. Tyrannosaur feeding traces on <i>Deinocheirus</i> (Theropoda:?
1322	Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia.
1323	Cretaceous Research 37: 186–190.
1324	Bremer JL. 1940. The pneumatization of the humerus in common fowl and the associated
1325	activity of theelin. Anatomical Record 77: 197–211.
1326	Brochu CA. 2003. Osteology of <i>Tyrannosaurus rex</i> : insights from a nearly complete skeleton
1327	and high-resolution computed tomographic analysis of the skull. Journal of Vertebrate
1328	Paleonotology 22: 1–138.
1329	Brusatte SL. 2013. The Phylogeny of Basal Coelurosaurian Theropods (Archosauria:
1330	Dinosauria) and Patterns of Morphological Evolution during the Dinosaur-Bird Transition.
1331	Unpublished PhD Dissertation, Columbia University, New York.
1332	Brusatte SL, Carr TD. 2016. The phylogeny and evolutionary history of tyrannosauroid
1333	dinosaurs. Scientific Reports 6: 1–8.
1334	Brusatte SL, Carr TD, Erickson GM, Bever GS, Norell MA. 2009. A long-snouted,
1335	multihorned tyrannosaurid from the Late Cretaceous of Mongolia. <i>Proceedings of the National</i>
1336	Academy of Sciences of the United States of America 106: 17261–17266.
1337	Brusatte SL, Carr ID, Norell MA. 2012. The osteology of <i>Altoramus</i> , a gracile and long-
1338	snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. Bulletin
1339	of the American Museum of Natural History 300: 1–197.
1340	Brusatte SL, Carr ID, Williamson IE, Holtz IR, Hone DWE, Williams SA. 2016. Dentary
1341	dinasour Comment on t "Distribution of the dentery measure of theread dinasours.
1042	Implications for theremod phylogeny and the validity of the genu. Cratagoous Research 65: 222
1343	niplications for theropod phylogeny and the validity of the genu. Cretaceous Research 05. 252–
1044	25%. Brusatta SL Llavd CT Wang SC Narall MA 2014 Gradual accombly of avian body plan
1345	aulmineted in renid rotes of evolution across the dineseur hird transition. Current Biology 24:
1040	2286 2202
1347	2300-2392. Brusatta SI Norall MA Carr TD Frickson CM Hutchinson IB Balanoff AM Bayar CS
1340	Chainiere IN Makovicky PI XII X 2010 Tyrannosaur naleobiology, new research on ancient
1350	evemplar organisms. Science 329: 1481_1485
1351	Carr TD 1999 Craniofacial ontogeny in Tyrannosauridae (Dinosauria Coelurosauria) <i>Journal</i>
1352	of Vertebrate Paleontology 19: 497–520
1353	Carr TD 2020 A high-resolution growth series of <i>Twrannosaurus rer</i> obtained from multiple
1000	Curr 11. Low of the men resolution growth series of Lyrunnosuurus rev obtained nom multiple

- 1354 lines of evidence. *PeerJ* 8: e9192.
- 1355 Carr TD. 2023. A reappraisal of tyrannosauroid fossils from the Iren Dabasu Formation
- 1356 (Coniacian–Campanian); Inner Mongolia; People's Republic of China. *Journal of Vertebrate* 1357 *Paleontology* e2199817.
- 1358 **Carr TD, Williamson TE. 2004**. Diversity of late Maastrichtian Tyrannosauridae (Dinosauria:
- 1359 Theropoda) from western North America. *Zoological Journal of the Linnean Society* 142: 479– 1360 523.
- 1361 Carr TD, Williamson TE. 2010. *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid
 1362 from New Mexico and the origin of deep snouts in Tyrannosauroidea. *Journal of Vertebrate*1363 *Paleonotology* 30: 1–16.
- 1364 Carr TD, Williamson TE, Britt BB, Stadtman K. 2011. Evidence for high taxonomic and
- 1365 morphologic tyrannosaurid diversity in the Late Cretaceous (Late Campanian) of the American
- Southwest and a new short-skulled tyrannosaurid from the Kaiparowits formation of Utah. *Naturwissenschaften* 98: 241–246.
- 1368 Carrano MT, Hutchinson JR. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex*
- 1369 (Dinosauria: Theropoda). Journal of Morphology 253: 207–228.
- 1370 Cau A, Madzia D. 2021. The phylogenetic affinities and morphological peculiarities of the bird-
- 1371 like dinosaur *Borogovia gracilicrus* from the Upper Cretaceous of Mongolia. *PeerJ* 9: e12640.
- 1372 Chinsamy-Turan, A. 2005. *The microstructure of dinosaur bone*. Johns Hopkins University 1373 Press, 1-216.
- 1374 Choiniere JN, Clark JM, Forster CA, Xu X. 2010. A basal coelurosaur (Dinosauria:
- 1375 Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucaiwan,
- 1376 People's Republic of China. Journal of Vertebrate Paleontology 30: 1773–1793.
- 1377 Cope ED. 1866. Discovery of a gigantic dinosaur in the Cretaceous of New Jersey. *Proceedings*1378 of the Academy of Natural Sciences of Philadelphia 18: 275–279.
- 1379 Csiki Z, Grigorescu D. 1998. Small theropods from the Late Cretaceous of the hateg basin
- 1380 (Western Romania) an unexpected diversity at the top of the food chain. *Oryctos* I: 87–104.
- Cullen TM, Simon DJ, Benner EKC, Evans DC. 2021. Morphology and osteohistology of a
- 1382 large-bodied caenagnathid (Theropoda, Oviraptorosauria) from the Hell Creek Formation
- (Montana): implications for size-based classifications and growth reconstruction in theropods.
- 1384 Papers in Palaeontology 7: 751–767.
- 1385 Currie PJ. 2003a. Theropods from the Cretaceous of Mongolia. In: Benton MJ,, In: Shishkin
- MA,, In: Unwin DM,, In: Kurochkin EN, eds. *The Age of Dinosaurs in Russia and Mongolia*.
 Cambridge: Cambridge University Press, 434–455.
- Currie PJ. 2003b. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper
 Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences* 40: 651–665.
- 1390 Currie PJ, Dong ZM. 2001. New information on *Shanshanosaurus huovanshanensis*, a juvenile
- 1391 tyronnsaurid (Theropoda, Dinosauria) from the Late Cretaceous of China. *Canadian Journal of*
- 1392 *Earth Sciences* 38: 1729–1737.
- Currie PJ, Funston GF, Osmólska H. 2016. New specimens of the crested theropod dinosaur
 Elmisaurus rarus from Mongolia. *Acta Palaeontologica Polonica* 61: 143–157.
- 1395 Currie PJ, Hurum JH, Sabath K. 2003. Skull structure and evolution in tyrannosaurid
- 1396 dinosaurs. *Acta Palaeontologica Polonica* 48: 227–234.
- 1397 Currie PJ, Peng JH. 1993. A juvenile specimen of *Saurornithoides mongoliensis* from the
- 1398 Upper Cretaceous of Northern China. *Canadian Journal of Earth Sciences* 30: 2224–2230.
- 1399 Currie J, Russell DA. 1987. Osteology and relationships of *Chirostenotes pergracilis*
- 1400 (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada.
- 1401 *Canadian Journal of Earth Sciences* 25: 972–986.

- 1402 Dalman SG. 2013. New Examples of *Tyrannosaurus rex* from the Lance Formation of
- 1403 Wyoming, United States. Bulletin of the Peabody Museum of Natural History 54: 241–254.
- 1404 Dong Z. 1977. On the dinosaurian remains from Turpan, Xinjiang. *Vertebrata PalAsiatica* 15:
 1405 59–66.
- 1406 Fanti F, Currie PJ, Badamgarav D. 2012. New Specimens of *Nemegtomaia* from the
- 1407 Baruungoyot and Nemegt Formations (Late Cretaceous) of Mongolia. *PLoS ONE* 7: e31330.
- Foster W, Brusatte SL, Carr TD, Williamson TE, Yi L, Lü J. 2021. The cranial anatomy of
- 1409 the long-snouted tyrannosaurid dinosaur *Oianzhousaurus sinensis* from the Upper Cretaceous of
- 1410 China. Journal of Vertebrate Paleontology 41: e1999251.
- 1411 Fowler DW, Woodward HN, Freedman EA, Larson PL, Horner JR. 2011. Reanalysis of
- 1412 'Raptorex kriegsteini;: a juvenile tyrannosaurid dinosaur from Mongolia. PLoS ONE 6: e21376.
- 1413 Funston GF. 2020. Caenagnathids of the Dinosaur Park Formation (Campanian) of Alberta,
- 1414 Canada: anatomy, osteo-histology, taxonomy, and evolution. Vertebrate Anatomy Morphology
- 1415 *Palaeontology* 8: 105–153.
- 1416 Funston GF, Chinzorig T, Tsogtbaatar K, Kobayashi Y, Sullivan C, Currie PJ,
- 1417 Tsogtbaatar K, Kobayashi Y, Sullivan C, Pj C. 2020a. A new two-fingered dinosaur sheds
- 1418 light on the radiation of Oviraptorosauria. *Royal Society Open Science* 7: 201184.
- 1419 Funston GF, Currie PJ. 2018. A small caenagnathid tibia from the Horseshoe Canyon
- Formation (Maastrichtian): Implications for growth and lifestyle in oviraptorosaurs. *Cretaceous Research* 92: 220–230.
- 1422 Funston GF, Currie PJ, Eberth DA, Ryan MJ, Ch T, Badamgarav D, Longrich NR. 2016.
- 1423 The first oviraptorosaur (Dinosauria: Theropoda) bonebed: evidence of gregarious behaviour in a 1424 maniraptoran theropod. *Scientific reports* 6: 1–13.
- 1425 Funston GF, Currie PJ, Tsogtbaatar C, Khishigjav T. 2021. A partial oviraptorosaur skeleton
- suggests low caenagnathid diversity in the Late Cretaceous Nemegt Formation of Mongolia.
 PLoS ONE 16: e0254564.
- 1428 Funston GF, Mendonca SE, Currie PJ, Barsbold R. 2018. Oviraptorosaur anatomy, diversity
- and ecology in the Nemegt Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 494:
 101–120.
- 1431 Funston GF, Powers MJ, Whitebone A, Brusatte SL, Scannella JB, Horner JR, Currie PJ.
- 1432 **2020b**. Baby tyrannosaurid bones and teeth from the Late Cretaceous of western North
- 1433 America.pdf. Canadian Journal of Earth Sciences 58: 756–777.
- 1434 Gao C, Morschhauser EM, Varricchio DJ, Liu J, Zhao B. 2012. A second soundly sleeping
- dragon: new anatomical details of the Chinese troodontid *Mei long* with implications forphylogeny and taphonomy. *PLoS ONE* 7: e45203.
- 1437 Gilmore CW. 1924. A new coelurid dinosaur from the Belly River Cretaceous of AlberT.
- 1438 *Canada Department of Mines Geological Survey Bulletin (Geological Series)* 38: 1–12.
- 1439 Gold MEL, Brusatte SL, Norell MA. 2013. The cranial pneumatic sinuses of the tyrannosaurid
- 1440 *Alioramus* (Dinosauria: Theropoda) and the evolution of cranial pneumaticity in theropod
- 1441 dinosaurs. American Museum Novitates 3790: 1-46.
- 1442 Goloboff P, Farris S, Nixon K. 2008. TNT, a free programm for phylogenetic analysis.
- 1443 Cladistics 24: 774–786.
- 1444 Harrison CJO, Walker CA. 1975. The Bradycnemidae, a new family of owls from the Upper
- 1445 Cretaceous of Romania. *Palaeontology* 18: 563–570.
- 1446 Holtz TR. 1998. A new phylogeny of the carnivorous dinosaurs. *GAIA Ecological Perspectives*
- 1447 on Science and Society 15: 5–61.
- 1448 Holtz TRJ. 2004. Tyrannosauroidea. In: Weishampel DB,, In: Dodson P,, In: Osmólska H, eds.
- 1449 *The Dinosauria*. Berkeley: University of California Press, .

- 1450 Huene F v. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte.
- 1451 Monographien zur Geologie und Palaeontologie, series 1 4: 1–361.
- 1452 Hurum JH, Sabath K. 2003. Giant theropod dinosaurs from Asia and North America: Skulls of
- 1453 *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica* 48: 161– 1454 190.
- 1455 Hutchinson JR. 2001. The evolution of femoral osteology and soft tissues on the line to extant
- birds The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131: 169–197.
- 1458 Hutt S, Naish D, Martill DM, Barker MJ, Newbery P. 2001. A preliminary account of a new
- tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of Southern England. *Cretaceous Research* 22: 227–242.
- 1461 Kurzanov SM. 1976. A New Carnosaur from the Late Cretaceous of Nogon-Tsav, Mongolia. In:
- Kramarenko et al., ed. Paleontology and Biostratigraphy of Mongolia. The Joint Soviet Mongolian Paleontological Expedition, Transactions.93-104.
- 1464 Kurzanov SM. 1981. An unusual theropod from the Upper Cretaceous of Mongolia. *Fossil*
- 1465 *Vertebrates of Mongolia. Joint Soviet-Mongolian Paleontological Expedition.*39–49.
- Kurzanov SM. 1987. Avimimidae and the problem of the origin of birds. *Trudy Sowmectnoj Cobwetcko-Mongolckoj Paleontologicheckoj Ekspedicii* 31: 1–92.
- 1468 Kurzanov SM, Osmólska H. 1991. Tochisaurus nemegtensis gen. et sp. n., a new troodontid
- 1469 (Dinosauria, Theropoda) from Mongolia. *Acta Palaeontologica Polonica* 36: 69–76.
- 1470 Lamanna MC, Sues HD, Schachner ER, Lyson TR. 2014. A new large-bodied
- 1471 oviraptorosaurian theropod dinosaur from the Latest Cretaceous of Western North America.
 1472 *PLoS ONE* 9: e92022.
- 1473 Lambe LM. 1914. On the fore-limb of a carnivorous dinosaur from the Belly River Formation
- 1474 of Alberta, and a new genus of Ceratopsia from the same horizon, with remarks on the
- 1475 integument of some Cretaceous herbivorous dinosaurs. *Ottawa Naturalist* 27: 129–135.
- 1476 Larson P, Parrish JM. 2013. The case for Nanotyrannus. Tyrannosaurid paleobiology.15–53.
- 1477 Lee S, Park J young, Lee Y nam, Kim S hwan, Lü J. 2019. A new alvarezsaurid dinosaur
- 1478 from the Nemegt Formation of Mongolia. *Scientific Reports* 9: 15493.
- Li D, Norell MA, Gao K qin, Smith ND, Makovicky PJ. 2010. A longirostrine tyrannosauroid
 from the Early Cretaceous of China. : 183–190.
- 1481 Loewen MA, Irmis RB, Sertich JJW, Currie PJ, Sampson SD. 2013. Tyrant dinosaur
- 1482 evolution tracks the rise and fall of late Cretaceous oceans. *PLoS ONE* 8: e79420.
- 1483 Lu J, Tomida Y, Azuma Y, Dong Z. 2005. Nemegtomaia gen. nov., a replacement name for the
- 1484 oviraptorosaurian dinosaur Nemegtia Lü et al. 2004, a preoccupied name. *Bulletin of the*
- 1485 *National Science Museum, Tokyo, Series C* 31: 51.
- 1486 Lu J, Yi L, Brusatte SL, Yang L, Li H, Chen L. 2014. A new clade of Asian Late Cretaceous
- 1487 long-snouted tyrannosaurids. *Nature Communications* 5: 3788.
- 1488 Madsen JH. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of*
- 1489 *Paleontology* 48: 27–31.
- Maleev EA. 1955. Giant carnivorous dinosaurs of Mongolia. *Doklady Akademii Nauk SSSR* 104:
 634–637.
- 1492 Maleev EA. 1974. Gigantic carnosaurs of the family Tyrannosauridae. he Joint Soviet-
- 1493 *Mongolian Paleontological Expedition Transactions* 1: 132–191.
- 1494 Naish D, Dyke GJ. 2004. Heptasteornis was no ornithomimid, troodontid, dromaeosaurid or
- 1495 owl: the first alvarezsaurid (Dinosauria: Theropoda) from Europe. *Neues Jahrbuch für Geologie*
- 1496 *und Paläontologie Monatshefte* 7: 385–401.
- 1497 Napoli JG, Ruebenstahl AA, Turner AH, Norell MA. 2021. A New Dromaeosaurid

- 1498 (Dinosauria: Coelurosauria) from Khulsan, Central Mongolia. American Midland Naturalist
- **1499 3982**: 1–48.
- 1500 Nesbitt S, RK DJ, Loewen M, Brusatte S, Smith N, Turner A, Kirkland J, McDonald A,
- 1501 Wolfe D. 2019. A mid-Cretaceous tyrannosauroid and the origin of NorthAmerican end-
- 1502 Cretaceous dinosaur assemblages. *Nature Ecology & Evolution* 3: 892–899.
- 1503 Norell MA, Makovicky PJ, Bever GS, Balanoff AM, Clark JM, Barsbold R, Rowe TB.
- **2009**. A review of the Mongolian Cretaceous dinosaur Saurornithoides . American Museum
 Novitates 3654: 1–63.
- 1506 Osborn HF. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the* 1507 *AMNH* 21: 259–265.
- 1508 **Osmólska H. 1981.** Coossified tarsometatarsi in theropod dinosaurs and their bearing on the 1509 problem of brid origins. *Paleontologia Polonica* 42: 79–95.
- 1510 Osmólska H. 1987. Borogovia gracilicrus gen. et sp. n., a new troodontid dinosaur from the
- 1511 Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 32: 133–150.
- 1512 Osmólska H. 1996. An unusual theropod dinosaur from the Late Cretaceous Nemegt Formation
- 1513 of Mongolia. *Acta Palaeontologica Polonica* 41: 1–38.
- 1514 Osmólska H, Roniewicz E. 1970. Deinocheiridae, a new family of theropod dinosaurs.
- 1515 *Palaeontologica Polonica* 21: 5–19.
- 1516 Osmólska H, Roniewicz E, Barsbold R. 1972. A new dinosaur, Gallimimus bullatus n. gen., n.
- sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia". *Palaeontologia Polonica* 27:
 103–143.
- 1519 **Ostrom JH**. **1970**. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous)
- of the Bighorn Basin area, Wyoming and Montana. Bulletin of the Peabody Museum of Natural
 History 35: 1–356.
- Padian K, Lamm ET. 2013. Bone Histology of Fossil Tetrapods. Berkeley, Los Angeles,
 California: University of California Press.
- 1524 Perle A, Chiappe LM, Barsbold R, Clarke JM, Norell MA. 1994. Skeletal morphology of
- 1525 *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *American*
- 1526 *Museum Novitates*: 1–29.
- Perle A, Norell MA, Chiappe LM, Clark JM. 1993. Flightless bird from the Cretaceous of
 Mongolia. *Nature* 362: 623–626.
- 1529 Rauhut OWM. 2000. The interrelationships and evolution of basal theropods (Dinosauria,
- 1530 Saurischia). Unpublished thesis, University of Bristol.
- 1531 Rauhut OWM. 2003. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal.
- 1532 *Palaeontology* 46: 903–910.
- 1533 Rauhut OWM, Milner AC, Moore-Fay S. 2010. Cranial osteology and phylogenetic position
- 1534 of the theropod dinosaur Proceratosaurus bradleyi (Woodward , 1910) from the Middle Jurassic 1535 of England. *Zoological Journal of the Linnean Society* 158: 155–195.
- 1536 **Rauhut OWM, Xu X. 2005**. The small theropod dinosaurs *Tugulusaurus* and *Phaedrolosaurus*
- 1537 from the Early Cretaceous of Xinjiang, China. Journal of Vertebrate Paleontology 25: 107–118.
- 1538 Sereno PC, Tan L, Brusatte SL, Kriegstein HJ, Zhao X, Cloward K. 2009. Tyrannosaurid
- skeletal design first evolved at small body size. *Science* 326: 418–423.
- 1540 Stefanic CM, Nesbitt SJ. 2019. The evolution and role of the hyposphene-hypantrum
- articulation in Archosauria: phylogeny, size and/or mechanics? *Royal Society Open Science* 6: 1–
 27.
- 1543 Tschopp E, Mateus O, Benson RB. 2015. A specimen-level phylogenetic analysis and
- 1544 taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). PeerJ, 3, e857.
- 1545 Tsuihiji T, Watabe M, Tsogtbaatar K, Tsubamoto T, Barsbold R, Suzuki S, Lee AH,

- 1546 Ridgely RC, Kawahara Y, Witmer LM. 2011. Cranial osteology of a juvenile specimen of
- 1547 Tarbosaurus bataar (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper
- 1548 Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31: 497–517.
- 1549 Voris JT, Therrien F, Zelenitsky DK, Brown CM. 2020. A new tyrannosaurine
- 1550 (Theropoda: Tyrannosauridae) from the Campanian Foremost Formation of Alberta, Canada,
- provides insight into the evolution and biogeography of tyrannosaurids. *Cretaceous Research*110: 104388.
- 1553 Voris JT, Zelenitsky DK, Therrien F, Ridgely RC, Currie PJ, Witmer LM. 2021. Two
- 1554 exceptionally preserved juvenile specimens of Gorgosaurus libratus (Tyrannosauridae,
- 1555 Albertosaurinae) provide new insight into the timing of ontogenetic changes in tyrannosaurids.
- 1556 *Journal of Vertebrate Paleontology* 41: 1–21.
- Wan X, Chen P, Wei M. 2007. The Cretaceous System in China. *Acta Geologica Sinica* 81:
 957–983.
- 1559 Wedel M. 2007. Postcranial pneumaticity in dinosaurs and the origin of the avian lung.
- 1560 Unpublished thesis, University of California.
- 1561 Witmer LM. 1997. The Evolution of the Antorbital Cavity of Archosaurs: A Study in Soft-
- 1562 Tissue Reconstruction in the Fossil Record with an Analysis of the Function of
- 1563 PneumaticiT. Journal of Vertebrate Paleontology, 17: 1–76.
- 1564 Xu X, Norell MA, Kuang X, Wang X, Zhao Q, Jia C. 2004. Basal tyrannosauroids from China
 1565 and evidence for protofeathers in tyrannosauroids. *Nature* 431: 680–684.
- 1567 FIGURES
- 1568 Figure 1. Mandible of *Bagaraatan ostromi* ZPAL MgD-I/108 in lateral (A); medial (B); dorsal
- 1569 (C); and posterior (D) view. E; the preserved part distal part of the mandible in anterior view. F;1570 dentary in anterior view.
- 1571

1566

- Figure 2. Details of the dentary of *Bagaraatan ostromi* ZPAL MgD-I/108 in dorsal (A); anterior
 (B); posterior (C); ventral (D); lateral (E); and medial (F) view.
- 1574

Figure 3. Comparison of *Bagaraatan ostromi* (A–B) and *Tarbosaurus bataar* (C–J) dentaries. A– B; ZPAL MgD-I/108 in medial (A); and lateral (B) view. C–D; ZPAL MgD-I/75 in medial (C); and lateral (D) view. E–F; ZPAL MgD-I/175 in medial (E); and lateral (F) view. G–H; ZPAL MgD-I/4 in medial (G); and lateral (H) view. I–J; ZPAL MgD-I/5 in medial (I); and lateral (J) view. Note the anterior margin of the dentary is steepens with ontogeny and the dentary becomes taller dorsoventrally. The 'chin' is distinct and the anterior end of the dentary is expanded through the ontogeny.

1582

Figure 4. Details of the posterior mandible of *Bagaraatan ostromi* ZPAL MgD-I/108 in lateral
(A); dorsal (B); ventral (C); medial (D); posterior (E); and anterior (F) view.

1585

Figure 5. Comparison of *Bagaraatan ostromi* (A) and *Tarbosaurus bataar* (B–E) distal end of the
mandible in lateral view. A; ZPAL MgD-I/108. B; ZPAL MgD-I/31. C; ZPAL MgD-I/3. D; MPCD 107/14. E; ZPAL MgD-I/4. F; ZPAL MgD-I/5. Note the exceptionally small surangular foramen

in the medium-sized individual MPC-D 107/14 (D) in comparison to similar-sized ZPAL MgD I/3 (C). Asterisks indicate the posterior surangular foramen. Note, that the placement of the double

surangular foramina in *B. ostromi* is similar to the enlarged posterior surangular foramen in *T. bataar*. During ontogeny, the surangular shelf is facing more laterally and the glenoid gets longer anteroposteriorly.

1594

Figure 6. Cervical vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; anterior cervical
vertebrae in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; posterior cervical vertebrae in anterior (G); left lateral (H); posterior (I); right lateral
(J); dorsal (K); and ventral (L) view.

1599

Figure 7. Anterior caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 4th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 5th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view.

1604

1609

Figure 8. Anterior caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 6th caudal
vertebra anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 7th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view.

Figure 9. Anterior caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 8th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 9th–10th caudal vertebrae in anterior (G); posterior (H); dorsal (I); left lateral (J); right
lateral (K); and ventral (L) view.

1614

Figure 10. Middle caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 11th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 12th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view.

1619

Figure 11. Middle caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 13th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 14th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view. M–R; 15th caudal vertebra in anterior (M); left lateral (N); posterior (O);
right lateral (P); dorsal (Q); and ventral (R) view.

1625

Figure 12. Middle caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 16th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 17th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view. M–R; 18th caudal vertebra in anterior (M); left lateral (N); posterior (O);
right lateral (P); dorsal (O); and ventral (R) view.

1631

Figure 13. Posterior caudal vertebrae of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; 19th caudal
vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; 20th caudal vertebra in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view. M–R; 21st–23th caudal vertebrae in anterior (M); left lateral (N); dorsal
(O); ventral (P); posterior (Q); and right lateral (R) view.

1637

1638 Figure 14. Posterior caudal vertebrae of Bagaraatan ostromi ZPAL MgD-I/108. A-F; 24th caudal vertebra in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F) 1639 view. G-L; indeterminate posterior caudal vertebra in anterior (G); left lateral (H); posterior (I); 1640 1641 right lateral (J); dorsal (K); and ventral (L) view. G-L; indeterminate posterior caudal vertebra in 1642 anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal (K); and ventral (L) view. M-R; 1643 indeterminate posterior caudal vertebra in anterior (M); left lateral (N); posterior (O); right lateral 1644 (P); dorsal (Q); and ventral (R) view. S-Y; indeterminate posterior caudal vertebra in anterior (S); left lateral (T); posterior (U); right lateral (W); dorsal (X); and ventral (Y) view. Z-E'; 1645 1646 indeterminate posterior caudal vertebra in anterior (Z); left lateral (A'); posterior (B'); right lateral 1647 (C'); dorsal (D'); and ventral (E') view.

1648

Figure 15. Two incomplete haemal arches of *Bagaraatan ostromi* ZPAL MgD-I/108. A–F; Haemal
arch A in anterior (A); left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F)
view. G–L; Haemal arch B in anterior (G); left lateral (H); posterior (I); right lateral (J); dorsal
(K); and ventral (L) view.

1653

1659

Figure 16. Ilium of *Bagaraatan ostromi* ZPAL MgD-I/108. A-B; fragment of left preacetabular
process in lateral (A) and medial (B) view. C–F; left postacetabular process in lateral (C); medial
(D); dorsal (E); and ventral (F) view. G–J; right postacetabular process in dorsal (G); ventral (H);
lateral (I); and medial (J) view. K–N; two fragments of ilium blade in lateral (K; M) and medial
(L; N) view.

Figure 17. Pubes of *Bagaraatan ostromi* ZPAL MgD-I/108. A–E; left pubis with proximal end of
the ischium in lateral (A); medial (B); dorsal (C); posterior (D); and anterior (E) view. F–G; right
pubis in lateral (F) and medial (G) view.

- 1663
 1664 Figure 18. Left pes phalanx IV-1 of *Bagaraatan ostromi* ZPAL MgD-I/108 in dorsal (A); lateral
 1665 (B); anterior (C); plantar (D); medial (E); and posterior (F) view.
 - 1666

Figure 19. Various bones of Caenagnathidae indet. ZPAL MgD-I/108/1. A-F; caudal vertebra in (A) anterior; left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F) view. G–

(A) anterior; left lateral (B); posterior (C); right lateral (D); dorsal (E); and ventral (F) view. C
H; proximal part of dorsal rib. I-N; manus ungual II-3 in dorsal (I); medial (J); ventral (K);

1670 lateral (L); anterior (M); and posterior (N) view. O-T; left manus phalanx II-1 in medial (O);

1671 ventral (P); lateral (Q); dorsal (R); anterior (M); and posterior (N) view. U–A'; left pedal phalanx

1672 II-2 in medial (U); ventral (W); lateral (X); dorsal (Y); anterior (Z); and posterior (A') view.

1673

1674	Figure 20. Left femur of Caenagnathidae indet. ZPAL MgD-I/108/1. A-E; proximal end of the
1675	femur in anterior (A); lateral (B); posterior (C); medial (D); and dorsal (E) view. F–J; distal end
1676	of the femur in anterior (F); lateral (G); posterior (H); medial (I); and ventral (J) view. K-L; thin
1677	section of the femoral cortex under polarized light. Red arrows indicate secondary osteons; green
1678	arrows point resorption cavities; yellow arrows indicate lamellar bone; and purple arrows point
1679	parallel-fibered bone.
1680	
1681	Figure 21. Left tibiotarsus of Caenagnathidae indet. ZPAL MgD-I/108/1. A-F; tibiotarsus in
1682	anterior (A); lateral (B); posterior (C); medial (D); dorsal (E); and ventral (F) view. G–K; proximal
1683	fibula in dorsal (G); anterior (H); lateral (I); posterior (J); and medial (K).
1684	
1685	Figure 22. Plots showing the relationship between the anteroposterior length of the surangular
1686	foramen to the skull length (as a proxy of body size) in tyrannosaurids. Bagaraatan ostromi
1687	measured for the single (posterior only) or double (posterior + anterior) foramina. A; regression
1688	analysis including specimens shows a negative slope and a high correlation coefficient. B;
1689	regression analysis for specific taxa shows the same trend. No small-medium-large size of the
1690	surangular foramen distinction can be noticed in the tyrannosaurids.
1691	
1692	Figure 23. Strict consensus tree of the Theropod Working Group (TWiG; Brusatte et al.; 2014)
1693	phylogenetic analysis, Bagaraatan ostromi ZPAL MgD-I/108 is found as basal tyrannosauroid.
1694	
1695	Figure 24. Strict consensus tree of the tyrannosaurid phylogeny (the Nesbitt et al.; 2019 version
1696	of the Brusatte & Carr, 2016 dataset), Bagaraatan ostromi ZPAL MgD-I/108 is placed in a
1697	polytomy within tyrannosaurids.
1698	
1699	Figure 25. Reconstruction of Bagaraatan ostromi ZPAL MgD-I/108 including only
1700	tyrannosaurid bones found in the assemblage and life reconstruction of the dinosaur by Jakub
1701	Zalewski.
1702	
1703	TABLES
1704	Tab. 1. Measurements of the tooth alveoli (anteroposterior length to labiolingual width) in dorsal
1705	view [mm].
1706	
1707	Table 2. Measurements of the caudal vertebrae [mm]. * – incomplete.
1708	
1709	