

An Ankylosaurid Dinosaur from Mongolia with in Situ Armour and Keratinous Scale Impressions

Authors: Arbour, Victoria M., Lech-Hernes, Nicolai L., Guldberg, Tom E., Hurum, Jørn H., and Currie, Philip J.

Source: *Acta Palaeontologica Polonica*, 58(1) : 55-64

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0081>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

An ankylosaurid dinosaur from Mongolia with in situ armour and keratinous scale impressions

VICTORIA M. ARBOUR, NICOLAI L. LECH-HERNES, TOM E. GULDBERG, JØRN H. HURUM, and PHILIP J. CURRIE



Arbour, V.M., Lech-Hernes, N.L., Guldberg, T.E., Hurum, J.H., and Currie P.J. 2013. An ankylosaurid dinosaur from Mongolia with in situ armour and keratinous scale impressions. *Acta Palaeontologica Polonica* 58 (1): 55–64.

A Mongolian ankylosaurid specimen identified as *Tarchia gigantea* is an articulated skeleton including dorsal ribs, the sacrum, a nearly complete caudal series, and in situ osteoderms. The tail is the longest complete tail of any known ankylosaurid. Remarkably, the specimen is also the first Mongolian ankylosaurid that preserves impressions of the keratinous scales overlying the bony osteoderms. This specimen provides new information on the shape, texture, and arrangement of osteoderms. Large flat, keeled osteoderms are found over the pelvis, and osteoderms along the tail include large keeled osteoderms, elongate osteoderms lacking distinct apices, and medium-sized, oval osteoderms. The specimen differs in some respects from other *Tarchia gigantea* specimens, including the morphology of the neural spines of the tail club handle and several of the largest osteoderms.

Key words: Dinosauria, Ankylosauria, Ankylosauridae, *Tarchia*, *Saichania*, Late Cretaceous, Mongolia.

Victoria M. Arbour [arbour@ualberta.ca] and Philip J. Currie [philip.currie@ualberta.ca], Department of Biological Sciences, CW 405 Biological Sciences Building, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9;

Nicolai L. Lech-Hernes [nicolai.lech-hernes@bayerngas.com], Bayerngas Norge, Postboks 73, N-0216 Oslo, Norway;

Tom E. Guldberg [tguldberg@miswaco.com], Fossekleva 9, N-3075 Berger, Norway;

Jørn H. Hurum [j.h.hurum@nhm.uio.no], Natural History Museum (Geology), University of Oslo, Postboks 1172 Blindern, N-0318 Oslo, Norway.

Received 18 July 2011, accepted 10 February 2012, available online 17 February 2012.

Copyright © 2013 V.M. Arbour et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Mongolian dinosaur specimens are often preserved in articulation, and in the case of ankylosaurs, osteoderms are sometimes found in situ (Kielan-Jaworowska and Dovchin 1969; Kielan-Jaworowska and Barsbold 1972). However, osteoderm arrangements in Mongolian ankylosaurs have rarely been described in detail. ZPAL MgD I/113, collected from Altan Uul III in the Nemegt Basin of Mongolia during the 1971 Polish-Mongolian Palaeontological Expedition, preserves in situ osteoderm and soft tissue scale impressions. In 1998, the specimen was sent to the Geological Museum in Oslo, Norway for preparation and study, and we describe it here.

The specimen was originally referred to “*Dyoplosaurus*” *giganteus* Maleev, 1956 by Maryańska (1977). Maleev (1956) named the new species *Dyoplosaurus giganteus* based on caudal and pedal elements (PIN 551-29). The referral of a new species to the genus *Dyoplosaurus*, the type species of which

is *Dyoplosaurus acutosquameus* Parks, 1926, was based on the similarity of the caudal vertebrae and osteoderms. However, Coombs (1978) and subsequent workers considered *Dyoplosaurus acutosquameus* a junior subjective synonym of *Euoplocephalus tutus* Lambe, 1910 (= *Stereocephalus tutus* Lambe, 1902), based on a revision of the Ankylosauria by Coombs (1978). Recently, Arbour et al. (2009) suggested that *Dyoplosaurus acutosquameus* is a distinct and valid taxon. Maryańska (1977) erected the new genus and species *Tarchia kielanae* based on a partial skull roof (ZPAL MgD I/111). Tumanova (1987) synonymised *Tarchia* with “*Dyoplosaurus*” *giganteus* to form the new combination *Tarchia gigantea*, and retained *Tarchia kielanae* as a distinct species. The holotype of “*Dyoplosaurus*” *giganteus* (PIN 551-29) includes only postcranial material whereas the holotype of *Tarchia kielanae* (ZPAL MgD I/111) includes only cranial material. PIN 3142/250, the specimen most typically associated with the genus *Tarchia* in both the scientific and popular literature, is known from both cranial and postcranial material, but the

Table 1. Information on specimens of *Tarchia* in the collections of the Palaeontological Institute (Moscow) and the Institute of Paleobiology (Warsaw). Other than the two specimens, whose status is marked as “unknown”, each of the others has been studied by at least one of the authors over the past few years. The specimen in Ulaanbaatar is on display at the Museum of Natural History.

Specimen	Material	Locality	Formation	Current Location
PIN 551-29	tail, metacarpals, manual phalanges, osteoderms	Nemegt	Nemegt	Moscow, Russia
PIN 3142/250	skull and skeleton	Hermiin Tsav I	Nemegt	Moscow, Russia
ZPAL MgD I/42	tail, tail club	Altan Uul IV	Nemegt	Warsaw, Poland
ZPAL MgD I/43	tail, tail club	Altan Uul IV	Nemegt	Ulaanbaatar, Mongolia
ZPAL MgD I/49	right humerus	Altan Uul IV	Nemegt	unknown
ZPAL MgD I/111	skull roof, occiput, braincase	Khulsan	Baruungoyot	unknown
ZPAL MgD I/113	postcranium	Altan Uul III	Nemegt	Oslo, Norway

postcrania are currently undescribed. In a recent visit (2009, VMA) to the ZPAL collections, the holotype skull of *Tarchia kielanae* could not be located. There are currently at least seven specimens of *Tarchia gigantea* in Moscow, Ulaanbaatar, and Warsaw (Table 1), most of which were examined during the course of this study.

Another ankylosaur from the Late Cretaceous of Mongolia, *Saichania chulsanensis* (MPC 100/151), is known from a good skull and the anterior portion of the skeleton. There are several postcranial specimens that have also been referred to *Saichania*, including the tail club PIN 3142/251, and MPC 100/1305, a nearly complete skeleton with in situ osteoderms. Although MPC 100/1305 is nearly complete, it lacks a skull, making comparison with the holotype difficult, and referral of this specimen to *Saichania* is largely because it is from the Baruungoyot Formation, like the holotype.

Presently, *Saichania* appears to be restricted to the Baruungoyot Formation, whereas *Tarchia* is known from both the Baruungoyot and Nemegt Formations. The holotype specimen of *Tarchia kielanae* was collected from Khulsan, the same locality as the holotype of *Saichania*, although ZPAL MgD I/42, ZPAL MgD I/43, ZPAL MgD I/49, ZPAL MgD I/113, PIN 551-29, and PIN 3142/550 are all from the Nemegt Formation (Maryńska 1977). Although there is little overlapping material between MPC 100/1305 and the holotype, the referral of MPC 100/1305 to *Saichania* based on stratigraphic grounds will be upheld here. In the same vein, despite the uncertainty surrounding the referral of specimens to *Tarchia*, ZPAL MgD I/113 will be referred to *Tarchia gigantea* on the grounds that it comes from the same formation as the holotype of “*Dyoplosaurus*” *giganteus*. With the recent description of MPC 100/1305 (*Saichania*) by Carpenter et al. (2011) and new information in this paper (ZPAL MgD I/113, *Tarchia*), comparisons can be made between the postcranial skeletons of *Tarchia* and *Saichania* for the first time.

Institutional abbreviations.—MPC, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; NHMUK, Natural History Museum, London, UK; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Systematic palaeontology

- Dinosauria Owen, 1842
- Ornithischia Seeley, 1887
- Thyreophora Nopcsa, 1915
- Ankylosauria Osborn, 1923
- Ankylosauridae Brown, 1908
- Tarchia* Maryńska, 1977

Type species: *Dyoplosaurus giganteus* (Maleev, 1956); Hermiin Tsav, Mongolia; Nemegt Formation, Late Campanian–Early Maastrichtian.

Tarchia cf. *gigantea* Maleev, 1956

Material.—ZPAL MgD I/113, posterior portion of abdomen including fragmentary ribs, partial pelvis, and in situ osteoderms and skin impressions; nearly complete caudal series including tail club handle and in situ osteoderms, but missing tail club knob.

Description.—ZPAL MgD I/113 consists of a large piece of the left side of the posterior abdomen and most of the tail (Figs. 1–5). Several ribs from the left side articulate with the dorsal vertebrae, most of which are only preserved as impressions. Both ilia are broken, but there is an imprint of the left ilium. The tail is nearly complete, but lacks the tail club knob. Several blocks of uncertain position include vertebrae, ribs, and a limb element. Numerous osteoderms were recovered with the specimen, including a layer of osteoderms and soft tissue imprints on the trunk (Fig. 3), and in situ osteoderms alongside the caudal vertebrae (Figs. 4, 5). In addition, more than a hundred loose pieces containing bone elements of unknown origin have been identified.

The section of trunk from the posterior left side of the body is about 92 cm in length, and the body is 86 cm wide. It is split in half along the vertebral column. There are seven poorly preserved ribs, and all except the first and last contact the poorly preserved transverse processes. It is unclear how many of these represent dorsosacral vertebrae. A layer 3–10 cm thick and 45–50 cm wide covers part of the trunk dorsally, and contains numerous flat and oval dorsal osteoderms (Fig. 3). The sacrum includes five almost complete verte-

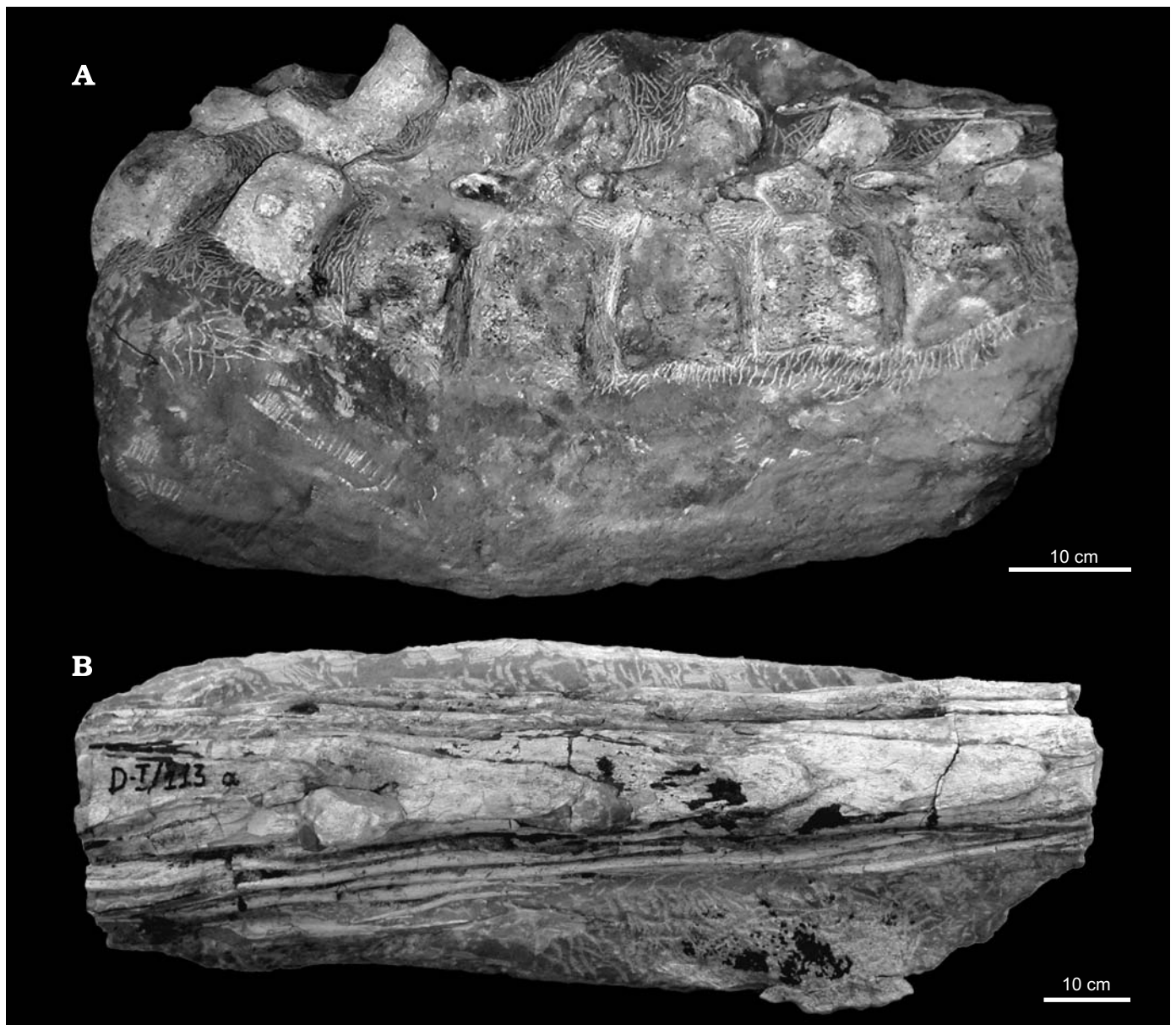


Fig. 1. Caudal vertebrae of an ankylosaurid dinosaur *Tarchia* cf. *gigantea*, ZPAL MgD I/113 from the Nemegt Formation at Altan Uul III, Mongolia. **A.** Free caudal vertebrae 1–7 in left lateral view. **B.** Handle caudal vertebrae 4–8 in dorsal view; anterior is to the left.

brae, including one caudosacral. The centrum is not fused to the last sacral and is thus not part of the sacral rod.

The tail is composed of at least 28 caudal vertebrae, 14 of which are free caudals (Table 2). The free caudals (Figs. 1, 4) occur in two separate blocks of sandstone (free caudals 1–7 in a block 77 cm long, and free caudals 8–11 in a block 48 cm long), and are visible in right lateral view. Free caudal 8 is split in half and the two halves can be seen in anterior and posterior view in their respective blocks. The total length of the free caudals is 1.245 m. More proximal caudals are of almost the same height and width, while distally the caudals become more elongate. All the neural arches except for the neural arch of the first free caudal are fused to the centra. The neural spines decrease in height posteriorly, and become more inclined posteriorly. The neural spine of

free caudal 2 is vertically oriented, while the neural spine of free caudal 7 is tilted some 45° posteriorly. The neural arches become progressively lower and more elongate. The prezygapophyses are long, narrow, and horizontal; their length increases posteriorly along the tail. The postzygapophyses are very short for the first three free caudals and disappear completely after free caudal 3. The lengths of the prezygapophyses of free caudals 2, 7, and 10 are 42 mm, 53 mm, and 59 mm, respectively. The transverse processes become reduced posteriorly and are not visible posterior to free caudal 8. The haemal spines are largely obscured by the surrounding matrix.

The 17 caudals (handle vertebrae, following the terminology of Coombs, 1995) making up the handle (Figs. 1, 4) of the tail club are partly embedded in five separate blocks of

Table 2. Dimensions (in mm) of the vertebrae of ZPAL MgD I/113. The tilde marks indicate approximate values.

		Centrum length	Centrum width	Centrum height
Dorsals	X	120	–	140
	Y	90	110	90
Presacrals	1	~100	65	–
	2	105	85	–
	3	105	90	–
Sacrats	1	105	85	~130
	2	105	95	~130
	3	105	130	~130
	4	95	160	~135
Sacrocaudal		85	170	140
Free caudals	1	85	130	140
	2	85	~125	~135
	3	80	~125	~135
	4	90	~125	~135
	5	95	~125	~135
	6	93	~125	~135
	7	88	~125	~135
	8	90	120	130
	9	103	–	70
	10	116	–	65
	11	123	–	62
Handle caudals	1	122	91	63
	2	119	–	–
	3–7	~115	–	–
	8	102	71	48
	9	101	–	–
	10	101	63	44
	11	101	61	42
	12	100	–	–
	13	102	50	35
	14	95	51	33
	15–17	~95	–	–

sandstone. Generally, the ventral sides of the vertebrae are all covered by matrix, except for the block containing the last three vertebrae. The total length of the handle caudals is 1.965 m. These caudals are typical for ankylosaurids, with elongate prezygapophyses and neural spines that form interlocking Vs in dorsal view. The neural spines and prezygapophyses diverge at an average angle of 35°. Ossified tendons are preserved on the lateral sides of the handle. The total length of the tail is 3.1 m.

Ten different types of osteoderms have been identified in the specimen and these vary in size, shape and surface detail (Fig. 2). An attempt to organise and generalise armour termi-

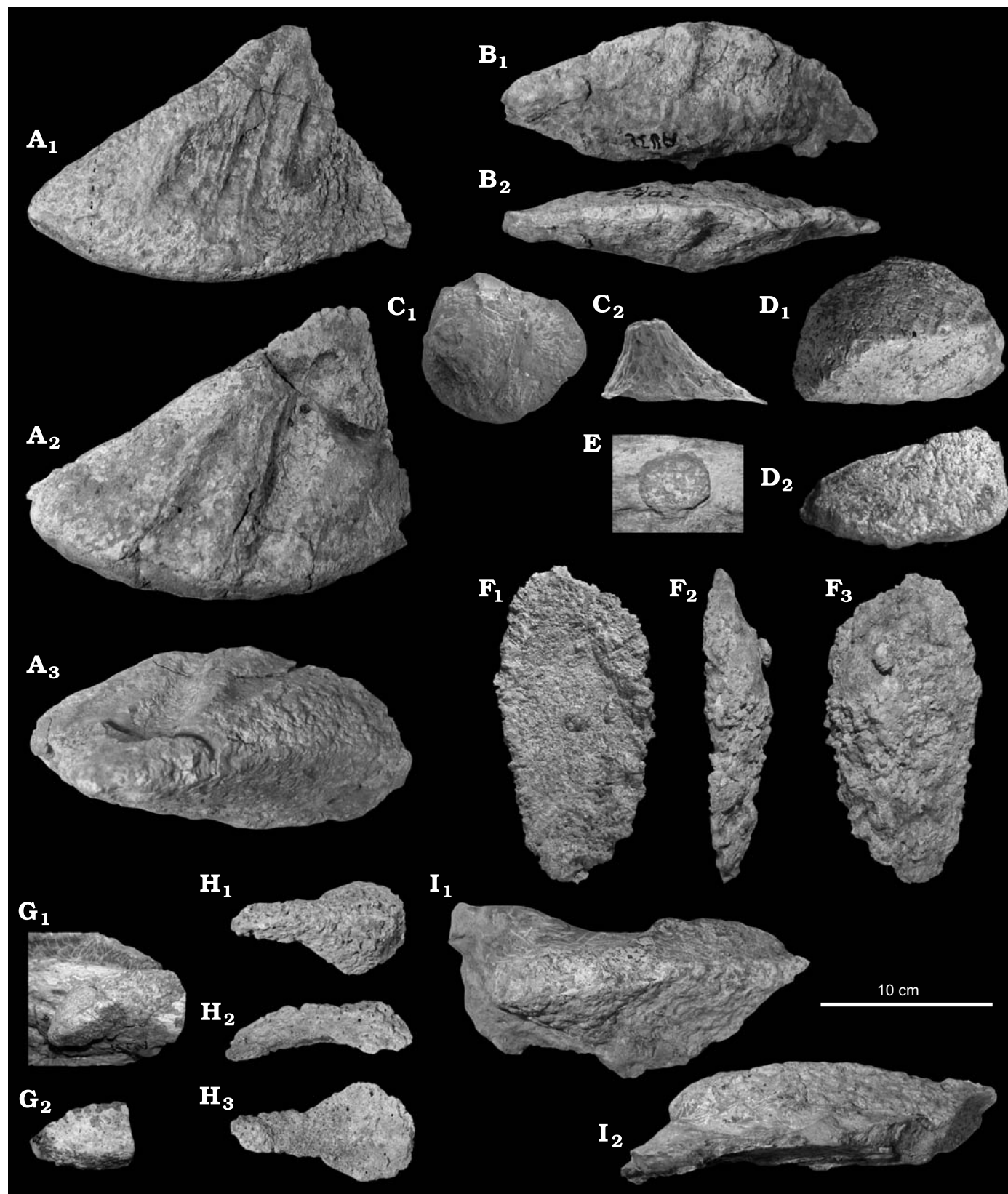
nology was made by Blows (2001), although several osteoderms described herein do not correspond to any of these terms, or to the terms initially used by Maryńska (1969).

The large, backswept Type 1 plates of Maryńska (1969) are not preserved in ZPAL MgD I/113, nor are morphologies corresponding to Type 3 (slightly compressed keeled osteoderms with a sharp, slightly backswept tip). Osteoderms corresponding to Types 2 and 4–6 are preserved. However, morphologies not described by Maryńska (1969) are also present, and these are designated as Types 7 through 10 herein.

Type 2 osteoderms (Fig. 2A, B) are sharply keeled and located along the lateral edges of the tail. In the anterior region of the tail, Type 2 osteoderms are triangular in dorsal view with sharp apices (Fig. 2A). Type 2 osteoderms in the posterior part of the tail have more rounded apices (Fig. 2B). A Type 4 osteoderm is conical with a circular base (Fig. 2C). In lateral view, the osteoderm is a tilted cone with a rugose surface. Type 5 is a medium-sized osteoderm with an oval base (Fig. 2D). A distinct keel extends from the pointed end to meet the longitudinal base line in the rounded end. The keel is strongly angled in dorsal view near the tapered end. Small, flattened osteoderms with circular bases are referred to here as Type 6 (Fig. 2E). The dorsal surface is rugose but lacks any additional structures. Large, flattened, keeled, osteoderms with slightly concave ventral surfaces are identified as Type 7 (Fig. 2F). These osteoderms are thin-walled and rugose. Type 8 osteoderms are small, nearly flat, elongate ovals (Fig. 2G). These are thin-walled, and each has a central or displaced keel and a slightly concave ventral surface. One unusual Type 8 osteoderm is ornamented by ridges and grooves, and has a notched peak (Fig. 5). A Type 9 osteoderm has a teardrop-shaped outline in dorsal view (Fig. 2H). The keel extends from the tapered end and terminates in a small apex at the centre of the broad end. The base is deeply concave. A strongly keeled osteoderm with an elongate oval base that is pointed at both ends is referred to as Type 10 (Fig. 2I). Three Type 10 osteoderms have been identified on the dorsal surface of the end of the tail.

The remains of in situ abdominal osteoderms are generally fragmentary and incomplete. A few disarticulated osteoderms identified as being from the trunk (Types 4, 7, and 10) have been recognized. Most impressively, a detached layer containing an almost complete pattern of dorsal trunk integument with imprints from keratinous scales between the larger bony osteoderms is present. This layer is from the dorsal side of the torso, and extends parallel to the vertebral column (Fig. 3). Keratinous scale impressions are large, keeled and approximately rectangular. Single or paired sequences of imprints separate and surround the bony osteoderms.

Fig. 2. Types of osteoderms in an ankylosaurid dinosaur *Tarchia cf. gigantea*, ZPAL MgD I/113 from the Nemegt Formation at Altan Uul III, Mongolia. **A.** Representative Type 2 osteoderm from the anterior portion of the tail in dorsolateral (A₁), posterior (A₂), and oblique (A₃) views. This large caudal osteoderm is from the right side of the tail and has five distinct grooves on the dorsal side. **B.** Representative Type 2 osteoderm from the posterior region of the tail in lateral view (B₁) showing two distinct grooves on the dorsal surface, and dorsal view (B₂) showing the slightly backward pointing groove and the outline of the keel. **C.** Representative Type 4 osteoderm in dorsal (C₁) and lateral (C₂) views. **D.** Representative Type 5 osteoderm in dorsal (D₁) and lateral (D₂) views. →



Note the angled keel and the two parallel grooves on the left side. **E**. Representative Type 6 osteoderm in dorsal view. This osteoderm is positioned near the posterior end of the tail. **F**. Representative Type 7 osteoderm in dorsal (**F₁**), lateral (**F₂**), and ventral (**F₃**) views. Note the extremely rugose surface, which is unique to this type. **G**. Two representative Type 8 osteoderms in situ; dorsal view in situ (**G₁**), and dorsal view when removed from tail (**G₂**). A slightly displaced keel runs in the longest direction. **H**. Sole Type 9 osteoderm in lateral (**H₁**), dorsal (**H₂**), and ventral (**H₃**) views. A distinct keel is present at the posterior end and terminates in an anterior crest (broken). **I**. Representative Type 10 osteoderm in dorsal (**I₁**) and lateral (**I₂**) views.

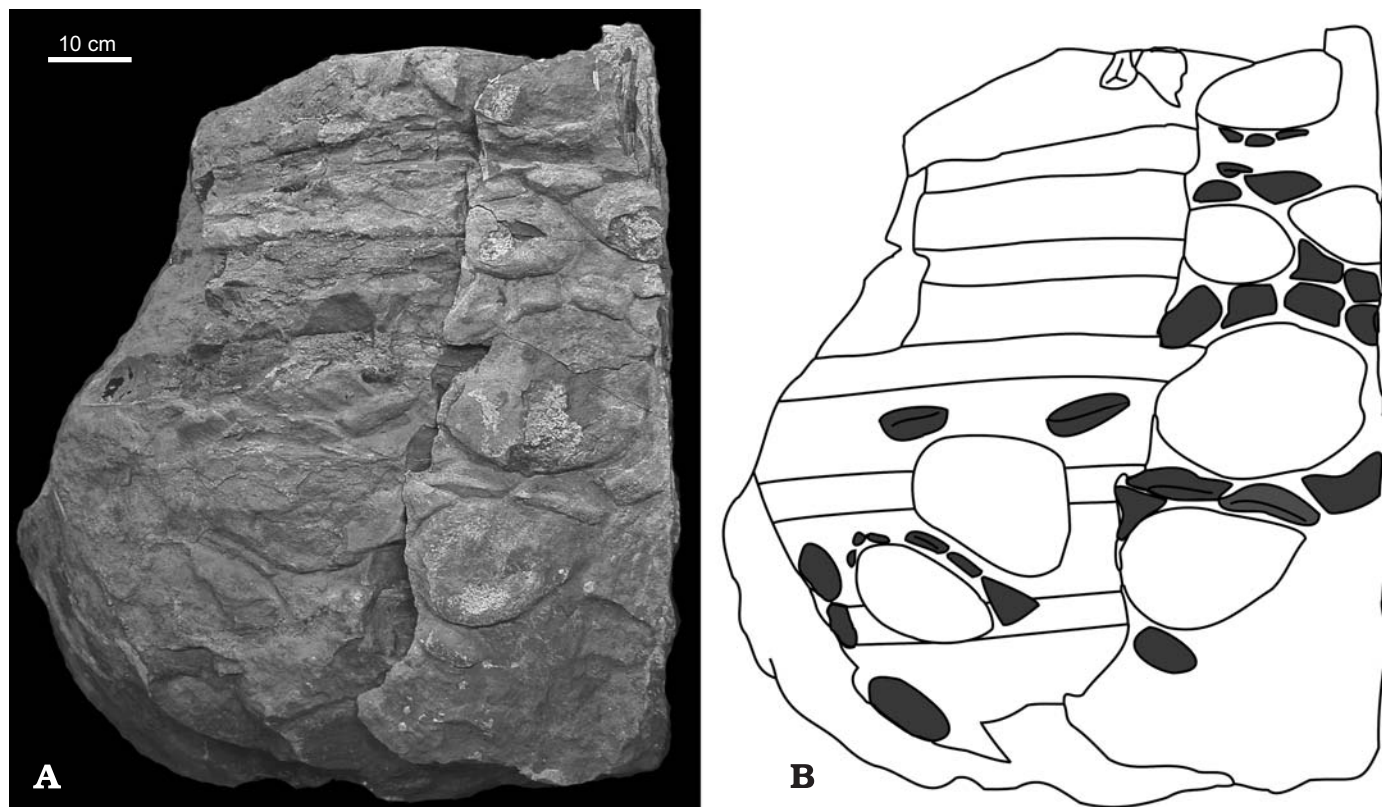


Fig. 3. An ankylosaurid dinosaur *Tarchia* cf. *gigantea*, ZPAL MgD I/113 from the Nemegt Formation at Altan Uul III, Mongolia. **A.** Dorsal view of the trunk. Skin impressions and osteoderms are visible on the trunk. Osteoderms are positioned in situ along the vertebral column. The specimen only represents the posterior part of the trunk. **B.** Interpretive drawing of osteoderms (white) and scale imprints (grey).

The caudal armour is mostly composed of Type 2 and 5 osteoderms (Fig. 4). Type 2 plates in the specimen originate from the base of the tail. It is reasonable to assume that the Type 2 osteoderms that are still in matrix are in situ (or close to being in situ) because the longest axis of each is parallel to the axis of the tail, they all have dorsal grooves, and each is positioned adjacent to a vertebral centrum. All of the Type 2 osteoderms in the specimen have large grooves on their dorsal surfaces. The last three vertebrae are covered by small osteoderms of Types 6 and 8 (Fig. 5). Unfortunately, ZPAL MgD I/113 does not have a tail club knob, which presumably was lost prior to collection.

Discussion

There is sufficient overlapping material to allow ZPAL MgD I/113 to be compared to most other referred *Tarchia* specimens. PIN 551-29 preserves one caudosacral vertebra, nine free caudal vertebrae, and nine handle vertebrae (two of which are partially obscured by the knob osteoderms). Free caudal centrum heights range from 8.2 to 12.6 cm. The handle vertebrae have sharply pointed, V-shaped neural spines. The tail club knob is broken, but was probably more than 20 cm wide. The osteoderms are porous, with similar texture as the other body osteoderms. The postcranium of

PIN 3142/250 has not been described, and so cannot be compared with the other specimens in this study. ZPAL MgD I/43 is the largest known ankylosaurid tail club, with a maximum knob width of 62 cm. Handle neural spines are sharply pointed and V-shaped in dorsal view. ZPAL MgD I/42 includes a fragmentary caudal vertebra, the tail club, and osteoderms. Six handle vertebrae are preserved in the tail club, and have sharply pointed V-shaped neural spines. Only the left major osteoderm of the knob is preserved, which has a width of 7.6 cm. The total width of the knob was probably around 20 cm.

With at least seventeen vertebrae incorporated into the tail club handle, ZPAL MgD I/113 has more handle caudals than *Dyoplosaurus* (approximately eleven) and *Saichania* (approximately twelve). Only *Pinacosaurus* incorporates more vertebrae into the handle of the tail club, with at least eighteen present in ZPAL MgD I/9. The complete caudal series is unknown in other *Tarchia* specimens. ZPAL MgD I/113 differs from all other *Tarchia* specimens in the morphology of the neural spines of the handle vertebrae. The neural spines and prezygapophyses diverge at an average angle of 35°, intermediate between the V-shaped morphology seen in other *Tarchia* specimens (and in all other ankylosaurids where the handle is known) and the U-shaped morphology of *Ankylosaurus* (Arbour et al. 2009). Because the average angle of divergence is between 20–25° in almost all ankylosaurid handle specimens

(except for *Ankylosaurus*), it seems unlikely that the 35° angle in ZPAL MgD I/113 represents intraspecific variation within *Tarchia*. This suggests that either ZPAL MgD I/113 is not referable to *Tarchia*, or the other ZPAL specimens are not referable to *Tarchia*. At present it cannot be determined which morphology belongs to the genus *Tarchia*.

The tail of ZPAL MgD I/113 is the longest complete tail of any known ankylosaurid (Fig. 4); it is more than twice the length of that of *Saichania* (MPC 100/1305) and longer than that of *Dyoplosaurus* (ROM 784). In both *Saichania* and ZPAL MgD I/113, the tail club accounts for about 65% the length of the tail, and in *Dyoplosaurus* the tail club represents about 60% of the total tail length.

Additional ankylosaurid taxa that preserve in situ osteoderms on the tail include, *Dyoplosaurus* (ROM 784), *Euoplocephalus* (NHMUK R5161, ROM 1930), *Pinacosaurus* (ZPAL MgD II/31, PIN 614) and *Saichania* (MPC 100/1305). *Dyoplosaurus* does not preserve osteoderms along the handle of the tail club, but there are Type 2 osteoderms immediately anterior to the handle. *Euoplocephalus* appears to lack Type 1 and 2 osteoderms; osteoderms preserved in the anterior portion of the tail have circular bases and low keels. Type 2 osteoderms are present on the tail of *Pinacosaurus*.

ZPAL MgD I/113 and MPC 100/1305 (*Saichania*) preserve some of the most complete sets of caudal osteoderms of any ankylosaurid, and comparisons between these two specimens can illuminate potential differences between *Saichania* and *Tarchia* (Fig. 4). In both *Saichania* and *Tarchia*, Type 2 osteoderms become smaller and more rounded in dorsal view towards the handle. In *Saichania*, the lateral osteoderms of the knob are semicircular in dorsal view, as are the lateral osteoderms immediately anterior to the knob. Although the knob osteoderms are not preserved in ZPAL MgD I/113, based on the length of the tail it is likely that the handle preserves the penultimate pair of osteoderms. In contrast to *Saichania*, *Tarchia* appears to lack osteoderms along the handle that are semicircular in dorsal view.

The Type 1 osteoderms of Maryńska (1969) probably represent the large lateral osteoderms towards the posterior of the pelvis, near the tail base, as *Saichania* shows these large osteoderms only in this region. ZPAL MgD I/113 does not preserve any Type 1 osteoderms. It is not clear if these were absent in ZPAL MgD I/113 or just not preserved; even though osteoderms are preserved on the dorsal surface of the pelvis, no lateral osteoderms are preserved. Type 5 osteoderms, with kinked keels, are present on the lateral sides of the torso in *Saichania*. In *Saichania*, the anterior part of the keel is kinked dorsally. The shape of the keel in the Type 5 osteoderm from ZPAL MgD I/113 indicates it may be derived from the right side of the body. Type 6 osteoderms are present in both *Saichania* and *Tarchia*, but in different regions. In *Tarchia*, they occur on the dorsal surface of the tail club. In *Saichania*, they are present on the dorsal surface of the pelvis.

ZPAL MgD I/113 does not have a tail club knob preserved, even though there are osteoderms present on the

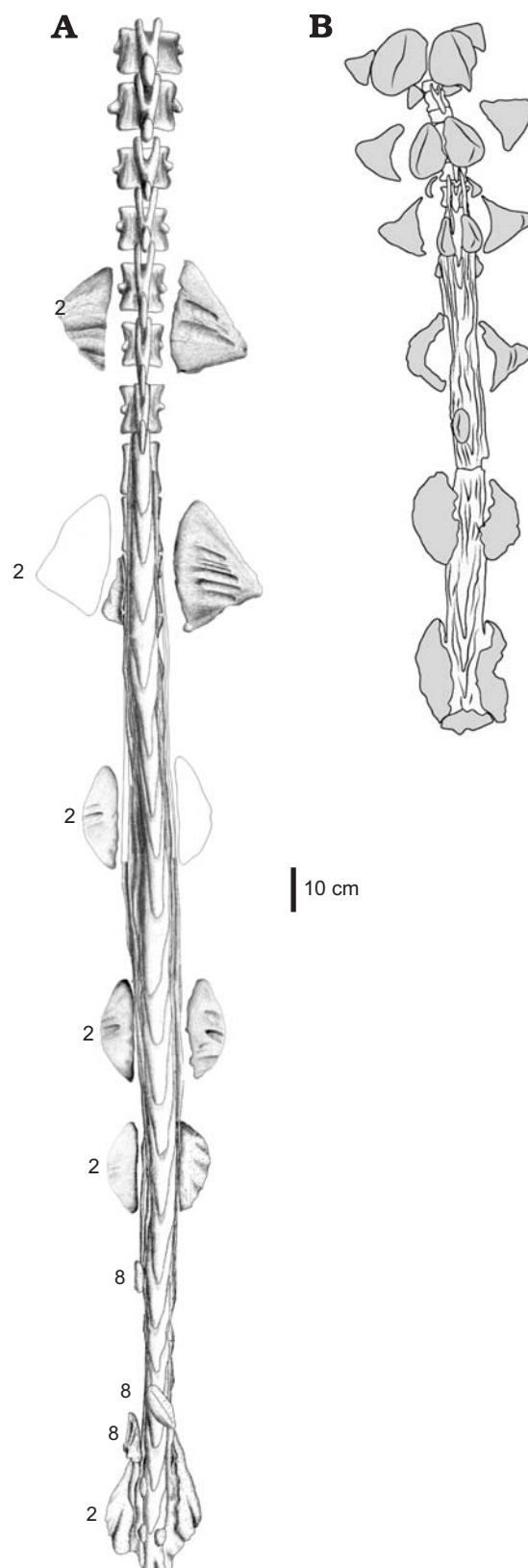


Fig. 4. Tail of an ankylosaurid dinosaur *Tarchia* cf. *gigantea*, ZPAL MgD I/113 from the Nemegt Formation at Altan Uul III, Mongolia, compared to tail of *Saichania* (MPC 100/1305) from the Baruungoyot Formation at Khulsan, Mongolia. Osteoderms found attached to the tail of ZPAL MgD I/113 are marked by numbers according to the Types 1–10 description in the text.

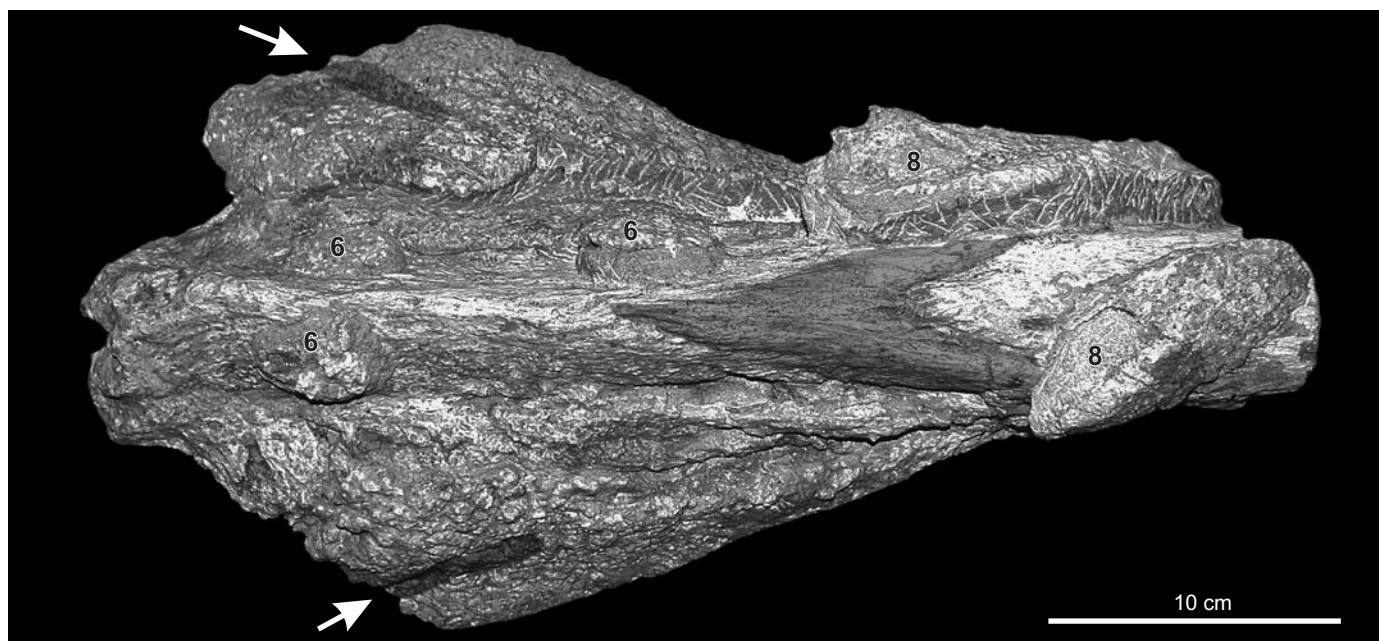


Fig. 5. Dorsal view of the most distal part of the tail preserved in an ankylosaurid dinosaur *Tarchia* cf. *gigantea*, ZPAL MgD I/113 from the Nemegt Formation at Altan Uul III, Mongolia. Five relatively small scutes cover the vertebrae (Types 6 and 8). Two large plates fuse to the centra of the three most distal vertebrae. Note the large grooves on both plates (darkened and arrowed), and the shapes of the distal keels. One handle vertebra is darkened to show the interlocking prezygapophyses and neural spines. Anterior is to the right.

distal end of the preserved tail. Osteoderms forming the tail club knob typically each have rounded lateral edges in dorsal view (except for a few specimens referred to *Euoplocephalus*, which are triangular in dorsal view, such as AMNH 5245), and sigmoidal medial edges. Osteoderms of the tail club knob overlap and surround the distal vertebrae dorsally and ventrally, even in the case of small knobs such as those in *Dyoplosaurus acutosquameus* (ROM 788) or *Saichania* (PIN 3142/251). There are typically a variety of small osteoderms forming the terminal end of the knob structure. It appears as though the tail club handle vertebrae in ZPAL MgD I/113 broke just anterior to the actual knob, and so the knob is not preserved in this specimen and cannot be compared to other *Tarchia* specimens. However, it is of interest that tail club knobs in specimens referred to *Tarchia* have a wide variety of shapes and sizes. PIN 551-29 has a poorly preserved but small tail club knob, as does ZPAL MgD I/42. In ZPAL MgD I/42, the keels on the major osteoderms are located at approximately the mid-height level of the osteoderms. In contrast, ZPAL MgD I/43 has anterolaterally-directed keels on the major osteoderms. It is difficult to determine the effects of ontogeny on tail club knob development, making it impossible to say whether ZPAL MgD I/43 represents one of the largest individuals of the genus *Tarchia* or whether it represents a distinct taxon.

Penkalski (2001) stated that in general each individual has a consistent osteoderm surface texture. This statement corresponds to the osteoderms in specimen ZPAL MgD I/113, with all osteoderms having rugose surfaces. Burns and Sullivan (2011) note, however, that although osteoderm texture is consistent within an individual, the tail club knob tex-

ture often differs substantially from the other body osteoderms. This provides further support that the most posterior preserved osteoderms in ZPAL MgD I/113 do not represent the terminal knob, as these osteoderms share a similar texture with the other caudal osteoderms.

The deep grooves on the Type 2 osteoderms are unusual features of ZPAL MgD I/113. Maleev (1956) noted the presence of two osteoderms with fluted ornamentation in *Talarurus*. However, these have numerous parallel ridges originating on the osteoderm surface about half way between the peak and the base line. The ridges increase in height and width towards the base line. Penkalski (2001) also noted the presence of ribbed, fluted osteoderm textures in several specimens referred to *Euoplocephalus*. Coombs (1995) described a small tail club from Alberta with distinct deep grooves on the dorsal surface; the texture of this specimen (ROM 7761) closely resembles that of ZPAL MgD I/113. A large tail club from Alberta (ROM 788) also has large furrows (Arbour and Currie 2011). A ridge and groove structure similar to those in *Euoplocephalus* and *Talarurus* is only present in one osteoderm in specimen ZPAL MgD I/113 (the Type 6 caudal osteoderm). The large grooves of the Type 2 plates, especially in the anterior part of the tail, are unique to ZPAL MgD I/113.

The functions of the grooves in the Type 2 plates remains unknown. It is unlikely that they were vascular in origin as their inner surfaces are smooth in contrast to the outer rugose and perforated surface areas of all osteoderms in the specimen. Coombs (1995) postulated that the grooves on ROM 7761 were not caused by abrasion from tail dragging, and instead may have been related to growth or the position

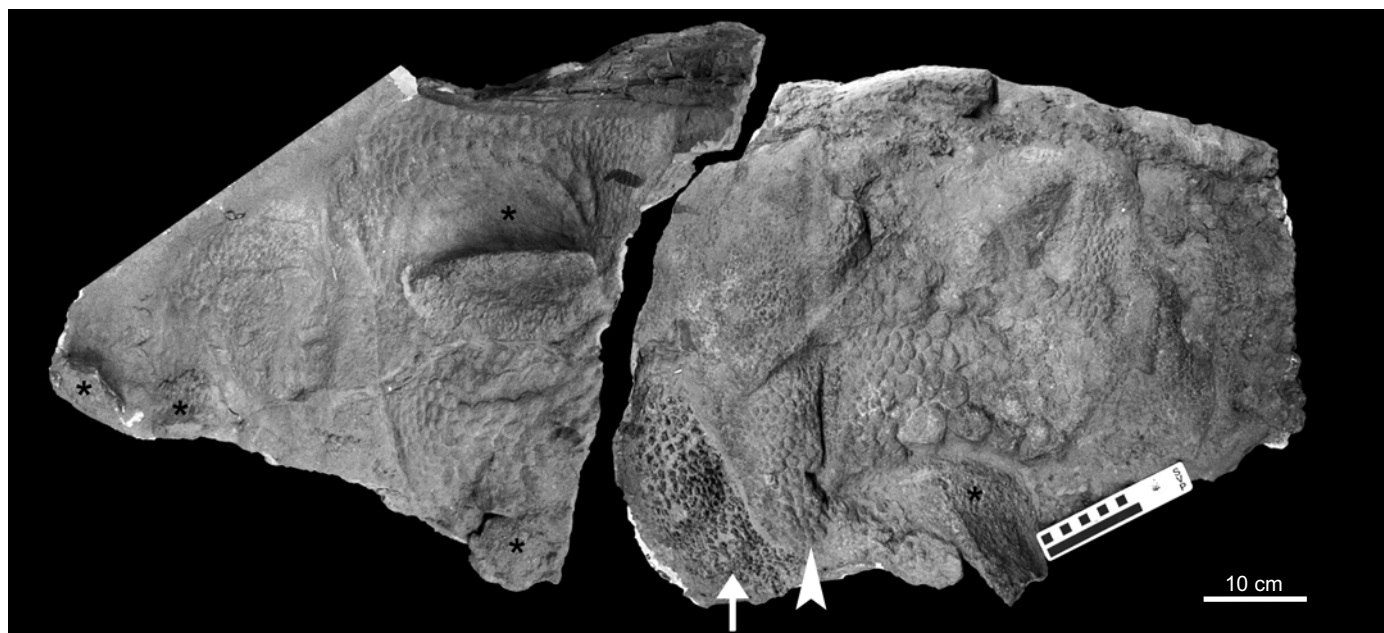


Fig. 6. Dorsal view of two blocks from an indeterminate ankylosaurid, ROM 813 from the Dinosaur Park Formation of Alberta, Canada, showing relationships between large osteoderms, smaller ossicles, and keratinous scale impressions. Large osteoderms are marked with an asterisk. Scale impressions are found in a layer (indicated by the arrowhead) above that containing the dark, shiny ossicles (indicated by the arrow).

of blood vessels. A potential explanation for the grooves could be the presence of keratinous ornamentation. As shown by ZPAL MgD I/113, ankylosaur osteoderms were covered with horny keratinous scales as in extant squamates and crocodilians; however, there is currently little data correlating keratinous texture with underlying bone surface texture. Ridged and grooved textures on the nasal boss of *Pachyrhinosaurus* were correlated with the presence of a cornified pad similar to that in *Ovibos*, the muskox (Hieronymus et al. 2009), so it is perhaps possible that the grooves on ZPAL MgD I/113 are associated with particularly thick keratinous coverings.

ZPAL MgD I/113 is the first Mongolian ankylosaurid specimen to preserve keratinous scale impressions. Similar impressions are found in the North American ankylosaurid specimen ROM 813 (Fig. 6). However, ZPAL MgD I/113 appears to lack the small, mm-sized ossicles in ROM 813 that occur ventral to the keratinous scale impressions, in the layer also containing large osteoderms. Both ZPAL MgD I/113 and ROM 813 show rosettes of scales around the larger osteoderms. ROM 813 preserves a greater variety of scale sizes and shapes, but those surrounding the large osteoderms are smaller and squarer than those in ZPAL MgD I/113, which are longer and more rectangular.

Conclusions

There are several features in ZPAL MgD I/113 that are not present in other specimens referred to *Tarchia*, or in other ankylosaurids. The angle of divergence of the neural spines

in the handle vertebrae, 35° , differs from all other ankylosaurids, which typically have an average angle around 20° (except for *Ankylosaurus*). The large number of vertebrae incorporated into the handle of the tail club is more like the condition in *Pinacosaurus* than in *Dyoplosaurus* or *Saichania*. The large grooves on the Type 2 osteoderms are also unique to this specimen. The arrangement of osteoderms on the tail differs from that of *Saichania*, as ZPAL MgD I/113 lacks osteoderms that are semicircular in dorsal view, as are found in *Saichania*.

ZPAL MgD I/113 is also the first Mongolian ankylosaurid to preserve keratinous scale impressions, and the pattern differs from that found in *Euoplocephalus*. Bell (2012) proposed that variations in keratinous scale arrangements among hadrosaurs may be of taxonomic value.

The angle of divergence of the neural spines, and the deep grooves on the osteoderms, are not found in other specimens referred to *Tarchia*, and it is possible that these features do not represent intraspecific variation. However, it is impossible to say at present whether ZPAL MgD I/113 represents the true condition for *Tarchia*, or whether it may represent a distinct taxon from *Tarchia* and *Saichania*. The non-overlapping nature of the holotypes of “*Dyoplosaurus*” *giganteus* and *Tarchia kielanae* makes it difficult to assign postcranial specimens to *Tarchia*. Until the postcrania of PIN 3142/250 are described, it will continue to be challenging to assess the taxonomic diversity of ankylosaurids in the Nemegt Formation. ZPAL MgD I/113 still provides an excellent opportunity to document morphological variation in the postcranial skeleton of ankylosaurids, and, if referable to *Tarchia*, provides additional information on postcranial differences between *Tarchia* and *Saichania*.

Acknowledgements

We thank Robert Sullivan (State Museum of Pennsylvania, Harrisburg, USA) and James Kirkland (Utah Geological Survey, Salt Lake City, USA) for reviewing this manuscript, and David Bruton (University of Oslo, Norway) and Teresa Maryńska (Muzeum Ziemi PAN, Warsaw, Poland) for comments on early versions of this manuscript. Bjørn Lund (University of Oslo) provided assistance with preparation of ZPAL MgD I/113. Many thanks also to Magdalena Borsuk-Białynicka (ZPAL), Tatyana Tumanova (PIN), David Evans (ROM), and Khishigjav Tsogtbaatar (MPC) who provided access to collections. The authors gratefully acknowledge funding support from the National Sciences and Engineering Research Council (Discovery Grant, Canada Graduate Scholarship-Doctoral, and Michael Smith Foreign Study Supplement), Alberta Ingenuity, the Dinosaur Research Institute, and the Korea-Mongolia International Dinosaur Project.

References

- Arbour, V.M. and Currie, P.J. 2011. Ankylosaur tail and pelvis pathologies. *Historical Biology* 23: 375–390.
- Arbour, V.M., Burns, M.E., and Sissons, R.L. 2009. A redescription of the ankylosaurid dinosaur *Dyoplosaurus acutosquameus* Parks, 1924 (Ornithischia: Ankylosauria) and a revision of the genus. *Journal of Vertebrate Paleontology* 29: 1117–1135.
- Bell, P.R. 2012. Standardized terminology and potential taxonomic utility for hadrosaurid skin impressions: a case study for *Saurolophus* from Canada and Mongolia. *PLoS ONE* 7: e31295.
- Blows, W.T. 2001. Dermal armor of the polacanthine dinosaurs. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 363–385. Indiana University Press, Bloomington.
- Brown, B. 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum of Natural History* 24: 187–201.
- Burns, M.E. and Sullivan, R.M. 2011. The tail club of *Nodocephalosaurus kirtlandensis* (Dinosauria: Ankylosauridae), with a review of ankylosaurid tail club morphology and biostratigraphy. *New Mexico Museum of Natural History Bulletin* 53: 179–186.
- Carpenter, K., Hayashi, S., Kobayashi, Y., Maryńska, T., Barsbold, R., Sato, K., and Obata, I. 2011. *Saichania chulsanensis* (Ornithischia, Ankylosauridae) from the Upper Cretaceous of Mongolia. *Palaeontographica Abteilung A* 294: 1–61.
- Coombs, W.P., Jr. 1978. The families of the ornithischian dinosaur order Ankylosauria. *Journal of Paleontology* 21: 143–170.
- Coombs, W.P., Jr. 1995. Ankylosaurian tail clubs of middle Campanian to early Maastrichtian age from Western North America, with description of a tiny club from Alberta and discussion of tail orientation and tail club function. *Canadian Journal of Earth Sciences* 32: 902–912.
- Hieronymus, T.L., Witmer, L.M., Tanke, D.H., and Currie, P.J. 2009. The facial integument of centrosaurine ceratopsids: morphological and histological correlates of novel skin structures. *The Anatomical Record* 292: 1370–1396.
- Kielan-Jaworowska, Z. and Dovchin, N. 1969. Narrative of the Polish-Mongolian Palaeontological Expeditions 1963–1965. *Palaeontologia Polonica* 19: 7–30.
- Kielan-Jaworowska, Z. and Barsbold, R. 1972. Narrative of the Polish-Mongolian Palaeontological Expeditions 1967–1971. *Palaeontologia Polonica* 27: 5–13.
- Lambe, L.M. 1902. New genera and species from the Belly River Series (mid-Cretaceous). *Geological Survey of Canada Contributions to Canadian Palaeontology* 3: 25–81.
- Lambe, L.M. 1910. Note on the parietal crest of *Centrosaurus apertus* and a proposed new generic name for *Stereocephalus tutus*. *Ottawa Naturalist* 14: 149–151.
- Maleev, E.A. 1956. Armoured dinosaurs from the Upper Cretaceous of Mongolia [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 62: 51–91.
- Maryńska, T. 1969. Remains of armoured dinosaurs from the uppermost Cretaceous in Nemegt Basin, Gobi Desert. *Palaeontologia Polonica* 21: 23–41.
- Maryńska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica* 37: 85–151.
- Nopcsa, F. 1915. Die dinosaurier der Siebenbürgischen landesteile Ungarns. *Communications of the yearbook of the Royal Hungarian Geological Imperial Institute* 23: 1–24.
- Osborn, H.F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates* 95: 1–10.
- Owen, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Sciences* 9: 60–204.
- Parks, W.A. 1924. *Dyoplosaurus acutosquameus*, a new genus and species of armoured dinosaur. *University of Toronto Studies, Geological Series* 18: 5–25.
- Penkalski, P. 2001. Variation in specimens referred to *Euoplocephalus tutus*. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 287–288. Indiana University Press, Bloomington.
- Seeley, H.G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43: 165–171.
- Tumanova, T.A. 1987. The armoured dinosaurs of Mongolia [original in Russian; translation by R. Griffith, 1999]. *The Joint Soviet-Mongolian Paleontological Expedition Transaction* 32: 1–77.