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A new ankylosaurid from the late Cretaceous Two Medicine Formation of Montana, USA

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Oohkotokia horneri gen. et sp. nov. is described based on a specimen in the collections of the Museum of the Rockies, Montana, USA. *Oohkotokia* exhibits a unique combination of characters not seen in other late Campanian North American ankylosaurids: prominent, horn-like, trihedral squamosal bosses, a small, undistinguished median nasal plate on the dorsal surface of the rostrum, a relatively small occipital condyle, a smooth, finely pitted osteoderm external texture, and triangular lateral osteoderms. Other specimens from the Two Medicine Formation are referable to *Oohkotokia*. *O. horneri*, *Euoplocephalus tutus*, *Dyoplosaurus acutosquameus*, and *Scolosaurus cutleri* separate stratigraphically.

Key words: Dinosauria, Ornithischia, Ankylosauridae, ankylosaur, systematics, Campanian, Cretaceous, Two Medicine Formation, Montana, USA.

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Introduction

The late Campanian Two Medicine Formation of northern Montana has yielded a unique dinosaur fauna including hadrosaurs, hypsilophodontids, ceratopsians, dromaeosaurids, theropods, and ankylosaurs (Gilmore 1917, 1930, 1939; Horner 1984; Horner et al. 1992; Weishampel et al. 2004; Chinnery and Horner 2007). The Upper Two Medicine Formation is especially rich; discoveries include hadrosaur eggs and hatchlings (Horner and Makela 1979; Horner 1982, 1983, 1999b), *Troodon* eggs with embryos (Horner and Weishampel 1988; Varricchio et al. 2002), and microraptorines (Burnham et al. 2000). Interestingly, several dinosaur groups are represented by unusual types that appear to be morphologically intermediate between Judithian and Maastrichtian forms (Horner et al. 1992; Sampson 1995; Horner 1999a).

Ankylosaur remains from the Two Medicine Formation include nodosaurids and ankylosaurids. Gilmore (1930) described *Edmontonia rugosidens* (as *Palaeoscincus rugosidens*) based on a fine specimen including the skull, much of the axial skeleton, and armour. In the same paper, Gilmore described an ankylosaurid skull (USNM 11892), which he referred to *Dyoplosaurus acutosquameus* Parks, 1924 from the Dinosaur Park Formation of Alberta. Other ankylosaurid taxa established on material from this region include *Scolosaurus cutleri* Nopcsa, 1928 from the Dinosaur Park Formation and *Anodontosaurus lambei* Sternberg, 1929 from the younger Horseshoe Canyon Formation of Alberta. Coombs (1971, 1978) synonymized all three of these with *Euoplocephalus tutus* (Lambe, 1902), and for several decades, the only recognized late Campanian ankylosaurid from western North America was *E. tutus*.

In a survey of variation among specimens referred to *Euoplocephalus*, Penkalski (2001) suggested that the material actually represents several taxa. Vickaryous and Russell (2003) redescribed the skull of *Euoplocephalus* using referred specimens, arguing that they all represent a single, highly variable taxon. Arbour et al. (2009) then reinstated *Dyoplosaurus* based on differences between that holotype (ROM 784) and material referred to *Euoplocephalus*. *Dyoplosaurus* has since been accepted as a valid taxon (Thompson et al. 2012), and *Scolosaurus* is valid, too (Penkalski and Blows 2013). Moreover, Arbour (2010) concluded that *Anodontosaurus* is distinct as well, and Arbour and Currie (2013) formally reinstated it. Thus the taxonomy has come full circle.

The taxonomic flux highlights the difficulties in separating taxa. Even derived Asian ankylosaurines are similar to North American forms in their overall skull proportions and in many details. Similarly, many postcranial characters that might at first seem unique are in fact ubiquitous—dorsal osteoderms with folded keels, for example, and spine-like osteoderms on the tail (Penkalski and Blows 2013). Other, seemingly minor differences can be significant.

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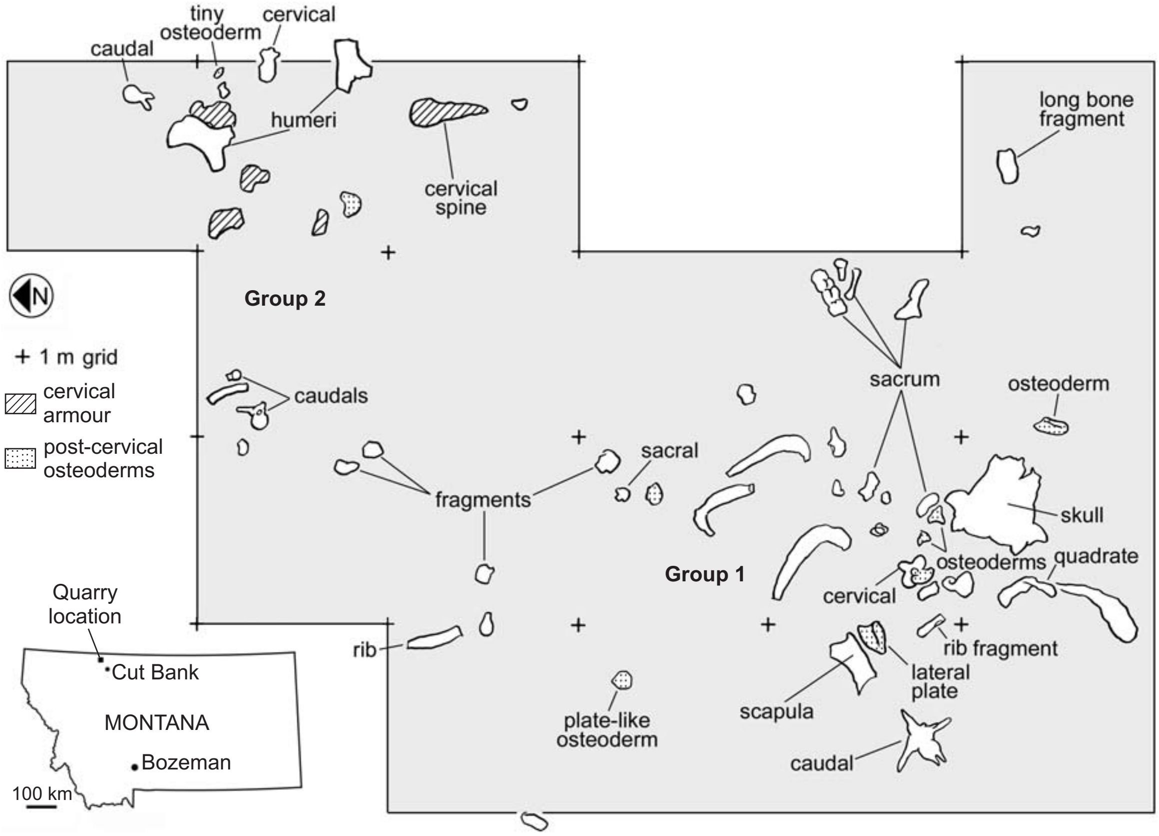

Fig. 1. Quarry map for holotype of *Oohkotokia horneri* gen. et sp. nov. (MOR 433) from the late Campanian Upper Two Medicine Formation of Montana, USA.

An undescribed specimen from the Upper Two Medicine Formation, MOR 433, is not referable to any of the above four nominal ankylosaurid taxa and represents a previously unknown taxon. It is the first new ankylosaurid from Montana or Alberta to be described in more than 80 years. Previously unknown ankylosaurids have been described in recent years from New Mexico (*Nodocephalosaurus kirtlandensis* Sullivan, 1999 and *Ashislepelta minor* Burns and Sullivan, 2011), Utah (*Cedarpelta bilbeyhallorum* Carpenter, Kirkland, Birge, and Bird, 2001), and China (*Tianzhenosaurus youngi* Pang and Cheng, 1998; *Pinacosaurus mephistocephalus* Godefroit, Pereda-Superbiola, Li, and Dong, 1999; *Crichtonsaurus bohlini* Dong, 2002; *Zhongyuansaurus luoyangensis* Xu, Lu, Zhang, Jia, Hu, Zhang, Wu, and Ji, 2007). Other ankylosaurs known from Montana include *Sauropelta edwardsorum* (Ostrom, 1970) and *Tatankacephalus cooneyorum* (Parsons and Parsons, 2009) from the Cloverly Formation, and *Ankylosaurus magniventris* (Brown, 1908) from the Hell Creek Formation.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Canada (formerly National Museums of Canada); FPDM, Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; MOR, Museum of the Rockies, Bozeman, USA; NHMUK, Natural History Museum, London, UK (formerly British Museum of Natural History); NSM PV, National Museum of Japan, Tokyo, Japan; ROM, Royal Ontario Museum, Toronto, Canada; SDNHM, San Diego Natural History Museum, San Diego, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Canada; USNM, United States National Museum (Smithsonian), Washington DC, USA.

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Geological setting

The specimen described here, MOR 433, was found disarticulated in a grey siltstone. Recovered in 1986–87 by field crews from the MOR, the material as catalogued includes an ankylosaurid skull, typical ankylosaur axial material, a partial scapula, several thin-walled, ankylosaurid-type osteoderms, nodosaurid-like cervical armour, a very large humerus, and various fragments. The material ranges in colour from red to grey; however, the colouration does not appear to carry any taphonomic or taxonomic signature, and the variation likely arises from weathering.

The quarry (Fig. 1) contained two loose concentrations of bones, the centres of which were separated by about three metres. Most or all of the nodosaurid-like material (humeri and cervical armour) lay in one concentration (Group 2) while the skull and other ankylosaurid material lay mostly in the other (Group 1); no unambiguously ankylosaurid elements were found in Group 2. John R. Horner (personal communication, 2012) felt that the material was from a single animal. While there is no obvious duplication of skeletal elements, there may be overlap in the preserved sacral centra as discussed below. Because of the quarry topography, I describe the material in three sections: first, the Group 1 (ankylosaurid) material, then the sacrum (or sacra), and finally the other (Group 2) material. The diagnosis is based only on Group 1 elements that are unambiguously ankylosaurid in nature—specifically the skull and free osteoderms.

A nodosaurid-like tooth was found as float in the quarry, but its location is not shown on the field map. The crown measures 10.3 mm tall by 10 mm long, with divergent denticles and a pronounced cingulum on one side—a typical nodosaurid morphology (Coombs 1990). The tooth almost certainly is not from the present skull. However, some basal ankylosaurids such as *Cedarpelta* and *Gobisaurus* also had large (10+ mm) teeth, and there is no a priori reason to assume they were absent from all ankylosaurines.

Systematic palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Ankylosauria Osborn, 1923

Ankylosauridae Brown, 1908

Ankylosaurinae Nopcsa, 1918

Genus *Oohkotokia* nov.

Etymology: From the Blackfoot animate noun *ooh'kotoka*, meaning large stone or rock, plus the Latin *-ia*, indicating made of or derived from, literally "child of stone," an allusion to the all-encompassing armour. Intended pronunciation: "O-OH-ko-toke-ee-uh"; IPA pronunciation [ʻo:xkotokia]. The generic name honours the Blackfeet people, on whose land the specimen was found.

Type species: *Oohkotokia horneri* sp. nov., see below; monotypic.

Diagnosis.—As for the type species.

Oohkotokia horneri sp. nov.

Figs. 2A, 3A, 4, 5A–E, G, H.

Etymology: The specific name honours John R. Horner for his work on dinosaurs from Montana.

Holotype: MOR 433, a skull and fragmentary skeleton from Group 1 area of quarry.

Type locality: MOR Locality TM-034, northwest of Cut Bank, Montana, USA.

Type horizon: Upper Two Medicine Formation (upper Campanian) of northwestern Montana, about 55 m below the contact with the Bearpaw Shale. The Two Medicine Formation is about 650 m thick and consists primarily of mudstone, siltstone, and fine-grained lenticular sandstone, interbedded with bentonite layers of varying thickness (Dawson 1885; Stebinger 1914; Rogers et al. 1993). The Upper Two Medicine has been dated by Rogers et al. (1993) using radioisotopes at 74 Ma (10 m below top of formation), an age accepted by Eberth (1997) and Trexler (2001). The top of the Dinosaur Park Formation was given an age of 74–74.5 Ma by Eberth (1997), but of 75 Ma or older by Hamblin (1994). Eberth (2005) refined this to around 74.9 Ma. Thus, the uppermost Two Medicine sediments are slightly younger than the latest Dinosaur Park beds.

Referred specimens.—MOR 363, a fragmentary skull from 60 m below the top of the Upper Two Medicine Formation (John R. Horner, personal communication 2004), with supraorbital and quadratojugal bosses identical to those of the holotype; MOR 538; NSM PV 20381, an undescribed specimen recovered in 1995 from a bonebed (Tanoue 2005) that includes a partial skull, vertebrae, a partial pelvis, forelimb and hindlimb elements without feet, and one keeled osteoderm; FPDM V-35, another undescribed specimen from the Upper Two Medicine Formation; TMP 2001.42.19; USNM 7943; USNM 11892.

Diagnosis.—An ankylosaurine diagnosed by the following unique combination of characters: median plate on nasal area of skull roof small (<50 mm), not distinguished from surrounding osteoderms; prominent, horn-like, trihedral squamosal bosses; keel on squamosal boss flat rostrally, grading into a blunt keel dorsally; apex rounded and unkeeled, situated caudally; caudal surface of squamosal boss flat to gently rounded and unkeeled; broad, smooth quadratojugal bosses with strong caudal curvature; nuchal crest not visible in lateral view; occipital condyle small (≤16% basal skull length); orbit large; osteoderms basally excavated with a smooth, weakly ornamented external surface texture; steeply-pitched, triangular caudal osteoderms. The small nasal plate, caudally curved quadratojugal bosses, and horn-like squamosal bosses distinguish *O. horneri* from *Euoplocephalus tutus*. Nuchal crest morphology, supraorbital boss shape, and vertebral morphology separate *O. horneri* from *Dyoplosaurus* acutosquameus, and osteoderm shape and texture distinguish *O. horneri* from *D. acutosquameus* and *Scolosaurus cutleri*. The horn-like squamosal bosses distinguish *O. horneri* from *A. lambei*.

Description

Group 1 (ankylosaurid) material

Skull.—The skull (Figs. 1–3) is crushed but reasonably well preserved on its dorsal and lateral surfaces. It is cracked rostrally to the right of the midline (see Fig. 2A$_1$) where the left and right sides were split apart post-mortem. As a result, the midline rostrally (midline; Fig. 2) is offset to the animal's left side. To either side of the narrowly triangular gap, the dorsal surface is well preserved. The palatal side is weathered, with most of the palate having been removed by erosion. The premaxillary beak is missing, though fragments of the premaxillae remain. The skull measures 415 mm long (sagittally) as preserved. After accounting for crushing and lack of the premaxillary beak, basal length was probably around 375 mm, one of the larger Campanian North American skulls. Overall, it appears most similar to skulls that have been referred to *Euoplocephalus*. It is crucial to note, however, that some of those skulls do not represent *E. tutus* (Penkalski 2001; Arbour 2010).

The crushing is unusual. Rather than being more-or-less unidirectional, there is a roughly triangular area around which the skull has been splayed outward, as if it were stepped on. This flattened area is bordered caudally by the fracture or escarpment along the nuchal crest, laterally by the right supraorbital + preorbital bosses, and rostromedially by the crack that extends from the rostral triangular break toward the left squamosal boss (Fig. 2A$_1$). The overall distortion suggests dinoturbation.

The dorsal surface has numerous small, flat, polygonal osteoderms with weak overall bilateral symmetry, an ankylosaurid character (Coombs 1978; Thompson et al. 2012). The borders of the osteoderms are clearly delineated rostrally but become less well defined in the area between the supraorbital bosses; caudally, the borders are again well defined. This, too, is typical of ankylosaurids.

Rostrally, there is no large, median osteoderm or plate ("large sagittally positioned polygon" of Vickaryous and Russell 2003; "internarial ornamentation" of Carpenter et al. 2011) in the nasal region as there is in most ankylosaurid taxa. Despite crushing, the dorsal surface here is well preserved, and the outlines of most or all nasal region osteoderms can be traced with confidence; only along the crack to the right of the midline are the borders untraceable. Characteristically small osteoderms plainly surround a similarly small central nasal osteoderm (nasal plate; Fig. 2). In *Euoplocephalus tutus*, this plate is prominent, having a raised central area and spanning almost half the width of the snout. Some basal forms and earlier Asian ankylosaurids also lack this feature, although the Campanian *Saichania* and *Tarchia* both have a prominent nasal plate. The plate's absence—or more properly, its small size—in *Oohkotokia* is presumably a reversal. In *Oohkotokia*, the plates in the rostral region (sensu Vickaryous and Russell 2003) are presumed to be fused osteoderms; however, in some ankylosaurids at least, the cranial sculpturing arises instead from dermatocranial elaboration by the periosteum (Carpenter et al. 2001).

The skull is striking in several ways. For one, it has a relatively smooth overall surface texture compared to most other late Campanian ankylosaurid skulls. *Ankylosaurus magniventris* is similarly smooth, as is the holotype of *Euoplocephalus tutus* and several referred skulls. However, the majority are rugose, pitted, and more highly sculptured. In the present specimen, most of the osteoderms have light, subparallel nonvascular grooves and a pitted texture that is less pronounced than in most other skulls.

The squamosal and quadratojugal bosses (horn-like protuberances at the caudal corners of the skull) are prominent. These have variously been referred to as horns, bosses, and ornamentation, but Vickaryous et al. (2001) gave a good rationale for use of the term boss. The squamosal bosses are large and trihedral (Figs. 2, 3), with a degree of caudal curvature. The boss has a flat, narrowly triangular area rostrodorsally that grades into a blunt keel toward the caudally-situated apex of the boss. The keel ends 20–30 mm short of the apex; distal to this, the boss is unkeeled or very weakly keeled, rounded, and suboval in cross section. This morphology is unique and is also present in the referred specimens TMP 2001.42.19 and USNM 11892 (see Gilmore 1930: pl. 9). The right squamosal boss in MOR 433 is better preserved than the left, but the flat rostral area and unkeeled, subconical apex are present in both. Both bosses are missing fragments dorsally; the apices were not pitted. The overall morphology is similar in other specimens, including some from Asia, but the boss is relatively large in MOR 433. Medially, the boss is concave, while laterally and caudally it is relatively flat. These three surfaces form the three sides of the "trihedron". The only Campanian specimens from North America that have a larger boss are others from the Two Medicine Formation that are referred herein to *Oohkotokia*.

The scythe-like quadratojugal boss (Fig. 3) curves caudally, tapering to a point. This boss varies considerably in both size and shape among late Campanian ankylosaurids. However, in undisputed *Euoplocephalus* specimens (TMP 1991.127.1 and UALVP 31; see Penkalski 2001; Arbour et al. 2009; Burns and Sullivan 2011), the quadratojugal boss is more symmetrical, with a central apex. In *Nodocephalosaurus*, the quadratojugal bosses curve rostrally, and Sullivan (1999) found the curvature to be taxonomically useful within Ankylosauridae. Thus, although the caudal curvature is not exclusive to *Oohkotokia*, it is one of a unique suite of diagnostic characters.

On the lateral surface of each side of the skull between the squamosal and quadratojugal bosses is a small (25 mm) but distinct, caudally situated, bluntly pointed osteoderm or ossicle (Figs. 2, 3). Many referred *Euoplocephalus* specimens are smooth here, while others have small osteoderms between the bosses; however, in none is there a keeled or pointed ossicle as in MOR 433.

The orbit is large, measuring at least 63 mm horizontally on the better preserved left side. This diameter is as large as in any skull currently referred to *Euoplocephalus*; however, it is relatively smaller than in three other skulls referred herein to *Oohkotokia*: USNM 11892, TMP 2001.42.19, and NSM PV 20381. Hill and Norell (2008) concluded that the orbit was relatively larger in juvenile ankylosaurs. Yet, none of the three referred *Oohkotokia* specimens are juveniles; the

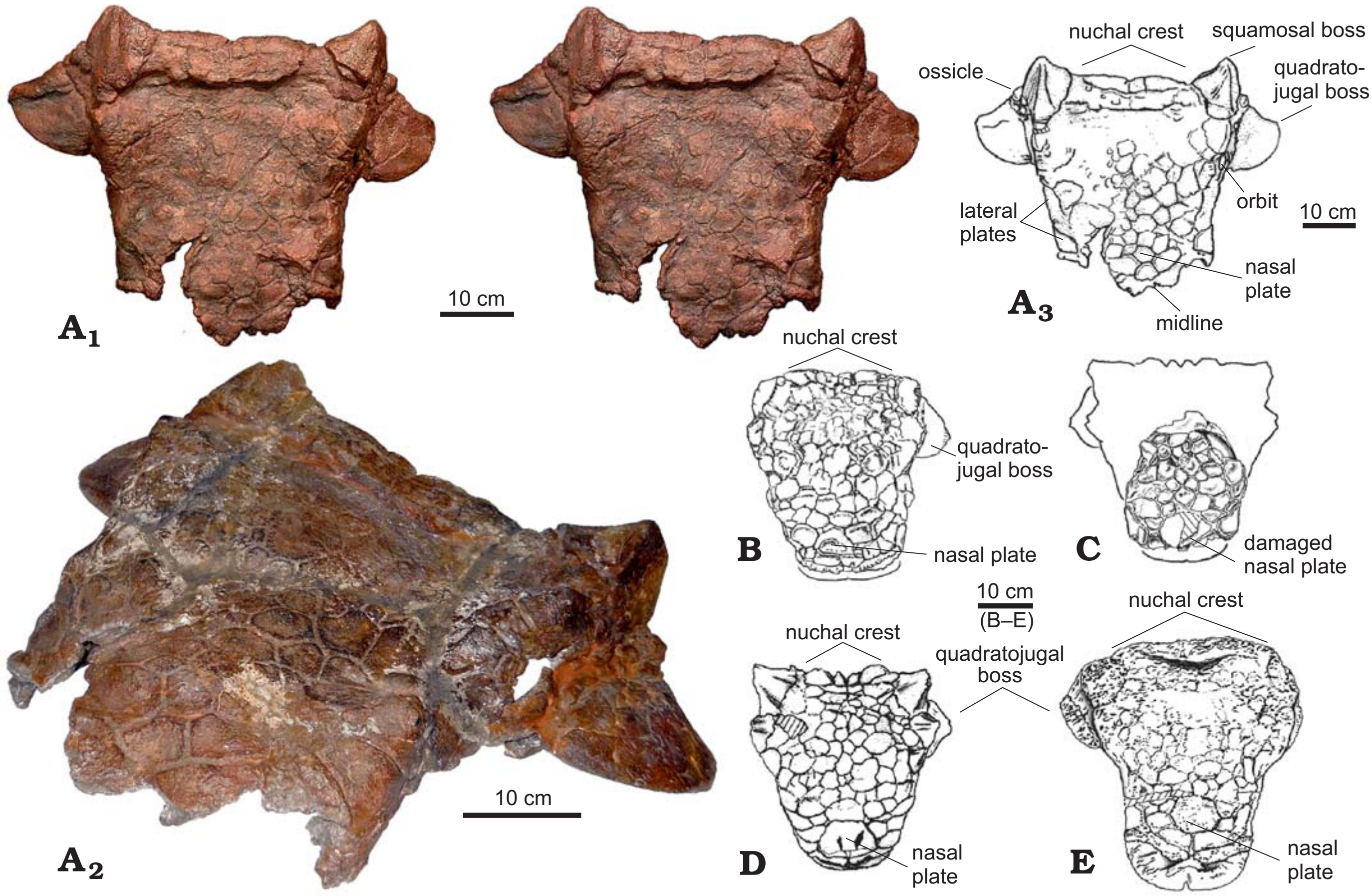

Fig. 2. Skull of ankylosaurid dinosaur *Oohkotokia horneri* gen. et sp. nov. from the late Campanian Upper Two Medicine Formation of Montana, compared with related taxa. **A**. MOR 433, holotype; stereo pair of high fidelity cast in dorsal view (A$_1$) with interpretive drawing (A$_3$); oblique rostrodorsal view of the actual skull (A$_2$). **B**. CMN 8530, holotype of *Anodontosaurus lambei* from the late Campanian–early Maastrichtian Horseshoe Canyon Formation of Alberta. **C**. CMN 0210, holotype of *Euoplocephalus tutus* from the late Campanian Dinosaur Park Formation of Alberta. **D**. TMP 1991.127.1, *Euoplocephalus tutus* from the late Campanian Dinosaur Park Formation of Alberta. **E**. AMNH 5403, ?*Euoplocephalus tutus* from the late Campanian Dinosaur Park Formation of Alberta. **B**–**E**. Interpretive drawings.

smallest measures about 340 mm in basal length—90% the size of MOR 433. Thus *Oohkotokia* apparently had a larger orbit than other taxa from Montana and Alberta. The antorbital margin is correspondingly narrower.

In the palatal region, crushing and erosion make detailed description impossible. Additionally, after preparation was finished, the skull was loaned for an exhibit and in the process was damaged (John R. Horner, personal communication 2011). Several fragments, e.g., portions of the right quadrate and left maxilla, are present in a cast (Fig. 3A$_2$) but no longer in the original skull (Fig. 3A$_1$).

Portions of both maxillae remain, but the alveolar borders are eroded and no teeth are preserved. Importantly, the nasal septum (or vomer) is present dorsally in the nasal cavity, making it possible to locate the midline on the dorsal surface. Note that the vomer is broken and offset along the diagonal fracture in the skull roof, showing how much the rostral portion of the skull is displaced to the animal's left side.

The occipital region is mostly intact although crushed, with the left paroccipital process incomplete distally. Both quadrates are nearly complete, but both are broken mid-shaft and the condyles are abraded. As in *E. tutus* and USNM 11892 (*O. horneri*), the paroccipitals were not fused to the quadrate, as evidenced by the contact on the left quadrate for the incomplete paroccipital process (paroccipital surface; Fig. 3). On the right side, the quadrate ramus of the pterygoid overlaps and is fused to the pterygoid wing of the quadrate, plausibly forming a scarf joint as described by Vickaryous and Russell (2003) for *E. tutus*.

The braincase is complete, but crushing and weathering make interpretation of nerve openings problematic. The large internal carotid foramen is visible piercing the basisphenoid, as in FPDM V-35, with a crescentic nerve III (oculomotor) foramen dorsal to that at the laterosphenoid border. Moving caudally, there is a smaller opening that may be the nerve V (trigeminal nerve) opening, but little else can be discerned with any certainty. Rostrally, the basioccipital tubera are preserved but distorted. The occipital condyle is chipped but otherwise well preserved and measures 61 mm in diameter.

The nuchal crest ("scutellum" of Tumanova 1987; "nuchal ridge" of Carpenter et al. 2011; "nuchal shelf" of Penkalski 2001)—that is, the caudal border of the skull roof excluding

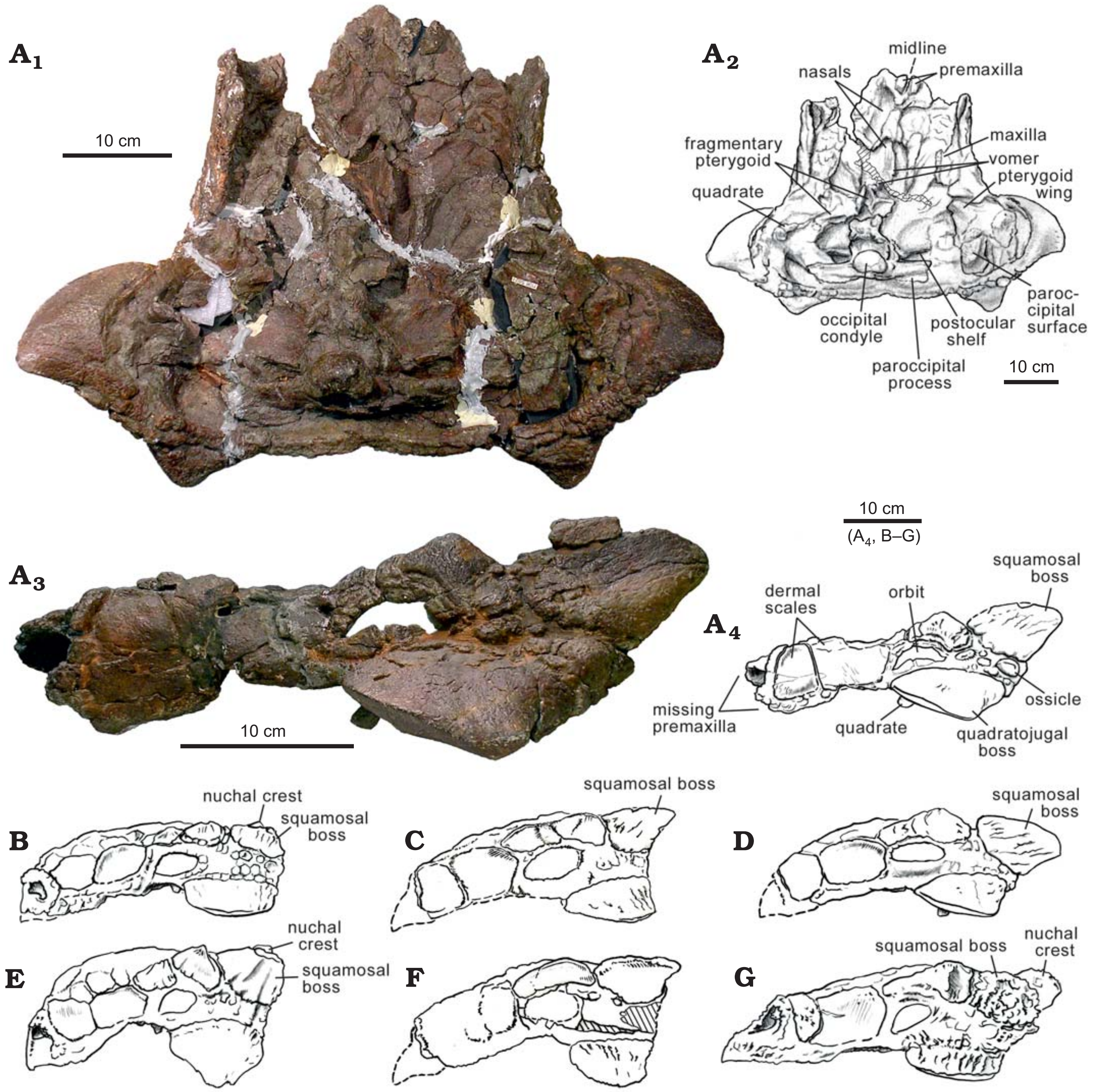

Fig. 3. Skull of ankylosaurid dinosaur *Oohkotokia horneri* gen. et sp. nov. from the late Campanian Upper Two Medicine Formation of Montana, compared with other late Campanian specimens. **A**. MOR 433, holotype, in ventral (A_1, A_2) and lateral (A_3, A_4) views. The ventral line drawing is based on a cast and shows fragments that are now missing from the actual fossil (see text for explanation). **B**. CMN 8530, *Anodontosaurus lambei* from the Horseshoe Canyon Formation of Alberta. **C**. NSM PV 20381, *Oohkotokia horneri* from the Two Medicine Formation of Montana. **D**. USNM 11892, *Oohkotokia horneri* (reversed) from the Two Medicine Formation, Montana. **E**. TMP 1991.127.1, *Euoplocephalus tutus* from the Dinosaur Park Formation of Alberta. **F**. TMP 2001.42.19, *Oohkotokia horneri* from the Two Medicine Formation, Montana. **G**. AMNH 5403, ?*Euoplocephalus tutus* from the lower Dinosaur Park Formation, Alberta.

the squamosal bosses—has four distinct osteoderms as in many ankylosaurid taxa. However, it is not deeply sculptured and is not visible in lateral view as it is in many of the Campanian specimens (compare Fig. 3B–G). This is due in part to the larger squamosal horns in MOR 433 (and the other Two Medicine specimens) but is also related to the width and caudodorsal expanse of the crest. In AMNH 5403, a referred *Euoplocephalus* specimen, the nuchal crest is elevated and rugose and is prominent in lateral view (Fig. 3G). The crest is also visible in TMP 1991.127.1 (= *E. tutus*; Penkalski 2001)

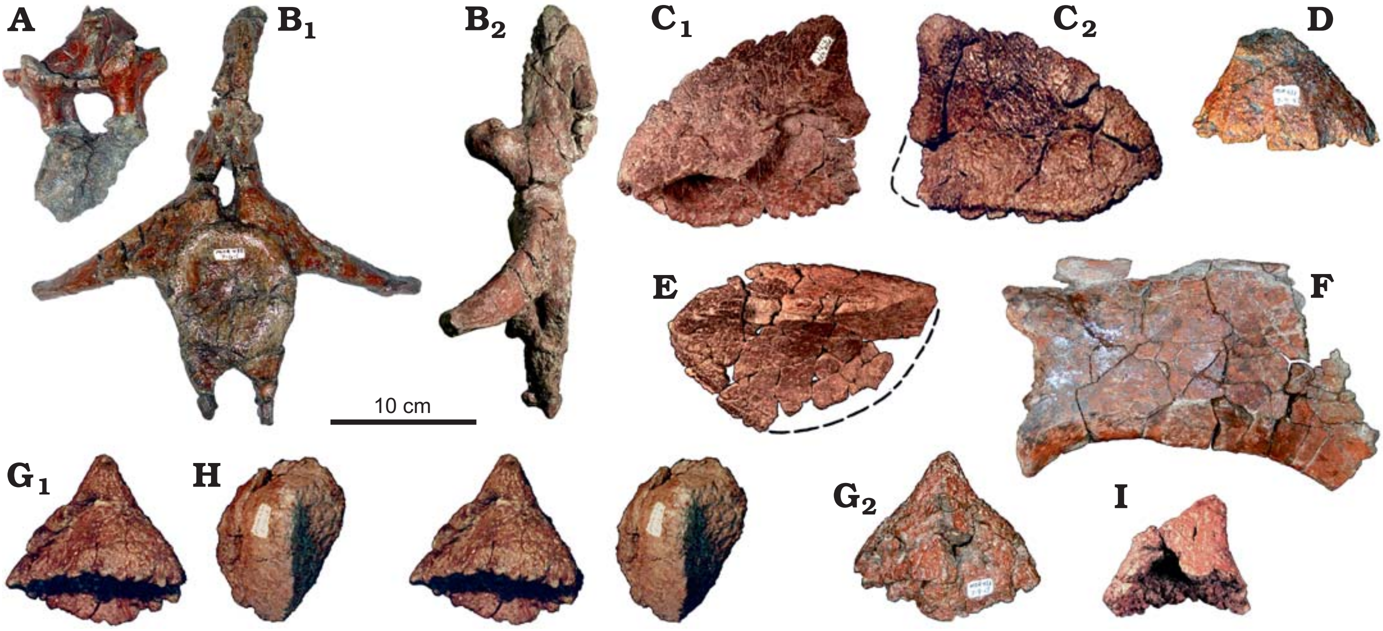

Fig. 4. Postcranial material of *Oohkotokia horneri* gen. et sp. nov. (MOR 433, holotype) from the late Campanian Upper Two Medicine Formation of Montana. **A**. Partial cervical vertebra in cranial view. **B**. Well-preserved fourth or fifth free caudal in distal and left lateral view. **C**. Lateral plate in ?ventral and ?dorsal view (C_1, C_2). **D**. Weakly ribbed subconical osteoderm. **E**. Oval, low-keeled osteoderm in external view. **F**. Partial scapula in ?lateral view. **G**. Conical osteoderm in caudal stereo (G_1) and cranial (G_2) views. **H**. High-keeled osteoderm in dorsal stereo. **I**. Smaller conical osteoderm.

and possibly UALVP 31 (= *E. tutus*; Arbour and Currie 2012) after accounting for crushing, as well as in the Asian *Pinacosaurus*, *Saichania*, *Tarchia*, *Talarurus*, *Tianzhenosaurus*, and *Crichtonsaurus benxiensis* Lü, Ji, Gao, and Li, 2007.

Axial skeleton.—One partial mid-cervical vertebra (Fig. 4A) was found just behind the skull (see Fig. 1). The dorsal half of the neural spine is missing, but judging from its base, the spine was grooved caudally but not compressed craniocaudally into a flange as in *Ankylosaurus* and cf. *Euoplocephalus* (AMNH 5337, AMNH 5403). The neural canal is taller than wide and D-shaped (wider dorsally) as in *Ankylosaurus* and as in the cervical described below with the Group 2 material. In referred *Euoplocephalus* specimens (e.g., AMNH 5403, AMNH 5404), the cervical neural canal is quadrangular. The narrowly oval diapophyses are more strongly inclined than in AMNH 5337 or AMNH 5404.

Only one other isolated vertebra was found in Group 1: a well-preserved ankylosaurid caudal (Fig. 4B), probably the fourth or fifth caudal judging by the presence of the chevron and the length of the transverse processes. The zygapophyseal surfaces are strongly inclined, making an acute angle between them of about 70°. This contrasts with the condition in *Dyoplosaurus* (ROM 784) where the zygapophyseal surfaces of the proximal tail form an obtuse angle of 120–150°. The neural spine is relatively taller than in cf. *Euoplocephalus* (AMNH 5404; Coombs 1971) or *Dyoplosaurus* (Arbour et al. 2009: fig. 4).

In addition to these two vertebrae, parts of the sacrum were found in Group 1, as discussed below. There are also several L-shaped thoracic ribs (Fig. 1), including the distal third of a rib (rib fragment; Fig. 1) with an uncinate process attachment virtually identical to that figured by Brown (1908: fig. 14) for *Ankylosaurus*.

Forelimb.—A poorly preserved scapula (Fig. 4F) consists only of the central portion of the scapular blade; the distal and proximal ends including all but the caudalmost corner of the glenoid are missing. The piece measures 12 cm at its narrowest width. There is no sign of the transverse pseudoacromial process present in most nodosaurids.

Osteoderms.—All of the basally-excavated, ankylosaurid-type osteoderms were found in Group 1, several in close proximity to the skull (see Fig. 1). They all have a similar external surface texture consisting of fine pitting, particularly on the keel, with ordered (sensu Hieronymus et al. 2009) neurovascular channels over much of the surface (Fig. 4). The degree of vascularization and pitting is variable, but all of the osteoderms are of the "smooth" type (sensu Arbour et al. 2009). One is a steeply-pitched, triangular osteoderm (Fig. 4C) that resembles the curved, lateral caudal "plates" (sensu Blows 2001) of some primitive ankylosaurs (e.g., *Polacanthus foxii*; Blows 2001). However, in *Oohkotokia*, this osteoderm is basally excavated and thin-walled, only being thicker along the keel. Similar osteoderms are present laterally in cf. *Saichania* on the flanks and tail (Carpenter et al. 2011).

Another osteoderm (Fig. 4G) is conical and weakly keeled cranially (Fig. 4G_2), with an oval base that is wider (transversely) than long. Plate-like osteoderms (sensu Penkalski 2001) are represented by the one with a damaged keel shown in Fig. 4E and by a smaller, flat fragment with a preserved edge. Many of the osteoderms (Fig. 4C_2, E, G_1) have a double-edged perimeter (sensu Penkalski 2001) and some (e.g., Fig. 4D) have incipient radial ribbing as well.

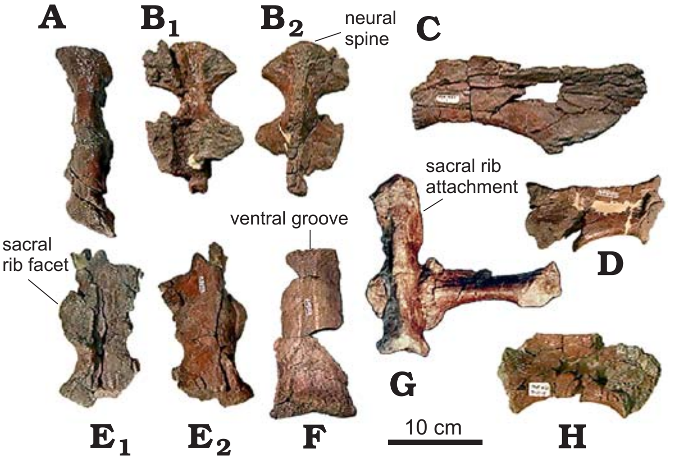

Fig. 5. Sacrum (or sacra) associated with ankylosaurid dinosaur *Oohkotokia horneri* gen. et sp. nov. (MOR 433, holotype) from the late Campanian Upper Two Medicine Formation of Montana. **A**. Presacral rod (?) in ventral view. **B**. Fused neural arches in ventral (B_1) and dorsal (B_2) views. **C**, **D**, **H**. Sacral ribs in cranial view. **E**. Dorsosacral (?) centra in dorsal (E_1) and ventral (E_2) views. **F**. Nodosaurid sacral fragment. **G**. Posterior sacrals with reattached ?s3 rib in ventral view.

Sacral elements.—There appear to be two partial synsacra in the quarry (Fig. 5), supporting the count of two animals. Most of the synsacral material is poorly preserved, so conclusions regarding overall pelvic morphology must be made with caution. The majority of it appears to be ankylosaurid.

Ankylosaurid sacrum.—The preserved elements include three broken segments (Fig. 5A, E, G) representing at least six vertebrae. There is no positive fit between the three segments, suggesting that one or more centra are missing. Where the segments are unbroken, the centra are fused. On each end, the face has a notochordal prominence. Two of the segments (Fig. 5A, G) are crushed laterally. The ribs and their transverse processes are fused and T-shaped in cross-section. The caudalmost is fused to its centrum; the others seem to have been unfused or poorly fused.

The segment with two vertebrae only (Fig. 5A) is poorly preserved dorsally but appears to be the cranial part of a presacral rod. The wider segment (Fig. 5E) consists of two fused centra missing their arches. This piece is obliquely crushed with the ?cranial centrum broken and incomplete. On each side are two large attachment points for sacral ribs, both intervertebral and facing dorsolaterally. The unit is interpreted as the last two dorsosacrals. The two largest ribs are the caudalmost dorsosacral and first sacral rib from the animal's left side (compare Coombs 1978: fig. 13). Most of one sacral (i.e., s1) is apparently missing from between the wide segment (Fig. 5E) and the third segment (Fig. 5G) which then consists of the caudal bit of s1 plus s2 and s3 (sensu Coombs 1986). The presumed presacral rod (Fig. 5A) and medium-sized rib (Fig. 5H) were found close to the skull (see Fig. 1).

Another piece (Fig. 5B) consists of two fused neural arches and appears to match the wide centrum segment. The ?cranialmost arch was poorly fused to its centrum on one side (upper left in Fig. $5B_1$). Dorsally, there is a broken longitudinal surface where a bladelike neural process was broken off. It appears that the pre- and post-zygapophyses were fused, but incomplete fusion with the centra—and the partial fusion of the ribs—suggests that this animal was immature. The caudal face of the presumed s3 centrum (bottom in Fig. 5G) is an articular face, so no sacrocaudals were fused to the synsacrum (yet).

Nodosaurid sacrum.—The preserved nodosaurid sacral piece (Fig. 5F) comprises the ?caudal end of a synsacrum. It is badly weathered dorsally, and only the ventral surface remains (Fig. 5F). It preserves part of an articular face and the medial groove described by Gilmore (1930) for *E. rugosidens*. Such a groove is also present in the nodosaurid *Peloroplites* and the basal ankylosaurid *Cedarpelta* (Carpenter et al. 2008). The ?ankylosaurid synsacrals described above lack the ventral groove, so even if there is no overlap, i.e., no duplication of elements, this piece is likely from a different animal. Judging by its length (18 cm), the piece represents two vertebrae. Its location was not recorded on the field map or in field notes, but if it was found near similarly numbered items, it was located between Group 1 and Group 2.

Group 2 material

Most or all of these elements likely belong to an edmontoniid (sensu Bakker 1988) that was deposited near the *Oohkotokia* holotype. However, some elements differ from typical *Edmontonia*, and there is the possibility, however remote, that they are from the same animal as the Group 1 material.

Vertebrae.—Four vertebrae were found in Group 2: a mid-cervical and three caudals (Figs. 1, 6A–C). The base of the cervical's broken neural spine is abraded but is solid and not a laterally expanded flange as in some ankylosaurids. An incomplete proximal caudal (Fig. 6C) is similar to the third caudal of *E. rugosidens* described by Gilmore (1930) and is nominally referable to that genus. The neural canal is excavated into the centrum, resulting in a heart-shape to the centrum in axial view. The preserved caudals of cf. *Euoplocephalus* (AMNH 5404, ROM 1930) do not show this morphology, but those of *Nodocephalosaurus* do (Sullivan and Fowler 2006) as does the one preserved caudal of CMN 8530 (*Anodontosaurus*). There is some positional variation in the shape of the centrum and neural canal. Another caudal (Fig. 6B) is unremarkable except that the neural spine is mostly complete and shorter than in the ankylosaurid caudal (Fig. 4B) described above. The fourth Group 2 vertebra is a poorly preserved mid-caudal centrum.

Forelimb.—Two partial humeri are present. The left (Fig. 6I) is more complete than the right but is missing the proximal end and the ulnar condyle. It is unclear whether the deltopectoral crest extended distally past the midpoint of the humerus as it typically does in ankylosaurids and *Gastonia* (Kirkland 1998). The radial condyle is weathered, but the shape is roughly correct, and the rest of the bone is well preserved. This humerus was certainly very large, comparable in size to that of *Edmontonia rugosidens* or *Ankylosaurus*.

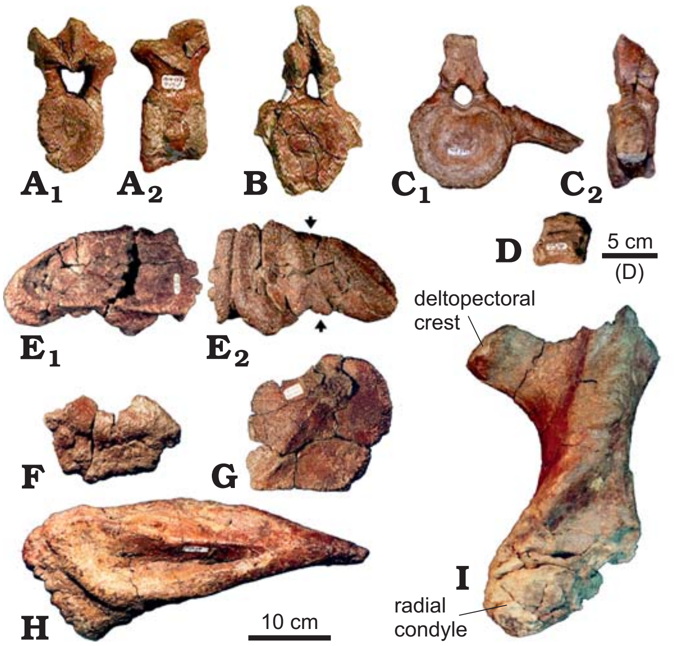

Fig. 6. Nodosaurid (Group 2; see text) material from the quarry, catalogued as MOR 433, including cervical armour and vertebrae referable to *Edmontonia* sp. **A**. Cervical vertebra in cranial (A_1) and lateral (A_2) views. **B**. Cadual vertebra in distal view. **C**. ?Third caudal in ?distal (C_1) and lateral (C_2) views. **D**. Phalanx. **E**. Part of the first cervical half-ring including one distal end, in ventral (E_1) and dorsal (E_2) views; arrows point to bony half-ring layer (see text). **F**. Partial osteoderm fused to underlying bone. **G**. Plate from ?second half-ring. **H**. Cervical/pectoral spine in external view. **I**. Left humerus in caudal view.

Cervical armour.—Most of one-half of the first cervical half-ring is present (Fig. 6E) including a distal end. The two complete osteoderms are oval and keeled, with apices that overhang the caudal border. The lateral osteoderm (sensu Penkalski 2001) is in close contact with the medial one—typical for nodosaurids—but does not contact the distal osteoderm, and the underlying bony half-ring is visible where their curvature forms an angle cranially and caudally (Fig. 6, arrows). The osteoderms are crushed and were evidently hollow underneath.

There is also a large (210 mm) polygonal, keeled cervical osteoderm preserved. It is damaged along one edge, while the opposite border (to the right in Fig. 6G) is a complete edge that abutted another plate (the bony layer can just be seen protruding at lower right). The keel is damaged ?cranially. The bony layer has a woven texture (underneath) that runs roughly parallel to the lower (straight) edge in Fig. 6G, indicating that this is the transverse direction. The element is likely a medial plate from the second half-ring.

The largest osteoderm is a distal cervical or pectoral spine (Fig. 6H) measuring 41 cm long. The end opposite the point has a rugose, undulating sutural contact for the half-ring segment medial to the spine. The spine is crushed and was either basally hollow or filled with cancellous bone as in cf. *Edmontonia* (Hayashi et al. 2010). The dorsal side is keeled for most of its length but becomes rounder in cross section near the apex; along the keel are one or two small, additional points. Carpenter (1990) referred the spine to *E. rugosidens*.

Referred specimens

USNM 11892.—This specimen (Fig. 3D) from the Upper Two Medicine Formation consists of a partial skull and five teeth. It was described in detail by Gilmore (1930), so here I add only a few comments relevant to its taxonomic status. Unfortunately, Gilmore's field notes and map do not give the elevation at which it was collected, and the quarry has not been relocated (John R. Horner, personal communication 2012).

Gilmore (1930) referred the specimen to *Dyoplosaurus acutosquameus* based primarily on tooth morphology. Although dentition may not be taxonomically useful for ankylosaurs below the familial level (Coombs and Demere 1996; personal observations), the teeth of USNM 11892 do represent a morphological extreme among teeth of late Campanian ankylosaurid specimens from Montana and Alberta. The teeth have a shelf-like labial cingulum and a unique Z-shape to the carina in occlusal view. They also lack the severe, random fluting described by Vickaryous and Russell (2003) for *E. tutus*. Conversely, the preserved teeth of *Dyoplosaurus* (ROM 784) lack the sharp cingula and Z-shaped carinae.

Gilmore (1930) believed that the skull lacked the large nasal plate (he called them scutes) while acknowledging that he had "great difficulty" making out the shapes due to fracturing and poor preservation in this region (Gilmore 1930: 32); however, it appears that Gilmore (1930) was correct, as discussed below. Gilmore (1930) also noted two large plates on the side of the snout and claimed that in *Euoplocephalus* (UALVP 31) there were three; in fact, most or all known ankylosaurines including *Euoplocephalus* have two, not including the narrow lacrimal ossification just rostral to the orbit. Even the Asian forms *Saichania* and *Tarchia* (and probably *Tianzhenosaurus*) have a very similar morphology here (e.g., Tumanova 1987).

USNM 11892 has the largest squamosal bosses—indeed, they could reasonably be called horns—of any known Upper Campanian/Lower Maastrichtian ankylosaurid specimen from North America. The bosses are very similar to those of the holotype, although the medial surface of the "trihedron" is not concave. It is noteworthy that Vickaryous and Russell (2003) did not mention USNM 11892 in their redescription of the skull of *Euoplocephalus*, nor did Arbour et al. (2009) sustain Gilmore's (1930) referral to *Dyoplosaurus*.

USNM 7943.—This is a partial first cervical half-ring found north of Milk River, near Landslide Butte, Glacier County, Montana, USA. Gilmore (1917: 44) states that it was found "a short distance from the place where the type of *Brachyceratops montanensis* was discovered, at a slightly higher horizon". According to Sampson (1995), *Brachyceratops* was found about 60 m below the Bearpaw contact; hence, USNM 7943 must be from about the same horizon as MOR 433. The specimen (Fig. 7A) includes both medial osteoderms and a partial lateral osteoderm (sensu Penkalski 2001), solidly

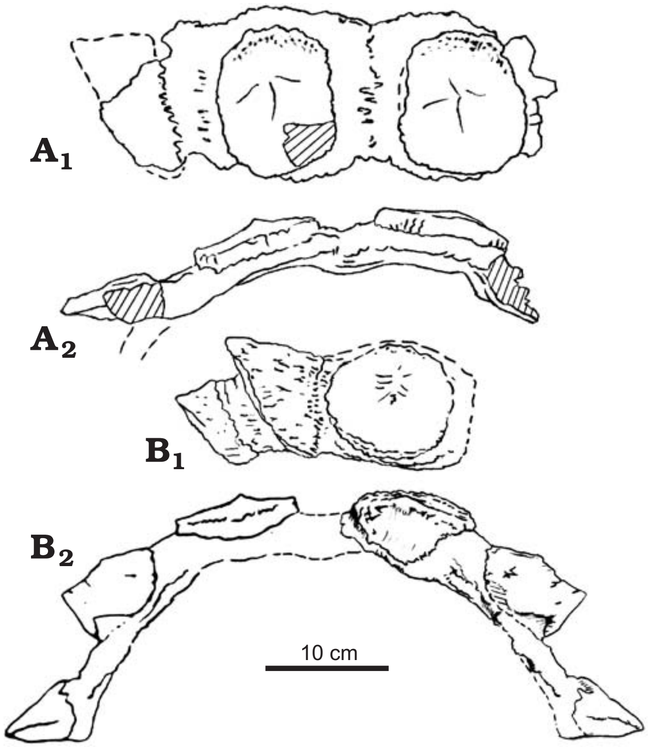

Fig. 7. Drawings of first cervical half-rings of *Oohkotokia horneri* sp. et gen. nov. from the late Campanian Two Medicine Formation of Montana. **A**. USNM 7943 in dorsal (A_1) and caudal (A_2) views. **B**. TMP 2001.42.19 in dorsal (B_1) and caudal (with left half mirrored) (B_2) views.

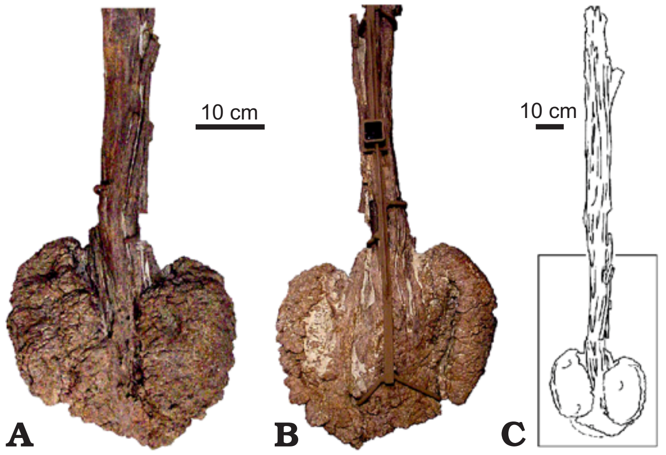

Fig. 8. Well preserved tail club of ankylosaurid dinosaur TMP 2001.42.19, referred specimen of *Oohkotokia horneri* sp. et gen. nov. from the late Campanian Two Medicine Formation of Montana, in dorsal (**A**) and ventral (**B**) views. The complete tail club (**C**); rectangle shows area of photos.

coossified with that section of the underlying bony half-ring. The medial osteoderms are subrectangular and unkeeled, with low, blunt central apices. The lateral osteoderm is steeply-pitched and keeled, although the exact shape is uncertain as the half-ring is dorsoventrally crushed. The shapes match those of the first half-ring of TMP 2001.42.19.

TMP 2001.42.19.—An undescribed specimen from the Two Medicine Formation of Montana, USA, TMP 2001.42.19 includes a partial skull without teeth (Fig. 3F), axial and limb elements, a tail club, and some armour. The specimen was found southwest of Cut Bank, Montana, USA by a private collector, but detailed stratigraphic data were not recorded. The specimen is from a bonebed (Brandon Strilisky, personal communication 2011) so the association of elements is uncertain. The skull has been heavily reconstructed; only the caudal skull roof and occipital regions are well preserved. In overall shape, the skull is similar to that of USNM 11892. The squamosal bosses are horn-like and unkeeled caudally and have the subconical apex present in MOR 433 and USNM 11892.

Most of the axial and appendicular elements are of limited value as they are largely reconstructed. The proximal third of the humerus is missing, but the element appears to match that of NSM PV 20381 in being small but very robust. The one well-preserved pedal ungual is typically hooflike and unlike the wide, triangular unguals of *Dyoplosaurus*.

The right half of the first cervical half-ring is preserved (Fig. 7B), including all three osteoderms from that side. The half-ring is distorted craniomedially, but the overall morphology is comparable to the preserved portion in USNM 7943 (Fig. 7A), although in the latter the medial osteoderm is more rectangular. Several free osteoderms are also present; these are keeled and have a smooth (sensu Arbour et al. 2009) texture, with sparse, subparallel neurovascular grooves.

There is a well-preserved tail club, the first to be described from the Two Medicine Formation. The club (Fig. 8) includes both major osteoderms and an almost complete handle but is damaged and incomplete distally. It is a round (sensu Coombs 1995), average-sized knob measuring 320 mm wide. The keeled major osteoderms are offset to the dorsal side of the knob, giving the club a somewhat "elf-eared" (dorsolaterally pointed) outline in distal view, though not as pronounced as in some other clubs, e.g., AMNH 5245 and UALVP 16247 (Coombs 1995: fig. 2C; Arbour and Snively 2009: fig. 2D). In dorsal view, the major osteoderms are not laterally pointed as in AMNH 5216 and AMNH 5245 from the Horseshoe Canyon Formation. The surface has a hummocky (sensu Hieronymus et al. 2009), cauliflower-like texture that may in part be a taphonomic artefact, although the major osteoderm of another partial club (MOR 538) from the Upper Two Medicine has a similar texture and is about the same size as TMP 2001.42.19.

Discussion

In a morphometric analysis of Late Campanian ankylosaurids from Alberta and Montana, MOR 433 and USNM 11892 plotted as outliers to the ten other specimens in that study (Penkalski 2001). These two specimens have the smallest occipital condyles (adjusted for basal skull length; Penkalski 2001: fig. 13.5) and the largest squamosal bosses (along with TMP 2001.42.19) of any known Late Campanian specimens from North America. NSM PV 20381 is also similar overall to USNM 11892, and these four specimens share numerous characters including squamosal boss morphology, caudally-curved quadratojugal bosses, large orbits, and probably the lack of a large nasal plate on the skull roof.

The skulls do have some notable differences. MOR 433 is larger than USNM 11892, yet the surface texture of the skull roof in MOR 433 is smoother, the opposite of what might be expected as increased rugosity is typically associated with larger size and, indirectly, with more advanced age (Penkalski 2001). The more highly sculpted, hummocky texture on USNM 11892 is at least partly due to taphonomic alteration. USNM 11892 also has a noticeable hump on the skull roof (in rostral view), though the lack of this feature in the holotype (MOR 433) could be due to crushing. The hump, or doming, is present but less pronounced in TMP 2001.42.19 and NSM PV 20381.

Comparison to *Euoplocephalus tutus*.—As Coombs (1978) pointed out, ankylosaurs are a conservative group with limited morphological diversity. In this light, Vickaryous and Russell's (2003) statement that *Euoplocephalus* has a distinctive pattern of plates ornamenting the preorbital snout might be reworded to say that all specimens that have been referred to *Euoplocephalus* have a pattern more similar to one another than to other known ankylosaurids. However, a new ankylosaurid from the Upper Campanian of New Mexico also has a *Euoplocephalus*-like scale pattern (Sullivan et al., 2013), and *Talarurus plicatospineus* Maleev, 1952 has a similar mosaic of small osteoderms instead of the larger, bulbous ones seen in *Saichania*, *Tarchia*, *Tianzhenosaurus*, and *Nodocephalosaurus*. Moreover, there are notable differences among specimens that have been referred to *Euoplocephalus* (Penkalski 2001). Although *Oohkotokia horneri* shares many characters with *E. tutus*, many of those characters are common to most or all derived ankylosaurines.

The lack of a large median nasal osteoderm or plate on the skull roof is rare in ankylosaurines. The vast majority have a prominent sagittal osteoderm (nasal plate; Fig. 2), typically situated just caudal to two bilaterally symmetric, subrectangular or strap-like plates that border the external nares. Regarding CMN 8530 (*Anodontosaurus*), Sternberg (1929: 29) wrote that the nasal plate is "not conspicuously larger than the others" around it. However, that specimen is badly crushed, and although the plate is smaller than in *E. tutus*, it is still conspicuous, as noted by Vickaryous and Russell (2003). Interestingly, other skulls from the Horseshoe Canyon Formation (AMNH 5223, ROM 832, TMP 97.59.1) also have a relatively small median nasal plate; in ROM 832, it is particularly small (<50 mm)—truly no larger than the osteoderms around it, as in *Oohkotokia*. In contrast, the Maastrichtian *Ankylosaurus* has the most prominent nasal plate of any known ankylosaurid, larger even than that of *E. tutus*. Unless this character was unusually plastic, we should expect to find another new ankylosaurid taxon in the late Campanian–early Maastrichtian of North America—one with a prominent nasal plate. Significantly, all skulls from the Dinosaur Park Formation have prominent nasal plates. The very small size of this plate—in essence, its absence as an autapomorphy—in *Oohkotokia* is thus significant, doubly so given that the only other known skull with such a small nasal plate is ROM 832 from the younger Horseshoe Canyon Formation. Thus it is likely that Gilmore was correct, and USNM 11892 (and presumably the other Two Medicine skulls) also lack the large nasal plate. Recent work (e.g., Bell 2012) has demonstrated the utility of epidermis, i.e., scale pattern, in hadrosaurian dinosaur taxonomy.

Squamosal boss morphology varies greatly among specimens—from rugose blobs in some to prominent horns in others, with most specimens having apical resorption pits. Specimens of *O. horneri* show little or no pitting. Some of the variation may be due to ontogeny and/or sexual dimorphism (Penkalski 2001), although the pitting is not size-dependent as the smallest skull (TMP 1991.127.1) has large apical pits. In MOR 433, the squamosal boss is slightly smaller than in USNM 11892 and is not unlike the shape in certain referred *Euoplocephalus* specimens. AMNH 5404 and 5405 have similar bosses with a tapering flat surface rostrally, a concave medial surface, and a flat caudal surface. The flat rostral area is present in most other specimens as well and is homologous to the triangular surface in *Saichania* bordered by the rostral edge of the boss, the keel, and the lateral surface (see Maryańska 1977: pl. 28: 1a; Carpenter et al. 2011: fig. 4F). In ROM 1930, the boss is larger than in either of the AMNH specimens, though still smaller than in MOR 433. ROM 1930 also occurs higher stratigraphically, though still much lower (older) than MOR 433. Various such trends are observable in the group of skulls that have been referred to *Euoplocephalus* over the years and may be evidence of anagenesis in some lineages. The significance of the variation in squamosal boss morphology is not yet fully understood, but the larger, more horn-like bosses in the smaller USNM 11892 might be a sexual character.

Oohkotokia differs from referred *Euoplocephalus* specimens (AMNH 5337, AMNH 5404, ROM 1930) in other ways too, e.g., cervical and caudal vertebral morphology, but many of the referred specimens do not represent *E. tutus* (Penkalski 2001). For this reason, I emphasize comparisons with the other holotypes as well as with *Euoplocephalus* sensu stricto, i.e., specimens that can be confidently referred to *E. tutus* (AMNH 5406, TMP, 1991.127.1, UALVP 31; see Penkalski 2001; Arbour et al. 2009; Burns and Sullivan 2011). MOR 433 is not referable to *Euoplocephalus* based on the following characters: (i) nasal plate is small and inconspicuous, whereas in *Euoplocephalus* it is prominent and broad, with a raised central area; (ii) relatively large, horn-like squamosal bosses that lack apical pits; (iii) quadratojugal bosses curve caudally, while in *E. tutus* they are straight, with a central apex.

Osteoderm morphology.—Most ankylosaurid specimens do not preserve the majority of their armour, but the presence of certain osteoderm types and other factors such as consistency in the texture give an overall picture of a specimen's armour morphology. While isolated osteoderms are generally not diagnostic (Penkalski 2001), the pattern and variety within a specimen are.

Although the surface texture might have changed during ontogeny, the correlation between texture and shape trends among specimens suggests that some aspects of texture are taxonomic (Penkalski 2001). Tumanova (1987, 2000) noted distinct textures characteristic of the osteoderms of *Shamosaurus*, *Talarurus*, *Tarchia*, and *Saichania*. Carpenter (2004) noted the relatively smooth texture in *Ankylosaurus*. Burns (2008) analyzed external surface texture in ankylosaur osteoderms and concluded that it is diagnostic, at least for some taxa. Carpenter (1990) used armour texture (along with other characters) to separate *Edmontonia* (smooth armour) and *Panoplosaurus* (lumpy armour). Burns and Sullivan (2011) erected *Ahshislepelta* based largely on osteoderm texture. Thus there is consensus that the texture has taxonomic value, and osteoderm shape has taxonomic value as well, as noted by Arbour et al. (2009).

In *Oohkotokia*, the external texture is essentially the same on all of the preserved osteoderms and is different than in most upper Campanian specimens from Alberta and Montana. The texture is most similar to that in *Euoplocephalus* sensu stricto and CMN 8530 (*Anodontosaurus*) but with more widespread fine pitting and a less pronounced dendritic pattern to the neurovascular grooves. Similarly, the osteoderm surface texture in USNM 7943 from the Two Medicine Formation is less rugose than the otherwise similar half-rings of AMNH 5403, AMNH 5337, AMNH 5405, and NHMUK R5161. USNM 7943 has fine pitting and sparse, ordered neurovascular grooves as in MOR 433.

Comparisons with other taxa.—Few direct comparisons can be made with *Dyoplosaurus acutosquameus* (holotype ROM 784), but those elements in common suggest two very different animals. The fragmentary skull of *Dyoplosaurus* is slightly smaller but has a more rugose surface texture than *Oohkotokia* (MOR 433); yet, the sculpturing in the temporal region is better defined in *Oohkotokia*, though not as clearly as in *E. tutus*. In *Dyoplosaurus*, the supraorbital boss (in dorsal outline) is oval, whereas in *Oohkotokia* it is cauliflower-shaped. The nuchal crest in *Oohkotokia* has more relief, with more deeply sculpted but smaller osteoderms than in *Dyoplosaurus*. As noted above, the well preserved proximal caudal of MOR 433 differs from the proximal caudals of *Dyoplosaurus*. Although neither specimen preserves the majority of its osteoderms, the armour differs in significant ways based on the available evidence: (i) in MOR 433, the osteoderm surface texture is relatively smooth with tiny, shallow pitting and sparse, ordered neurovascular grooves, whereas *Dyoplosaurus*' osteoderms are rugose and perforate as in many Dinosaur Park specimens; (ii) MOR 433 has craniocaudally compressed cones that are not present in *Dyoplosaurus*; (iii) none of the *preserved* osteoderms of *Dyoplosaurus* matches the triangular lateral osteoderm in MOR 433—despite the fact that the pelvic region and entire tail with osteoderms are preserved in *Dyoplosaurus*. Note that in his reconstruction, Parks (1924) exaggerated the height, pointiness, and curvature of the lateral osteoderms (compare Parks 1924: pl. 3 with Arbour et al. 2009: fig. 1).

Based on the above, MOR 433, holotype of *Oohkotokia horneri*, represents a different taxon than ROM 784. This conclusion is supported by differences between ROM 784 and the referred *Oohkotokia* specimens. For instance, the tail club knob of TMP 2001.42.19 is different from that of *Dyoplosaurus*, which is small, elongate, and ventrally grooved.

There are some interesting points of comparison with *Scolosaurus*. In *Oohkotokia* (MOR 433), the well-preserved proximal caudal measures 26 cm across the transverse processes, each of which is longer than the width of the centrum (82 mm). In *Scolosaurus*, the span is about 27 cm for caudal no. 4 (the first with a chevron), but the centrum measures about 12 cm in width; thus, its transverse processes are noticeably shorter than the diameter of the centrum. In successive caudals, these processes become even shorter. Craniocaudally compressed cones similar to that preserved with MOR 433 are present dorsally in *Scolosaurus*. This osteoderm shape is unusual, but that alone is scant evidence to refer MOR 433 to *Scolosaurus*. Moreover, unlike MOR 433, *Scolosaurus* has no low-keeled, oval osteoderms (Penkalski and Blows 2013); thus the two preserved in MOR 433 are significant in distinguishing it from *Scolosaurus*. Nor did *Scolosaurus* possess any steeply pitched, triangular lateral osteoderms like those of MOR 433. The texture also differs between the two taxa—in *Scolosaurus* it is rugose and perforate as in most Dinosaur Park specimens. The two cervical half-rings referred herein to *Oohkotokia* (TMP 2001.42.19 and USNM 7943) are craniocaudally narrower than that of *Scolosaurus* and have differently shaped lateral osteoderms. Also, the humerus of TMP 2001.42.19 is relatively small compared to that of *Scolosaurus*, but the half-ring is not.

Ford and Kirkland (2001) erected *Aletopelta coombsi* based on SDNHM 33909, a specimen from the broadly contemporaneous Point Loma Formation of coastal California. The specimen was originally described by Coombs and Demere (1996) as Nodosauridae indet. Referral of *Aletopelta* to the Ankylosauridae is debatable as some of the characters used to identify it as ankylosaurid are unconvincing, e.g., limb and armour morphologies. The specimen also has large, nodosaurid-like teeth. The humerus of SDNHM 33909 is incomplete but was certainly large, as in *Edmontonia*. The scapular blade of *Aletopelta* is much wider than that of MOR 433. The femoral fourth trochanter is situated proximal to the femoral midpoint as in most nodosaurids (contra Ford and Kirkland 2001). *Aletopelta* does have a steeply-pitched, triangular caudal osteoderm similar to that of MOR 433, but with a different surface texture—sparse neurovascular grooves and deep pitting. Finally, *Aletopelta* has a pelvic shield consisting of fused, irregular polygons, typical of nodosaurids but not ankylosaurids (Arbour et al. 2011). Vickaryous et al. (2004) consider *Aletopelta* a nomen dubium.

Parsons and Parsons (2009) described *Tatankacephalus* *cooneyorum* from the Lower Cretaceous Cloverly Formation of Montana as an ankylosaurid. However, Thompson et al. (2012) recover it as a basal nodosaurid. The specimen has large, *Edmontonia*-like teeth, and the skull is typically nodosaurid in being longer than wide (although see Carpenter et al. 2008 on *Cedarpelta*) and in having paroccipital processes that are visible in dorsal view.

Oohkotokia differs from *Talarurus* in being bigger, in having a broader muzzle, in having larger, horn-like squamosal bosses, and in the reniform shape of the occipital condyle; in *Talarurus*, this element is narrowly oval (Tumanova 1987).

Anodontosaurus (CMN 8530) occurs stratigraphically higher than other referred *Euoplocephalus* specimens, as does *Oohkotokia* (MOR 433). *Anodontosaurus* also has a relatively small nasal plate (for an ankylosaurine), but the skull is otherwise strikingly different from that of *Oohkotokia* in having smaller, keeled squamosal bosses, centrally-pointed quadratojugal bosses, and ornamental rows of ossicles bordering and surrounding the supraorbital, squamosal, and quadratojugal bosses.

The recently described *Ahshislepelta minor* (Burns and Sullivan 2011) from New Mexico lacks a skull and has little to compare with *Oohkotokia*. The preserved osteoderms have similar, smooth textures but are differently shaped, suggesting two different animals. The humerus of *Ahshislepelta* is unusually slender for an ankylosaurid, whereas humeri of *Oohkotokia* (TMP 2001.42.19; NSM PV 20381) are much more robust with a more distally expanded deltopectoral crest. Burns and Sullivan (2011) concluded that *Ahshislepelta* was mature; thus it was fully grown or nearly so and was a smaller, more gracile animal than *Oohkotokia*.

One animal or two?—Dinosaur specimens are commonly found disarticulated and in association, particularly in the Two Medicine Formation (Trexler 2001). Because of the lack of extraneous skeletal elements, there is a temptation to assume that all the material here pertains to a single, extraordinary animal. Nevertheless, the most parsimonious conclusion is that two animals are present in the quarry (contra Penkalski 1998).

There are some differences between the nodosaurid-like MOR 433 material and those elements in *Edmontonia*. In MOR 433's first cervical half-ring, the bony layer is plainly visible (arrows; Fig. 6) as in ankylosaurids, while in typical *Edmontonia*, the plates are closely appressed (Gilmore 1930: pl. 5). The MOR 433 cervical (or pectoral) spine is also smaller than any similar, described *Edmontonia* spine, whereas the humerus is as large as in the largest specimen of *Edmontonia*; this presents an incongruity. Perhaps the spines only grew large late in ontogeny after the animal had reached adult size, as proposed by Arbour et al. (2009) for the ankylosaurid tail club. Individual variation can probably account for the observed differences, so MOR 433's nodosaurid-like (Group 2) material is referred to *E. rugosidens*.

Stratigraphic separation.—Many dinosaur taxa separate stratigraphically within the Dinosaur Park Formation (Ryan and Evans 2005; also see Arbour et al. 2009: fig. 7). Fig. 9 shows the stratigraphic distribution of ankylosaurid specimens that can be plotted with confidence. There are other good specimens that cannot be plotted accurately because precise elevation data was never recorded; unfortunately, this includes the holotype of *E. tutus*. Nevertheless, several things are apparent. For one, virtually all the ankylosaurid specimens are from the lower 40 m of the formation, with none from the top 20–25 m, as noted by Mallon et al. (2012). Based on AMNH field notes, most of those for which accurate elevation data is lacking appear to be from low in the formation. The holotypes of *D. acutosquameus* and *S. cutleri* are both from the bottom 10 m, the latter being from lower in the formation. The only undisputed *E. tutus* specimens (AMNH 5406, TMP 1991.172.1, and UALVP 31; triangles in Fig. 9) with reliable stratigraphic data are from higher in the formation. MOR 433 is from near the top of the Two Medicine Formation and hence from strata that are younger than any part of the Dinosaur Park Formation. CMN 8530 (holotype of *Anodontosaurus lambei*) is from even younger strata, around the middle of the non-equivalent Horseshoe

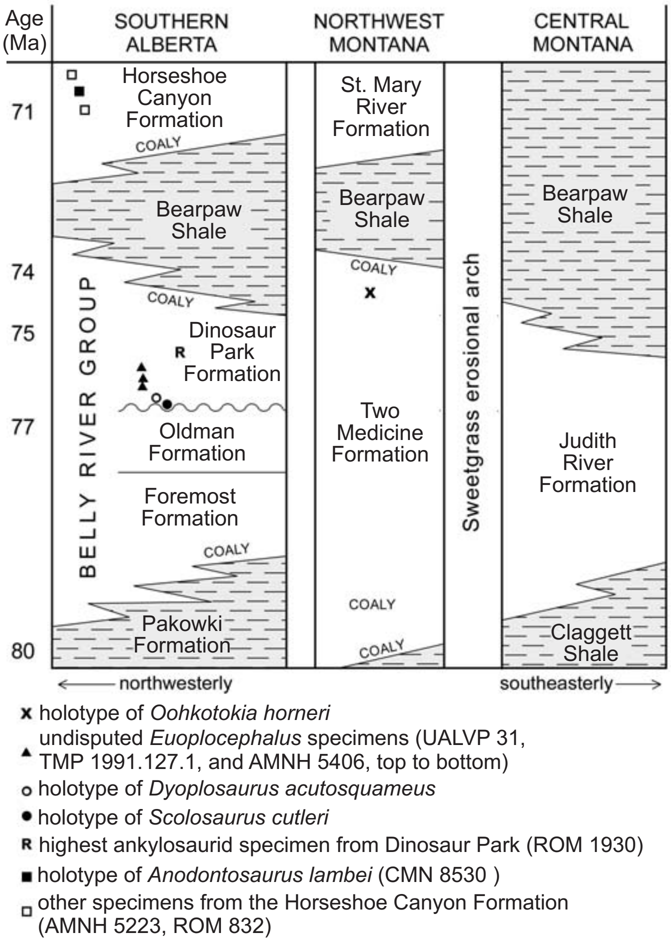

Fig. 9. Generalized chart showing the stratigraphic level at which important late Campanian ankylosaurid specimens have been found in Montana and Alberta. After Eberth (1997), with stratigraphic data from Stebinger (1914), Horner (1984), Hamblin (1994), Eberth (2005), and Eberth and Braman (2012).

Canyon Formation. Thus, at least four of the five holotypes fall at discrete stratigraphic levels—all five if the holotype of *E. tutus* is from the same stratigraphic range as the three *Euoplocephalus* specimens plotted in Fig. 9.

There appears to be a lateral component to the taxonomy as well. Béland and Russell (1978) divided Dinosaur Provincial Park into four arbitrary zones: tiers A–D, going from west to east. All undoubted *E. tutus* specimens (the holotype plus the three listed above) were found just south of Steveville, in "tier A". This suggests habitat preference in *E. tutus* and by inference for the other taxa. Alternatively, it could be that these undoubted *E. tutus* specimens are juveniles or subadults of a more inclusive taxon (Penkalski 2001) and that it is the juveniles that had a habitat preference. However, it is not plausible that juveniles lived in "tier A" of the Dinosaur Park Formation while adults of the same taxon only existed in the Upper Two Medicine Formation.

It is beyond the scope of this paper to analyze fully late Campanian paleoenvironments. However, the Judith River Formation of Montana and the laterally equivalent Dinosaur Park Formation of southern Alberta represent lowland, nearshore environments, whereas the Two Medicine Formation represents a more upland environment (Horner 1984; Horner et al. 1992; Dodson 1997; Eberth 1997; Rogers 1997; Trexler 2001). Hence there appears to have been habitat exclusion between the Dinosaur Park taxa (*Euoplocephalus, Dyoplosaurus*, and *Scolosaurus)* and *Oohkotokia*. Indeed, the same dinosaur taxon rarely or never occurs in both the Dinosaur Park and Two Medicine formations (Horner 1999a; Trexler 2001) though similar taxa do (Currie 2003; Ryan et al. 2007, although see McDonald and Horner 2010).

On generic separation.—Some of the specimens from Montana and Alberta plainly are more similar to one another than to others. A cladistic analysis based on skull characters (Fig. 10) of 15 specimens plus *Pinacosaurus grangeri* as the outgroup suggests probable relationships. Since the palatal side is fragile and poorly preserved in many specimens, most characters were taken from the external (dorsal and lateral) surfaces and the occipital region. Characters were scored based on personal examination of each specimen except for *Pinacosaurus*, which was coded from previously published literature. The characters and character states are listed in Appendix 1. The cladistic analysis with PAUP 4.0b10 (Swofford 2003) using the heuristic search algorithm returned 826 minimum-length trees (29 steps) with a consistency index (CI) of 0.79. The large number of most parsimonious trees (MPTs) was due to the inclusion of CMN 0210 (holotype of *E. tutus*) and ROM 784 (holotype of *D. acutosquameus*), both of which are fragmentary. When these two skulls were removed, the number of MPTs fell to 24 and the CI improved to 0.82. Significantly, the tree topology did not change. A strict consensus tree is shown in Fig. 10.

In the cladogram, CMN 8530 (holotype of *Anodontosaurus lambei*) clusters with *E. tutus* in an unresolved polytomy at node 2. MOR 433, holotype of *O. horneri*, forms a clade with USNM 11892 at node 6, with this clade situated basal to the other large grouping (node 4), which includes *D. acutosquameus*. One or more of the unresolved specimens at node 5 likely represent *Dyoplosaurus*, and one or more may represent *Scolosaurus*. Based on the tree topology, *Oohkotokia horneri* could be considered a distinct genus or a second species of *Dyoplosaurus*. The topology of the tree equally supports MOR 433 + USNM 11892 as a separate genus. Because MOR 433 has characters in common with *E. tutus*, *S. cutleri*, and specimens from the Horseshoe Canyon Formation, it is more parsimonious to establish a new genus rather than arbitrarily assigning *O. horneri* to one of the aforementioned genera.

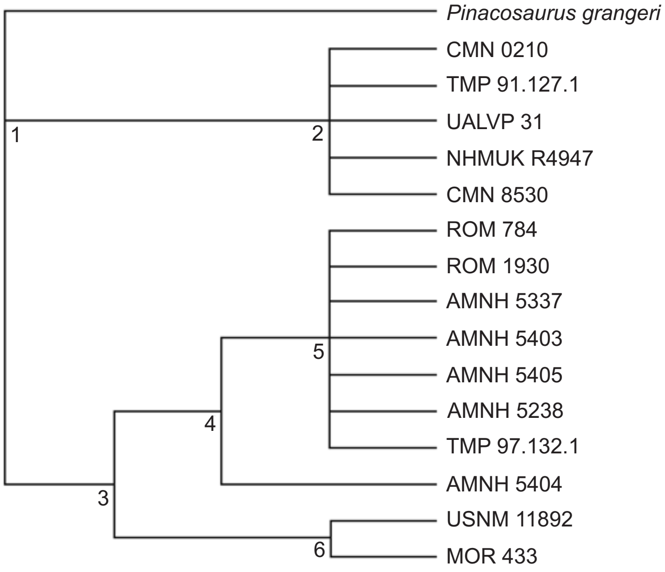

Fig. 10. Strict consensus tree based on 15 specimens—all of which were at one time referred to *Euoplocephalus tutus*—plus *Pinacosaurus grangeri*, generated using PAUP 4.0b10 (Swofford 2003). Nodes are discussed in the text. The tree has 29 steps, a Consistency Index of 0.793, and a Retention Index of 0.846.

Conclusions

Ankylosaurines must have existed in one form or another continuously in Montana and/or Alberta throughout the late Campanian and early Maastrichtian. Eventually, more specimens with accurate stratigraphic data will help to improve the phylogenetic resolution. Nevertheless, the current stratigraphic picture corroborates the morphometric and cladistic analyses and supports *O. horneri* as a separate taxon. *Oohkotokia horneri* possesses a unique combination of characters with several autapomorphies not seen in the Late Campanian taxa from Alberta. Meanwhile, the similarities largely encompass characters common to many ankylosaurids and are not diagnostic at the specific level; they may unite certain taxa in an as yet-unnamed clade endemic to North America (nodes 2+3 in Fig. 10). Contrary to what has generally been assumed for many years, *Euoplocephalus tutus* is unknown in Montana.

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Appendix 1

Character list

Characters used in the cladistic analysis. Where applicable, similar characters used in previous studies are listed. Many other characters used by previous authors are not included here because they would be uninformative in this restricted analysis. All characters were treated as unordered.

1. *Skull shape in dorsal view*: constricted preorbitally (0); trapezoidal (1). Some ankylosaurid specimens have a noticeable constriction of the snout just rostral to the orbits while others do not.
2. *Skull roof domed centrally*: no (0); yes (1). Related to Vickaryous et al. (2004) char. 2, Carpenter (2001) char. 53, and Thompson et al. (2012) char. 31.
3. *Premaxillary morphology caudoventrally*: undivided (0); divided (1). Although it is not always clear whether the vomer divides the premaxillae or overlaps them, some specimens have undamaged premaxillae that are ventrally grooved or divided for their entire length. This does not appear to be a juvenile feature because young *Pinacosaurus* lack the groove caudally (see Maryańska 1977; Burns et al. 2011).
4. *Quadratojugal bosses*: swept caudally (0); centrally situated apex (1). Modified version of Hill et al. (2003) char. 41, Vickaryous and Russell (2003) char. 7. The quadratojugal boss has several discrete morphologies that are likely taxonomic.
5. *Preorbital boss morphology*: confluent with supraorbital boss (0); distinct hornlet (1). This character attempts to qualify some of the variation in the supraorbital ornamentation.
6. *Median nasal plate*: undistinguished—no larger than surrounding osteoderms (0); noticeably larger than surrounding osteoderms (1); bulging and more than 40% the width of the snout (2). In *E. tutus* and *Ankylosaurus*, there is a prominent sagittal osteoderm on the snout caudal to the external nares, while in a few other ankylosaurids, this osteoderm is no larger than the ones around it.
7. *Raised nuchal osteoderms*: absent (0); present (1). Related to Carpenter (2001) char. 60, Vickaryous et al. (2004) char. 11. *Dyoplosaurus* is an extreme in its lack of relief or sculpturing along the nuchal crest.
8. *Medial nuchal osteoderms*: tabular (0); sharp and pointed (1). Some specimens in this analysis have tabular or quadrangular osteoderms of various relief, while others have smaller, pointy osteoderms there (this character is not related to the “tabular” bone of Maryańska 1977).

9. *Sharp lingual cingulum on maxillary teeth*: absent, invaded by fluting (0); present (1). Elaboration of Thompson et al. (2012) char. 64 and Vickaryous et al. (2004) char. 19. A few specimens have teeth with sharp cingula, but in most the fluting or sculpturing is not confined to the crown, resulting in poorly defined cingula.
10. *Shelf-like labial cingulum on maxillary teeth*: absent (0), present (1). Elaboration of Thompson et al. (2012) char. 64 and Vickaryous et al. (2004) char. 19. In most of the specimens in this analysis, the grooves or fluting on the lingual surface of the crown continue to the base; in others, they end abruptly at a protruding, shelf-like cingulum.
11. *Grooves vertically aligned between cusps*: yes (0); no, random fluting dominates (1). This character accounts for variation between specimens with teeth that are essentially divided by furrows into vertical leaves in line with the primary denticles and others in which the crown has much more random fluting unrelated to the positions of the denticles.
12. *Vomer-maxillary contact*: absent (0); present (1); expanded (2). Modified version of Carpenter (2001) char. 56, Thompson et al. (2012) char. 22. Some specimens have a more rectangular internal naris (and may also have an expanded secondary palate) as a result of increased vomer-maxillary range of contact.
13. *Basioccipital*: with two shallow, longitudinal depressions (0); with a small foramen near the basisphenoid contact (1); partially divided by a large foramen (2). Maryańska (1977) suggested that this feature changed during ontogeny, but it is coded here because none of the skulls in this study are less than 80% of adult size, with the exception of *Pinacosaurus*.
14. *Caudal intermandibular foramen*: completely within splenial (0); not enclosed by splenial (1). In some specimens, this foramen is completely surrounded by the splenial, whereas in others it is open dorsally or caudodorsally.
15. *Squamosal boss*: low, apically pitted (0); sharply keeled and pitted (1); pyramidal or trihedral and pitted (2); trihedral with subconical, horn-like apex (3). Hill et al. (2003), char. 42; Vickaryous et al. (2004) char. 6 modified. There is substantial variation in squamosal boss morphology among the specimens and among ankylosaurids in general. This character attempts to qualify that as appropriate for the included specimens.
16. *Lacrimal dermal morphology*: wide, ornamented with ossification (0); narrow, unornamented rim (1). In most specimens, the rostral edge of the orbit is wide enough to accommodate a vertical osteoderm, while in others this region is relatively narrow and lacks a distinct osteoderm, though it may have smaller ossicles there.
17. *Rostrolateral plate on snout*: drops to base of external naris (0); shorter and higher, above base of external naris (1). The rostral plate on the side of the ankylosaurine snout varies in shape more than the caudal one, particularly in how tall and strap-like it is.
18. *Narial ossifications*: narrow and arching (0); triangular, weighted laterally (1). This character qualifies differences in the rugose ornamentation that borders the external nares caudodorsally.

Character-specimen matrix

Specimen/taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
CMN 0210	?	?	1	?	?	2	?	?	?	?	?	2	?	?	?	?	1	?
ROM 784	?	1	?	?	?	?	0	0	0	?	1	?	?	?	?	?	?	?
TMP 1991.127.1	1	0	1	1	1	2	1	1	?	?	?	2	0	?	1	0	1	1
UALVP 31	1	0	1	1	1	1	1	1	?	?	?	?	?	1	1	0	1	1
CMN 8530	0	0	?	1	1	1	1	0	?	?	?	?	1	1	1	0	1	?
NHMUK R4947	1	0	?	1	1	2	1	0	?	?	?	?	1	?	?	0	0	0
ROM 1930	0	1	0	0	0	1	1	0	0	0	1	1	1	?	2	0	0	0
AMNH 5337	0	1	0	0	0	1	1	0	0	0	1	1	2	0	0	0	0	0
AMNH 5403	0	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0
AMNH 5404	0	1	0	?	0	1	1	0	0	1	0	1	1	?	2	0	0	0
AMNH 5405	0	1	0	0	0	1	1	0	0	0	1	1	1	0	2	0	0	0
AMNH 5238	0	1	?	0	0	1	1	0	0	0	1	?	?	?	2	?	0	?
TMP 1997.132.1	0	1	0	0	0	1	1	0	0	0	1	1	1	0	2	0	0	0
USNM 11892	0	1	?	0	0	?	1	0	1	1	0	?	0	?	3	1	0	0
MOR 433	?	?	?	0	0	0	1	0	?	?	?	?	?	?	3	1	0	0
Pinacosaurus grangeri	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	?	?	?

Key: 0–3 = character states; ? = missing data.