Title: Ankylosaurid dinosaur tail clubs evolved through stepwise acquisition of key features.

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ABSTRACT

Ankylosaurid ankylosaurs were quadrupedal, herbivorous dinosaurs with abundant dermal ossifications. They are best known for their distinctive tail club composed of stiff, interlocking vertebrae (the handle) and large, bulbous osteoderms (the knob), which may have been used as a weapon. However, tail clubs appear relatively late in the evolution of ankylosaurids, and seemed to have been present only in a derived clade of ankylosaurids during the last 20 million years of the Mesozoic Era. New evidence from mid Cretaceous fossils from China suggests that the evolution of the tail club occurred at least 40 million years earlier, and in a stepwise manner, with early ankylosaurids evolving handle-like vertebrae before the distal osteoderms enlarged and coossified to form a knob.

Keywords: Dinosauria, Ankylosauria, Ankylosauridae, Cretaceous

INTRODUCTION

Tail weaponry, in the form of spikes or clubs, is an uncommon adaptation among tetrapods. Among dinosaurs, stegosaurs have large conical bony spikes at the end of the tail, and the sauropod *Spinophorosaurus nigerensis* may also possess small distal tail spikes (Remes et al. 2009). Several species of extant lizards have prominent spiky scales along the length of the tail (e.g. *Uromastyx* spp., *Ouroboros cataphractus* and other cordylid lizards), and both Old and New World porcupines (Hystricidae and Erithizontidae) will use their tails, covered in barbed quills, for defense. Even rarer is the modification of the tail into a club-like structure, which appears to have evolved only a few times in mammals, turtles, and dinosaurs. Some glyptodonts (relatives of the extant armadillos) encased the distal portion of the tail in a sheath of rigid osteoderms, forming a club (Alexander et al. 1999), as did meiolaniid turtles (Gaffney, 1996). The sauropods *Mamenchisaurus hochuanensis* and *Shunosaurus lii* each have expanded and coossified distal caudal vertebrae that form a small, lumpy tail club (Dong et al. 1989; Xing et al. 2009). It is the ankylosaurid dinosaurs, however, that evolved the most extreme and robust tail weaponry among the tetrapods.

Derived ankylosaurid ankylosaurs had a unique tail club formed from modified, tightly interlocking distal caudal vertebrae (the handle, *sensu* Coombs, 1995) and enlarged osteoderms that envelop the terminus of the tail (the knob, *sensu* Coombs, 1995). The handle vertebrae are unlike those of any other club-bearing tetrapods, with elongate and robust prezygapophyses, neural spines/postzygapophyses, and haemal arches. Centra within the handle may be partially coossified, also contributing to the rigidity of the distal tail in ankylosaurids.

Carpenter et al. (2008) and Thompson et al. (2012) considered the tail club only to be present in adult ankylosaurine ankylosaurids, and absent in more basal ankylosaurids like *Shamosaurus scutatus*. However, this may be based on an alternate use of the term 'tail club' focusing primarily on the large knob osteoderms, which obscures the important role of the handle vertebrae in identifying the tail club in ankylosaurids. The term 'tail club' does not refer solely to the large terminal osteoderms, but to the entire distal structure of the ankylosaurid tail, and both the knob and handle are biomechanically important for tail club impacts (Arbour and Snively, 2009; Carpenter et al., 2011). The tail club represents modifications to two skeletal systems, the endoskeleton (caudal vertebrae), and the dermal skeleton (osteoderms), and the evolution of this structure has not been investigated in detail previously. We evaluate three hypotheses for interpreting the fossil record of ankylosaur tail clubs (Fig. 1): 1) the knob evolved first, in which case early ankylosaurids should have tapered tail vertebrae similar to nodosaurids and terminal osteoderms that fully envelop the terminal caudal vertebrae; 2) the handle evolved first, in which case early ankylosaurids should have distal caudal vertebrae modified into the handle morphology, but without knob osteoderms preserved enveloping the terminal caudals; or 3) the knob and handle evolved in tandem, in which case early ankylosaurids should possess both structures, but the handle could be short, the knob could be small, or other differences compared to derived ankylosaurines could be apparent.

Institutional abbreviations

CMN – Canadian Museum of Nature, Ottawa, Ontario, Canada; **DMNH** – Denver Museum of Nature and Science, Denver, Colorado, USA; **HGM** – Henan Geological Museum, Zhengzhou, Henan, China; **IVPP** – Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MWC** – Museum of Western Colorado Dinosaur Journey, Fruita, Colorado, USA; **NHMUK** – Natural History Museum, London, United Kingdom; **PIN** – Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **TMP** – Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP** – University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada

METHODS

We reviewed the caudal anatomy of ankylosaurs using firsthand examination of specimens (Supplementary Information 1) and references to the literature, and follow the taxonomic classification proposed by Arbour and Currie (in press). We use the character matrix presented by Arbour and Currie (in press) to examine changes to the tail of ankylosaurs in a phylogenetic context. This matrix (Supplementary Information 2; character statements can be found in Supplementary Information 1) includes 41 taxa and 177 characters; it does not comprehensively sample nodosaurid ankylosaurs because it was designed to test the interrelationships within Ankylosauridae and to investigate the affinities of some ambiguous ankylosaur taxa, and so taxa that are usually recovered outside of Ankylosauridae (e.g. Vickaryous et al. 2004, Thompson et al. 2012) were generally not included. Arbour and Currie (in press) used TAXEQ3 (Wilkinson 2001) to safely exclude *Bissektipelta archibaldi* (Averianov, 2002; Parish and Barrett, 2004), "*Minmi paravertebra*" Molnar, 1980, and "*Tianchisaurus nedegoapeferima*" Dong, 1993, from their phylogenetic analysis without removing phylogenetically important information; distal caudal vertebrae are also unknown for these taxa.

The character matrix was assembled in Mesquite version 2.75 (Maddison and Maddison, 2011) and analyzed in TNT v1.1 (Goloboff et al. 2008), with characters treated as unordered and of equal weight. The parsimony analysis was conducted in TNT using the Traditional Search option with one random seed and 1000 replicates of Wagner trees, and the tree bisection reconnection (TBR) swapping algorithm. Consistency and retention indices were calculated in Mesquite, and Bremer supports were calculated in TNT. In order to investigate the evolution of characters associated with the tail club, we used the "Trace Character History" tool in Mesquite. We used likelihood reconstruction and the Mk1 model (Markov k-state 1 parameter model) to investigate the evolution of character 109 (lengthening of the prezygapophyses in the distal caudal vertebrae), and a modified version of characters 176 and 177 (presence or absence of the knob, without information about its shape).

Phylogenetic Framework

Arbour and Currie (in press) found 3030 most parsimonious trees. The strict consensus tree shows poor resolution within Nodosauridae and ankylosaurine ankylosaurids, but recovered a suite of basal ankylosaurid taxa, Shamosaurinae, and Ankylosaurinae. The 50% majority rule tree shows that 1) *Cedarpelta bilbeyhallorum* Carpenter, Kirkland, Burge, and Bird, 2001, and *Chuanqilong chaoyangensis* Han, Zheng, Hu, Xu, and Barrett, 2014, were sister taxa in 86% of the trees, 2) Shamosaurinae was the sister taxon to Ankylosaurinae in 60% of the trees, 3) *Cedarpelta* is the most basal ankylosaurine in 60% of the trees, 4) *Pinacosaurus* Gilmore, 1930, was monophyletic in 85% of the trees, 5) *Saichania chulsanensis* Maryańska, 1977**,** *Tarchia kielanae* Maryańska, 1977, and *Zaraapelta nomadis* Arbour, Currie, and Badamgarav, 2014a*,* formed a clade in 89% of the trees, and 6) a derived clade of mostly North American ankylosaurines (Ankylosaurini) was present in 68% of the trees.

Ankylosaurinae includes *Ankylosaurus magniventris* Brown, 1908, *Anodontosaurus lambei* Sternberg 1929, *Crichtonpelta benxiensis* (Lü, Ji, Gao, and Li, 2007), *Dyoplosaurus acutosquameus* Parks, 1924, *Euoplocephalus tutus* (Lambe, 1902), , *Nodocephalosaurus kirtlandensis* Sullivan, 1999, *Pinacosaurus grangeri* Gilmore, 1933*, Pinacosaurus mephistocephalus* Godefroit, Pereda Suberbiola, Li, and Dong 1999, *Saichania chulsanensis*, *Scolosaurus cutleri* Nopcsa, 1928, *Talarurus plicatospineus* Maleev, 1952, *Tarchia kielanae*, *Tsagantegia longicranialis* Tumanova 1993, *Zaraapelta nomadis*, "*Zhejiangosaurus lishuiensis*" Lü, Jin, Sheng, Li, Wang, and Azuma, 2007, and *Ziapelta sanjuanensis* Arbour, Burns, Sullivan, Lucas, Cantrell, Fry, and Suazo, 2014b. Ankylosaurids that fall outside of Ankylosaurinae are *Gobisaurus domoculus* Vickaryous, Russell, Currie, and Zhao, 2001 and *Shamosaurus scutatus* Tumanova, 1983 (as Shamosaurinae), *Ahshislepelta minor* Burns and Sullivan, 2011, *Aletopelta* *coombsi* Ford and Kirkland, 2001, *Cedarpelta bilbeyhallorum*, *Chuanqilong chaoyangensis*, *Gastonia burgei* Kirkland, 1998, and *Liaoningosaurus paradoxus* Xu, Wang, and You, 2001. The basal position for *Ahshislepelta* and *Aletopelta* is at odds with their stratigraphic provenance, since both are derived from Campanian sediments in North America. *Liaoningosaurus paradoxus* may occupy a relatively basal position because it is a juvenile; juvenile individuals are sometimes recovered in more basal positions than adults of the same species when coded separately in phylogenetic analyses (Campione et al. 2013). On the other hand, a relatively basal position in Ankylosauridae is consistent with the Lower Cretaceous provenance of *Liaoningosaurus paradoxus*, and this taxon retains premaxillary teeth (Xu et al. 2001), which are lost in more derived ankylosaurines (Vickaryous et al. 2004).

Results

The anterior caudal vertebrae of ankylosaurs (e.g. Arbour and Currie 2013a: fig. 9; Arbour et al. 2009: fig. 9) are wider than long, with amphiplatyan centra, and transverse processes set at about the midheight of the centrum. The prezygapophyses are separate (unlike those of the dorsal vertebrae, which are joined at the midline), and are finger-like projections from the neural arch; the postzygapophyses do not extend far past the posterior border of the neural spine. The neural spine in ankylosaurids is usually mediolaterally thin (e.g. *Euoplocephalus,* Arbour and Currie 2013a*; Talarurus,* Maleev 1956), and in nodosaurids the neural spine can be more robust and with a substantial distal mediolateral expansion (e.g. *Polacanthus,* Blows 1987: figs. 2-3). The haemal arch often fuses to the posterior ventral edge of the centrum, and the haemal spine is about as long as the neural spine.

The distal caudal vertebrae in basal ankylosaurs (e.g. *Mymoorapelta maysi* Kirkland and Carpenter, 1994; Fig. 2F), basal ankylosaurids (e.g. *Gastonia*), and nodosaurids (e.g. *Nodosaurus textilis* Marsh, 1889, *Sauropelta edwardsorum* Ostrom, 1970) tend to be longer than wide, and dorsoventrally compressed relative to anterior caudals. The neural spine is reduced relative to the anterior caudals, and the haemal spine takes on a rounded, hatchet-shaped appearance (e.g. *Hungarosaurus tormai* Ősi, 2005: fig. 10C'). The prezygapophyses do not extend past the anterior edge of the centrum by more than about 25% of the centrum length (e.g. *Nodosaurus*, Lull 1921; *Mymoorapelta* MWC 5819, Fig. 2F). The distal tail of these ankylosaurs would have been flexible.

The distal caudal vertebrae of ankylosaurines are unique among dinosaurs. In basal nodosaurids and basal ankylosaurids, the morphological transition from anterior to posterior caudal vertebrae is smooth, but in ankylosaurines, this transition is abrupt and occurs at about the midpoint of the caudal series (e.g. Arbour et al. 2009: Fig. 1, Parks 1924: Pl. 1). In contrast, the distal caudal vertebrae of ankylosaurines interlock tightly, forming a series of interlocking Vs in dorsal view (Fig. 2A). The prezygapophysis of each caudal overlaps the adjacent anterior vertebra by at least 50% of its length, unlike in basal ankylosaurids, nodosaurids, or basal ankylosaurs, where the overlap is only about 25% of the centrum length (e.g. *Mymoorapelta* MWC 5819; Fig. 2F). The prezygapophyses are dorsoventrally deep, mediolaterally flattened, and with vertically oriented articular surfaces; the modified neural spine and postzygapophyses of the preceding vertebra completely fill the space between the prezygapophyses. Transverse processes are absent on most vertebrae in this region, although small bumps may be present on the first few handle vertebrae (Arbour et al. 2009). The haemal arches are similarly modified into a tightly interlocking series. The haemal spine is dorsoventrally short but anteroposteriorly long, and has a boat-like shape (e.g. Maleev 1956: fig. 35; Maryańska 1977: fig. 10). Anteriorly it is bifurcated, and posteriorly it tapers to a point. Flexibility in the distal portion of the tail in ankylosaurines was highly reduced, and where fusion of the vertebral centra occurred there would have been almost no flexibility whatsoever.

In ankylosaurines, knob osteoderms completely envelop and obscure the distalmost vertebrae. Two laterally positioned osteoderms (the major osteoderms, sensu Coombs, 1995) form the bulk of the knob and are usually keeled and dorsoventrally flattened rather than hemispherical. Two or more smaller osteoderms form the terminus of the knob, and the boundaries between these minor knob osteoderms can be indistinct (Arbour and Currie, 2013a). Only a few specimens preserve osteoderms along the more proximal portions of the tail, and the best example is MPC 100/1305, a large ankylosaurid tentatively referred to *Pinacosaurus* (Arbour and Currie 2013b). In this specimen, the lateral osteoderms are triangular and sharply pointed in the anterior and middle portions of the tail, and become smaller and less sharply pointed posteriorly (Carpenter et al. 2011: fig. 15; Arbour and Currie 2013: fig. 1). The penultimate pair of lateral osteoderms anterior to the knob are similar to the major knob osteoderms, with rounded lateral edges, but they are not as dorsoventrally deep and do not envelop the handle vertebrae to the same degree as the knob osteoderms.

We find direct evidence for two ankylosaurs with a tail club handle but not a tail club knob: *Gobisaurus domoculus* and *Liaoningosaurus paradoxus*. HGM 41HIII-0002 (the holotype of *Zhongyuansaurus luoyangensis* Xu, Lu, Zhang, Jia, Hu, Zhang, Wu, and Ji, 2007, but referred to *Gobisaurus* by Arbour and Currie, in press) clearly preserves the handle of a tail club (contra Xu et al. 2007 and Carpenter et al. 2008), even though knob osteoderms are not present (Fig. 2B,C). The vertebrae are indistinguishable from those of more derived ankylosaurine ankylosaurs, with elongated prezygapophyses and neural spines that interlock tightly together. The tail club of HGM 41HIII-0002 appears to preserve the distalmost caudal vertebra; the last three vertebrae in the handle abruptly shorten, and the terminal vertebra is rounded at the distal end, similar to what was observed in CT scans (Fig. 2D,E) of an Albertan tail club (UALVP 16247, Arbour 2009). The tail club of HGM 41HIII-0002 is unusual compared to other ankylosaurid tail clubs because it preserves no evidence for the large terminal knob osteoderms. No other ankylosaurid specimen preserves the distal end of the handle without at least some of the knob preserved, because the knob osteoderms envelop and are tightly appressed to the vertebrae and associated ossified tendons. This suggests that either a large terminal knob was not present in HGM 41HIII-0002, or that the knob osteoderms were smaller or more loosely associated with the handle vertebrae.

The second ankylosaur that preserves tail club handle vertebrae without a tail club knob is *Liaoningosaurus*. IVPP V12560, the holotype of *Liaoningosaurus paradoxus*, is one of the smallest known ankylosaur skeletons, at only about 33 cm in length (Fig. 2G). Unfused neural arches, small size, and the absence of osteoderms posterior to the cervical/pectoral region (as in juvenile *Pinacosaurus grangeri,* Burns et al. 2011) suggest that IVPP V12560 is a juvenile individual. *Liaoningosaurus paradoxus* does not possess an obvious tail club, but close observation of the distal caudal vertebrae show a close similarity to the handle vertebrae of ankylosaurines. The neural arches of the distal tail vertebrae interlock, and the prezygapophyses overlap the adjacent vertebra by at least 50% of the centrum length, as in ankylosaurines (Fig. 2H). Therefore, *Liaoningosaurus paradoxus* appears to have possessed a tail club handle, but does not appear to have had a tail club knob. However, osteoderms are only preserved in the cervical/pectoral region (Fig. 2G), it is possible that the full complement of osteoderms had not yet developed in the holotype specimen IVPP V12560. Intriguingly, *Chuanqilong* does not appear to have modified handle-like vertebrae in its distal tail (Han et al. 2014: fig. 3), despite its similar geologic age and provenance and possible close relationship to *Liaoningosaurus* (Han et al. (2014) recovered *Chuanqilong* as the sister taxon to *Liaoningosaurus*, although Arbour and Currie (in press) found *Chuanqilong* as the sister taxon to *Cedarpelta*).

Ancestral state reconstruction provides additional information on the origin of elongated prezygapophyses that overlap at least 50% of the preceding vertebral centrum length, and the origin of enlarged knob osteoderms (Fig. 4). Elongated prezygapophyses were present in the ancestor of all ankylosaurines more derived than *Crichtonpelta* (proportional likelihood = 1.000), and were most likely present in the ancestor of Ankylosaurinae+Shamosaurinae (proportional likelihood = 0.963). Whether or not the ancestor of the clade containing all ankylosaurids more derived than *Ahshislepelta* and *Gastonia* had elongated prezygapophyses is equivocal (proportional likelihood 0.501), because the base of this clade includes a polytomy that includes taxa with elongated prezygapophyses (*Liaoningosaurus*), and taxa that do not (*Aletopelta*, *Chuanqilong*). Knob osteoderms have a more restricted phylogenetic distribution: a tail club knob was most likely present in the ancestor of all ankylosaurines more derived than *Crichtonpelta* (proportional likelihood = 0.977), but not in the ancestor of Ankylosaurinae+Shamosaurinae (proportional likelihood = 0.023).

DISCUSSION

Ankylosaurid tail clubs are complex structures involving contributions from both the vertebral series and the dermal skeleton. Our results suggest that the tail club evolved in a stepwise fashion, in which modifications to the distal caudal vertebrae preceded modifications to the terminal osteoderms (Fig. 4).

Bonebed material at the DMNH of *Gastonia burgei*, the oldest ankylosaurid in this study (although some other analyses recover this taxon as a basal nodosaurid, e.g. Thompson et al. 2012), includes a large sample of caudal vertebrae of many sizes and positions within the vertebral series, and none have the distinctive morphology of handle vertebrae.

Isolated osteoderms that could be identified as disarticulated knob osteoderms are unknown in any formations prior to the Campanian. A tail club was described for *Tianchisaurus nedegoapeferima* from the Middle Jurassic of China (Dong, 1993), which would make this the earliest occurrence of a tail club in the fossil record. However, the "tail club" of IVPP V10614 does not appear to represent a tail club knob. The putative knob appears subdivided by deep grooves into three sections, with two larger sections flanking a small triangular area. In most ankylosaurid knobs, the major osteoderms are clearly separated at the midline in dorsal and ventral view, and the terminal end of the knob is made up of more than one osteoderm (e.g. Arbour and Currie, 2013a: Fig. 14). It is unclear what the putative knob of *Tianchisaurus nedegoapeferima* represents, but it is unlikely that it is a true tail club knob, and so this should not be considered the first occurrence of an ankylosaurine-like tail club in the fossil record. Another putative tail club-like structure was reported for *Polacanthus foxii* Owen vide Anonymous, 1865, from the Barremian Wessex Formation of England (Blows and Honeysett 2014). Blows (1987) described a 'caudal end mass' consisting of osteoderms, caudal vertebrae, and ossified tendons in NHMUK R175, and considered that this represented the terminus of the tail and fusion of these elements. Later, Blows (2001) suggested that the presence of ossified tendons in the caudal region of *Polacanthus* (which are also present in ankylosaurines with a tail club) may have been an adaptation for lateral tail swinging even in the absence of a fully developed tail club. Pereda-Suberbiola (1994) and Carpenter and Kirkland (1998) considered the 'caudal end mass' of NHMUK R175 to represent a more anterior portion of the tail, and suggested that it does not represent an incipient tail club. We agree that this structure does not represent the distal end of the tail or an incipient tail club.

The oldest ankylosaur to possess either of the two modifications present in derived ankylosaurid tail clubs (distal caudal vertebrae modified to form a handle, or terminal osteoderms enlarged and enveloping the tail terminus) is the holotype of *Liaoningosaurus paradoxus*, (122 Ma, Aptian; Xu and Norell, 2006; Fig. 4). In *Liaoningosaurus*, the prezygapophyses of the distal caudal vertebrae overlap the preceding vertebra by at least 50% of its length, a feature found only in more derived ankylosaurids with complete tail clubs (Fig. 2); this feature is not present in more basal ankylosaurids like *Gastonia*, nodosaurids like *Sauropelta* , or basal ankylosaurs like *Mymoorapelta* . *Liaoningosaurus* lacks knob osteoderms, but the holotype (and only published specimen to date) is a very small juvenile, and likely had not developed its full complement of osteoderms before it died. This makes it difficult to determine if *Liaoningosaurus* had a tail club knob in addition to the modified distal caudal vertebrae. However, one specimen of *Gobisaurus* (HGM 41HIII-0002) preserves a tail club handle without a knob. This specimen includes the terminal caudal vertebrae, so the absence of the knob is not because the end of the tail is missing. Although the skull for HGM 41HIII has some cranial sutures visible (Arbour and Currie in press), which suggests that the specimen is not fully mature, it is still a relatively large individual, and several post-cervical osteoderms were associated with it (Xu et al. 2007). Ontogeny does not seem to be the best explanation for the absence of knob osteoderms in this specimen. It is possible that knob osteoderms were present in life and disarticulated from the handle after death. However, in isolated tail club knobs from more derived ankylosaurids, there are often some fragments of the distal caudal vertebrae or ossified tendons associated with the knob or knob osteoderms; this is most likely because of the close association between these elements in the living animal (e.g. UALVP 16247, CMN 2251). Thompson et al. (2012) considered HGM 41HIII-0002 (as *Zhongyuansaurus)* to be the first known ankylosaurid in which the tail club was definitively absent, although this was in reference to a 'fully developed' tail club consisting of a handle and knob. However, 41HIII-0002 clearly preserves a tail club handle. After *Liaoningosaurus paradoxus*, *Gobisaurus domoculus* is the next youngest ankylosaurid known to have possessed a tail club, with an age of no more than 92 Ma (Turonian; Kobayashi and Lü 2003; Fig. 4). Given the close anatomical similarity between the overlapping elements of *Gobisaurus* and *Shamosaurus*, it seems likely that *Shamosaurus* also had a tail club handle; ancestral state reconstruction also suggests that the ancestor of *Gobisaurus* and Ankylosaurinae had a tail club handle. Ancestral state reconstruction suggests that *Tsagantegia* and "*Zhejiangosaurus"*, for which caudal material is unknown, most likely each had a tail club handle. *Cedarpelta*, from the Mussentuchit Member of the Cedar Mountain Formation (~104-98 Ma, Chure et al. 2010, Cifelli et al. 1997), is the oldest North American ankylosaurid besides *Gastonia*, and has been considered closely related to *Gobisaurus* and *Shamosaurus* (Carpenter et al. 2008). Unfortunately, no distal caudal vertebrae are known for *Cedarpelta*, and ancestral state reconstruction was ambiguous about the presence or absence of a tail club handle at this level in the phylogeny (Fig. 3). At present, no pre-Campanian North American ankylosaurids appear to have had a tail club handle.

The oldest and most basal ankylosaur known to possess terminal osteoderms that envelop the end of the tail is *Pinacosaurus*, from the Campanian (Dashzeveg et al. 2005) of Mongolia and China (Fig. 4). All ankylosaurid ankylosaurs that are more derived than *Pinacosaurus* either are known to have had a tail club (e.g. *Ankylosaurus*, *Euoplocephalus*), or occur in formations in which disarticulated tail clubs are known but cannot be attributed to a specific taxon (e.g. *Tarchia*, Arbour et al. 2014a; *Ziapelta*, Arbour et al. 2014b). Several ankylosaurid specimens from Mongolia (PIN 614 and MPC 100/1305, both tentatively assigned to *Pinacosaurus grangeri*, Arbour and Currie, 2013b, and ZPAL MgD I/113, an indeterminate ankylosaurid from the Nemegt Formation, Arbour et al. 2013) demonstrate that osteoderms were present along the length of the handle, not just at the terminus. Interestingly, in MPC 100/1305 the penultimate lateral osteoderms are rounded and similar in shape to the major knob osteoderms, although they are not as dorsoventrally deep.

Crichtonpelta is the earliest and most basal ankylosaurine (Fig. 4), but no caudal material has been described for this taxon. An undescribed mounted skeleton on display at the Sihetun Fossil Museum (Liaoning, China) is presented with a tail club, but it is unclear if this has been sculpted or if it represents real fossil material, and the tail vertebrae have not yet been described or figured. Ancestral state reconstruction suggests that *Crichtonpelta* probably had a tail club handle, but was ambiguous about whether or not *Crichtonpelta* was likely to have a tail club knob (Fig. 3); ankylosaurines more derived than *Crichtonpelta* were very likely to have a knob, but the ancestor of Shamosaurinae and Ankylosaurinae was unlikely to have had a knob.

Understanding trends within the evolution of the tail club among ankylosaurines is complicated by the dearth of tail clubs that can be referred to different species; for example, it is difficult to associate isolated tail club knobs from the Baruungoyot and Nemegt formations of Mongolia with any of the known ankylosaurids from those formations (*Saichania*, *Tarchia*, and *Zaraapelta*) because no specimens preserving a skull and tail club have been described in detail yet (Arbour et al. 2014a). Nevertheless, two patterns merit further investigation as more specimens are collected. First, the maximum size of tail club knobs seems to increase from the earliest known knob to later knobs in the late Campanian and Maastrichtian. The largest tail club knob from the Djadokhta Formation (on MPC 100/1305, ?*Pinacosaurus*), the stratigraphically oldest formation with tail club knobs, is 146 mm wide. The largest knob from the younger Nemegt, Dinosaur Park, and Horseshoe Canyon formations are 620 mm wide (ZPAL MgD I/43), 572 mm wide (ROM 788), and 593 mm wide (AMNH 5245), respectively, and the only known tail club from the youngest unit, the Scollard Formation is ~450 mm wide (AMNH 5214, a subadult *Ankylosaurus*). Testing this apparent trend is complicated by the lack of precise age estimates for the Djadokhta, Baruungoyot, and Nemegt formations, and the absence of information about ankylosaur knob osteoderm ontogeny. Secondly, although the morphology of the handle vertebrae is consistent across most species of ankylosaurines, it diverges significantly in two taxa. In most ankylosaurines, the edges of the neural spines diverge at an angle of about 22° in dorsal view, forming the distinctive interlocking V morphology. In ZPAL MgD I/113, an ankylosaur of unknown affinity from the Nemegt Formation, this angle is approximately 35°, and in *Ankylosaurus* (AMNH 5214), it is approximately 60° (Arbour et al. 2009). In *Ankylosaurus*, this results in a U-shaped neural spine rather than a V-shaped neural spine in the handle vertebrae. Why these two taxa diverged from the basal condition found in other ankylosaurines is not clear, but it is worth noting that these two specimens are among the largest of all known ankylosaurines, suggesting that overall body size increases may have necessitated a change in tail club morphology.

The absence of enlarged terminal osteoderms in taxa without handle vertebrae, and the absence of isolated knob osteoderms in formations without taxa that had a tail club handle, suggests that the hypothesis that the tail club knob evolved before the handle (Fig. 1) can be rejected. Biomechanically, a large knob of dermal bone at the end of a flexible tail (analogous to a flail, rather than a club) could result in damage to the ankylosaur if wielded as a weapon; the rotational inertia of a large mass at the end of the tail could lead to tearing of the soft tissues between the vertebrae, and twisting stresses could break the vertebrae. The absence of knob osteoderms in *Gobisaurus* suggests that the handle-first hypothesis (Fig. 1) may best explain the evolution of the ankylosaurid tail club. This is also supported by the results from ancestral state reconstruction (Fig. 3), which reconstruct a later and more derived first appearance of the tail club knob relative to the first appearance of elongated prezygapophyses. However, we cannot reject the hypothesis that the handle and knob evolved in tandem (Fig. 1), as the absence of knob osteoderms in the known specimens of *Gobisaurus* or *Liaoningosaurus* might be attributed to ontogenetic and/or taphonomic changes. Basal thyreophorans like *Scelidosaurus harrisonii* Owen, 1861, had spiky lateral tail osteoderms that would certainly have been effective weapons if the tails were swung from side to side, even if they were not being used to deliver forceful impacts. Ankylosaurid ankylosaurs evolved a stiffened distal tail composed of tightly interlocking caudal vertebrae. Although early ankylosaurids and shamosaurines may not have had the enlarged knob osteoderms found in later taxa, the end of the tail may still have been an effective bat-like weapon.

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SUPPLEMENTARY INFORMATION

Supplementary Information 1: Specimens Examined, and Character Statements (.docx)

Supplementary Information 2: Character matrix (.nex)

FIGURE CAPTIONS

Figure 1. Three hypotheses for the evolution of the ankylosaurid tail club. In the knob-first hypothesis, knob osteoderms that completely envelope the terminus of the tail should appear before handle vertebrae in the fossil record. In the handle-first hypothesis, handle vertebrae should appear in the fossil record before the knob osteoderms completely envelop the terminus of the tail. In the tandem hypothesis, the tail club handle and knob appear at about the same time in the fossil record. Lateral caudal osteoderm pattern modified after MPC 100/1305, cf. *Pinacosaurus*. [Planned for column width. Colour online; greyscale in print]

Figure 2. Caudal anatomy of ankylosaurs. A) UALVP 47273, *Dyoplosaurus acutosquameus* tail club, in slightly oblique dorsal view, anterior is to the left. This represents the typical morphology of derived ankylosaurine tail clubs, with lengthened prezygapophyses interlocking with the neural spines of the adjacent vertebra, and large terminal osteoderms that envelop the tip of the tail (although the knob can be substantially wider in some specimens). B) HGM 41HIII-002, *Gobisaurus domoculus* (="*Zhongyuansaurus*"), tail club handle in left dorsolateral view, drawn from Xu et al. (2007). C) HGM 41HIII-002, handle in right ventrolateral view; the deep groove along the bottom is the haemal canal. The terminal vertebra appears to be present: in X-ray images of the ankylosaurid tail club knob UALVP 16247 (X-ray in D, interpretive drawing in E; posterior is up), the terminal vertebra is a small nub compared to the long distal caudals of the handle. F) MWC 5819, *Mymoorapelta maysi*, two distal

caudal vertebrae in right lateral view, mirrored for comparative purposes (anterior is to the left), showing the typical distal caudal morphology for basal ankylosaurs and nodosaurids. The prezygapophyses overlap the preceding vertebra by about 25% the length of the centrum. G) IVPP V12560, *Liaoningosaurus paradoxus* whole specimen in ventral view, anterior is to the left, box outlines area magnified in (H). H) Distal caudal vertebrae of IVPP V12560, anterior is to the left, scale is in millimeters. The prezygapophyses overlap the preceding vertebra by at least 50% of the centrum length, similar to what is observed in ankylosaurid tail clubs. Abbreviations: c, centrum; ha, haemal arch; hc, haemal canal; kn, knob; ns, neural spine; prz, prezygapophyses; poz, postzygapophyses. [Planned for page width. Colour online; black and white in print]

Figure 3. Ancestral state reconstruction for the presence of elongated prezygapophyses (characteristic of the tail club handle), and enlarged knob osteoderms, showing proportional likelihoods, using the 50% majority rule phylogenetic tree from Arbour and Currie (in press). [Planned for page width. Colour online; black and white in print]

Figure 4. 50% majority rule phylogenetic tree from Arbour and Currie (in press) showing acquisition of characters of the tail club in a stratigraphic context. Unmodified distal caudal vertebrae are found in basal ankylosaurs (*Mymoorapelta maysi*), nodosaurids (*Sauropelta edwardsorum*), and the basal ankylosaurid *Gastonia burgei*; in these taxa the prezygapophyses overlap no more than 25% of the preceding vertebra. *Liaoningosaurus paradoxus* and *Gobisaurus domoculus* have distal caudal vertebrae with prezygapophyses that overlap at least 50% of the preceding vertebra. *Pinacosaurus grangeri* and all more derived ankylosaurines have a complete tail club with handle vertebrae and knob osteoderms. [Planned for page width. Colour online; black and white in print]

Proposed cover image:

How the ankylosaur got its tail club: Early ankylosaurs like *Mymoorapelta*, from the Jurassic of North America (blue), had flexible tails like other dinosaurs. By the mid Cretaceous, some ankylosaurs in China, like *Gobisaurus* (yellow), had evolved a stiffened distal tail. The large knob of bone at the tip of the tail evolved later, and is characteristic of the clade of ankylosaurs called ankylosaurines, represented here by *Ziapelta* (red and life restoration) from the Late Cretaceous of New Mexico. Image by V. Arbour; life restoration of *Ziapelta* by Sydney Mohr first appeared in Arbour et al. (2014), PLOS ONE 9:e108804, and is used here under the Creative Commons Attribution License.