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Authors: Persons, W. Scott, Currie, Philip J., and Norell, Mark A.

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Oviraptorosaur tail forms and functions

W. SCOTT PERSONS, IV, PHILIP J. CURRIE, and MARK A. NORELL



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Oviraptorosaur caudal osteology is unique among theropods and is characterized by posteriorly persistent and exceptionally wide transverse processes, anteroposteriorly short centra, and a high degree of flexibility across the pre-pygostyle vertebral series. Three-dimensional digital muscle reconstructions reveal that, while oviraptorosaur tails were reduced in length relative to the tails of other theropods, they were muscularly robust. Despite overall caudal length reduction, the relative size of the M. caudofemoralis in most oviraptorosaurs was comparable with those of other non-avian theropods. The discovery of a second *Nomingia* specimen with a pygostyle confirms that the fused terminal vertebrae of the type specimen were not an abnormality. New evidence shows that pygostyles were also present in the oviraptorosaurs *Citipati* and *Conchoraptor*. Based on the observed osteological morphology and inferred muscle morphology, along with the recognition that many members of the group probably sported broad tail-feather fans, it is postulated that oviraptorosaur tails were uniquely adapted to serve as dynamic intraspecific display structures. Similarities, including a reduced vertebral series and a terminal pygostyle, between the tails of oviraptorosaurs and the tails of theropods widely accepted as basal members of the Avialae, appear to be convergences.

Key words: Dinosauria, Theropoda, Oviraptorosauria, pygostyle, caudal musculature, functional morphology.

W. Scott Persons, IV [persons@ualberta.ca] and Philip J. Currie [philip.currie@ualberta.ca], University of Alberta, Department of Biological Sciences, Edmonton, Alberta, T6G2E9, Canada;
Mark A. Norell [norell@amnh.org], American Museum of Natural History, Central Park W & 79th St, New York, NY 10024, USA.

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Introduction

Oviraptorosaurs are a group of maniraptoriform theropod dinosaurs, characterized by numerous synapomorphies, including: a crenulated ventral margin of the premaxilla, a U-shaped mandibular symphysis, an edentulous dentary (except in basal members), pneumatized caudal vertebrae, an anteriorly concave pubic shaft, and a posteriorly curved ischium (Osmólska et al. 2004). Although absent in several taxa, prominent cranial crests are common and emblematic features within the group (Osmólska et al. 2004). Oviraptorosaurs ranged in size from the 0.69 meter long *Protarchaeopteryx robusta* (Ji et al. 1998) to the estimated 8 meter long *Gigantoraptor erlianensis* (Xu et al. 2007). At present, all confirmed oviraptorosaur material is limited to Cretaceous sediments of Asia, Europe, and North America (Osmólska et al. 2004), although tentatively identified oviraptorid fossils have also been reported from Australia (Currie et al. 1996). The absence of teeth and the inferred presence of keratinous beaks in advanced forms, along with the incisiform teeth of the basal taxon *Incisivosaurus gauthieri* (Xu et al. 2002a) and the in situ gizzard stone masses preserved in specimens of *Caudipteryx zoui* (Ji et al. 1998), suggest that oviraptorosaurs were predominantly herbivorous (Paul 1988; Barrett 2005; Zanno et al. 2009; Longrich et al. 2010). It has also been argued that oviraptorosaurs ate eggs (Osborn 1924; Currie et al. 1993), or clams (Barsbold 1977). Although all known forms are definitively flightless, direct proof of feather integument (including feathers of modern aspect) is preserved in specimens of *Caudipteryx*, *Protarchaeopteryx* (Ji et al. 1998), and *Similicaudipteryx* (Xu et al. 2010b). Structures tentatively identified as quill knobs are present on the ulna of *Avimimus portentosus* (Kurzanov 1987).

The tails of all oviraptorosaurs are remarkable for their reduced length. In the primitive oviraptorosaur *Similicaudipteryx yixianensis,* the last few caudal vertebrae are fused (He et al. 2008; Xu et al. 2010b). Soft tissue preservation confirms that, as in modern avians, these fused terminal vertebrae are a pygostyle, which served as an anchor for a fan of elongate caudal feathers (He et al. 2008; Xu et al. 2010b). *Caudipteryx* also had a caudal feather-fan (Ji et al. 1998), but lacks a pygostyle; nevertheless, the last five vertebrae appear to be tightly integrated into an inflexible unit (personal observation). The advanced oviraptorosaur *Nomingia gobiensis* has a series of

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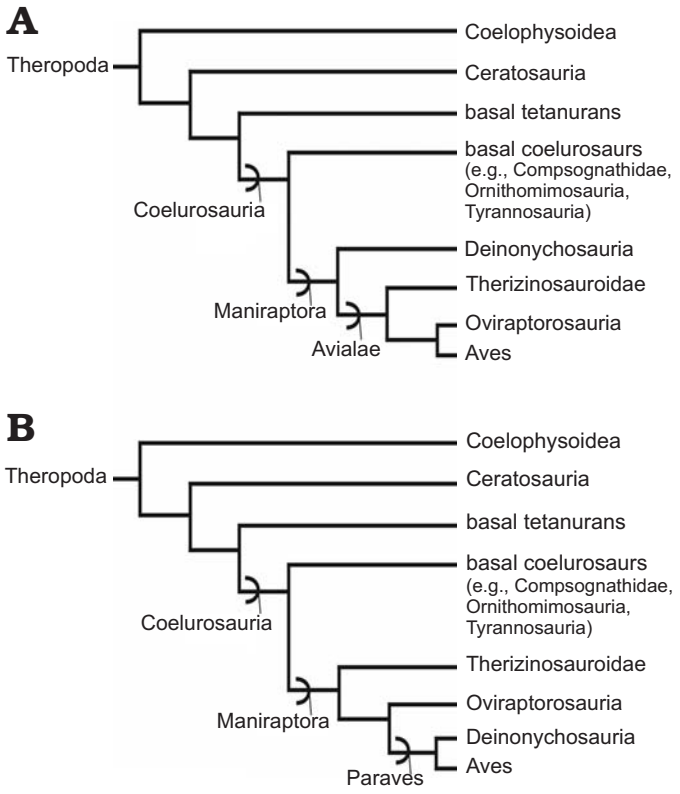


Fig. 1. Simplified theropod phylogenies, illustrating two competing hypotheses on the relationship between oviraptorosaurs and birds. **A**. Oviraptorosauria is the sister group to Aves and is positioned within Avialae (phylogeny modified from Maryańska et al. 2002). **B**. Oviraptorosauria is the sister group to Paraves, which includes Aves and Deinonychusauria (phylogeny modified from Senter 2007).

fused terminal caudal vertebrae and, based on this, a caudal feather-fan has been inferred (Barsbold et al. 2000b).

The elongate lower leg bones of most oviraptorosaurs indicate a moderate degree of cursoriality, particularly in avimimids (Kurzanov 1987), *Caudipteryx* (Ji et al. 1998), and caenagnathids (Currie and Russell 1988; Christiansen and Bonde 2002). Key to understanding the group's locomotor style is assessing the size of oviraptorosaur caudofemoral musculature. The M. caudofemoralis (composed of the m. caudofemoralis longus and the m. caudofemoralis brevis) originates on the lateral surfaces of the anterior caudal centra, chevrons, and the brevis fossa of the ilium and inserts onto the fourth trochanter of the femur (Persons and Currie 2011b). Among modern crocodilians and most non-serpentine squamates, the M. caudofemoralis functions as the primary femoral retractor and supplies most of the force during the locomotive power stroke (Snyder 1962; Gatesy 1990a, 1997). A large M. caudofemoralis is a characteristic of basal theropods (Gatesy 1990a; Persons and Currie 2011b). In avialans and deinonychosaurs, the M. caudofemoralis is greatly reduced in size or altogether absent, and the stroke mechanics of the hind limbs emphasize knee-flexion, rather than femoral retraction (Gatesy 1990a, b; Persons and Currie 2012).

The similarities between the tails of oviraptorosaurs and modern birds have been cited as support for a close relationship between the two groups (Lü et al. 2002; Maryańska et al. 2002) and as a correlate for bird-like knee-flexion-dominated locomotion (Maryańska et al. 2002). Based on a suite of morphological characters, Paul (2002) argued that oviraptorosaurs are most parsimoniously interpreted as secondarily flightless. On the basis of a cladistic analysis, Maryańska et al. (2002) concluded that oviraptorosaurs were not only secondarily flightless, but true members of the Avialae. More recent analyses tend to recover oviraptorosaurs as a clade close to the base of the Avialae (Osmólska et al. 2004; Longrich et al. 2010), as a sister clade to the Avialae (Xu et al. 2007), or most commonly as a sister clade to the Paraves (e.g., Makovicky et al. 2005; Senter 2007; Turner et al. 2012; Fig. 1B).

In this study, the caudal osteology and inferable caudal musculature of oviraptorosaurs is considered, with the aim of critically reevaluating claims of avian affinities and similarities in terrestrial locomotion. The uniqueness of oviraptorosaur tail osteology has not been thoroughly described elsewhere, and a new morphological overview is offered. The size and arrangement of dinosaur tail muscles has been the subject of several recent studies, and techniques for using the proportions of the caudal skeleton to reconstruct the caudal musculature have been developed and their accuracy verified with modern taxa (Allen et al. 2009; Arbour 2009; Mallison 2011; Persons and Currie 2011a, b). Based on simple observations of vertebrae and chevron dimensions and using a digital muscle reconstruction methodology refined from Persons and Currie (2011a, b), a qualitative and quantitative assessment of oviraptorosaur tail muscles is presented, with particular attention paid to three genera of advanced Asiatic oviraptorosaurs for which nearly complete and articulated caudal material is known: *Ajancingenia yanshini* (MPC-D 100/30), *Khaan mckennai* (MPC-D 100/1127), and *Nomingia gobiensis* (MPC-D 100/119). Finally, three newly discovered oviraptorosaur pygostyle specimens are reported.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York City, USA; BHI, Black Hills Institute of Geological Research, Hill City, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MPC-D, Paleontological Center of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

Description

Observations on general caudal osteology.—The tails of oviraptorosaurian dinosaurs are reduced compared to those of most other non-avian theropods, both in terms of length relative to body size and the total number of caudal vertebrae, which ranges from 22 vertebrae in *Caudipteryx zoui* (Ji et al. 1998) to 33+ in *Conchoraptor gracilis* (Barsbold 1986; Table 1). Typically, caudal centra in non-avian theropods increase in length/height and length/width ratios along the caudal series. Centra near the base of the tail in most non-avian thero-

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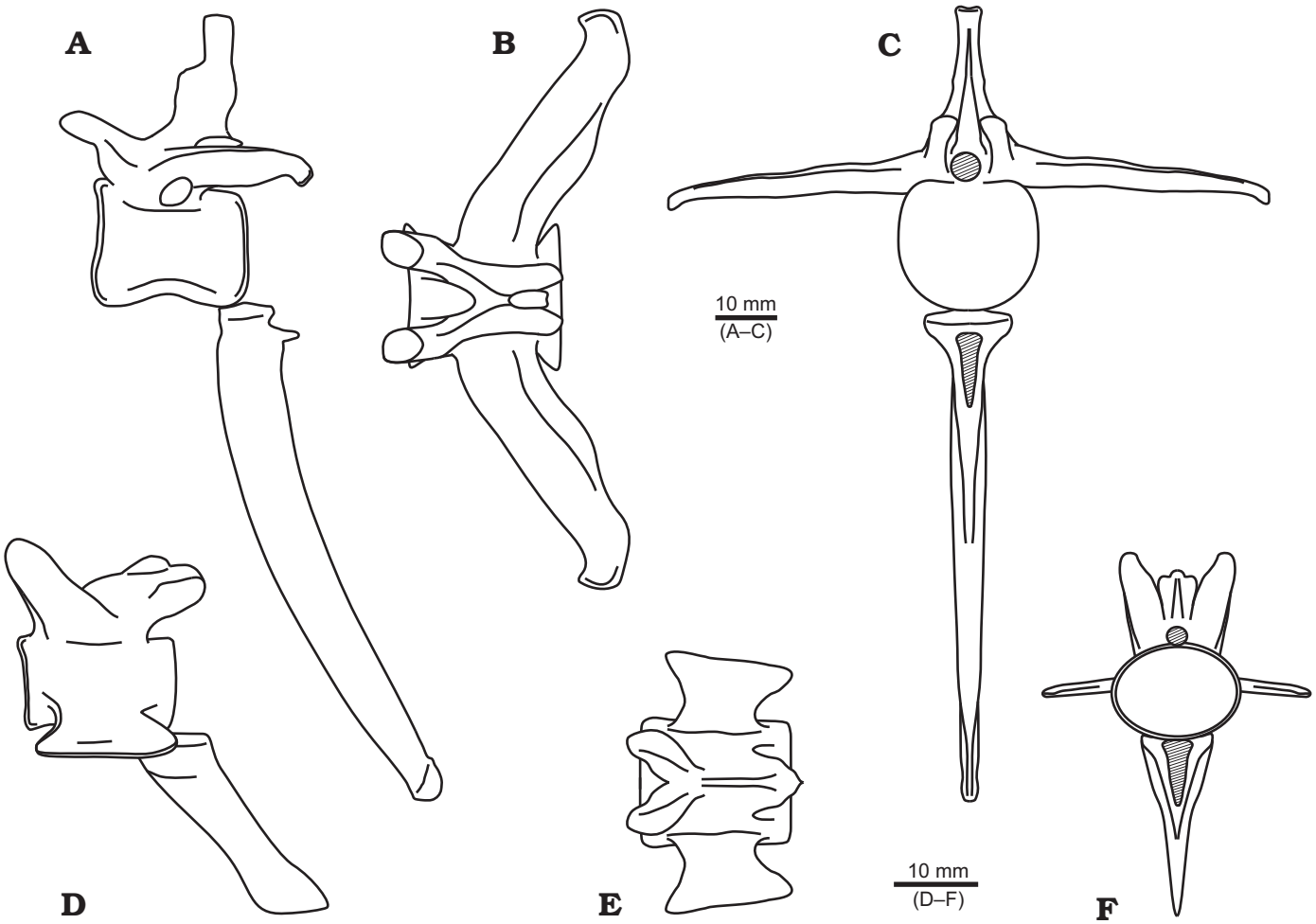


Fig. 2. Outline illustrations of the basic anterior and posterior caudal morphology of *Ajancingenia yanshini* (Barsbold, 1981). Caudal vertebra two and accompanyinposterior chevron in right lateral (**A**), dorsal (**B**), and anterior (**C**) views. Caudal vertebra nineteen and accompanying posterior chevron in right lateral (**D**), dorsal (**E**), and anterior (**F**) views.

Table 1. Comparative summary of theropod caudal-series composition. "+" follow minimal observed values that are likely smaller than the true values, "1?" denotes the single blade shaped terminal caudal vertebra of *Jeholornis prima*, which may have functioned as a pygostyle, and NA denotes the absence of a pygostlye, such that a count of the comprising vertebrae is not applicable.

Genus species	Caudals	Transverse processes	Pygostyle
Coelophysis bauri	40+	19	NA
Sinocalliopteryx gigas	46	16	NA
Gorgosaurus libratus	37	12	NA
Ornithomimus edmontonicus	33	14	NA
Caudipteryx zoui	22	13	NA
Khaan mckennai	29+	25	NA
Ajancingenia yanshini	30	25	NA
Citipati osmolskae	33	30	3
Conchoraptor gracilis	33+	27+	3
Nomingia gobiensis	24	18	5
Velociraptor mongoliensis	29+	11	NA
Anchiornis huxleyi	20+	9+	NA
Archaeopteryx lithographica	23	7	NA
Jeholornis prima	27	5	1?

pods are subequal in height, width, and length, while those near the tail tip are many times longer than they are tall or wide. The tails of oviraptorosaurs also follow this pattern of progressive centrum elongation, but the trend is more subtle (Fig. 2). As a result, the caudal centra of oviraptorosaurs remain dimensionally near-symmetrical further down the tail, and the caudal vertebrae are more densely packed per unit of length than in other dinosaurs.

Barsbold et al. (1990) briefly noted a similar morphological pattern in oviraptorosaur caudal prezygapophyses. Usually, the prezygapophyses of non-avian theropods increase in relative anterior/posterior length distally along the caudal series, eventually developing into long, finger-like projections that may equal or exceed the length of the adjacent centrum and that flank the lateral sides of the preceding vertebrae. Among advanced coelurosaurs, the caudal prezygapophyses tend to become particularly elongate, limiting both dorsoventral and lateral intervertebral flexibility. In oviraptorosaurs (although *Gigantoraptor erlianensis* may be an exception), the prezygapophyses of all but the most posterior caudal vertebrae remain short anteroposteriorly, have wide articular surfaces for the postzygapophyses, and maintain a

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dorsal (not lateral) position relative to the preceding vertebrae. Combined with reduced central lengths—which result in higher density of intervertebral flexure points—the short and broad articular surfaces of the prezygapophyses indicate that oviraptorosaurs had a high degree of tail flexibility per unit of absolute tail length.

The anterior transverse processes (and/or caudal ribs) of oviraptorosaurs generally have greater lateral widths relative to the widths of their associated centra than those of other theropod groups and, as noted by Barsbold (1986), the transverse processes persist far down the caudal series. Anteriorly, the transverse processes are often slightly lobate and have strong posterior inclinations—roughly 65°. The relative elevation of an oviraptorosaur transverse process is variable, but the most anterior transverse processes are more ventrally positioned than in most other non-avian theropods. Posteriorly, the transverse processes gradually reduce in size, extend roughly perpendicular to the vertebral midline, and have an increasingly more ventral position. In many oviraptorosaurs, including *Ajancingenia yanshini* and *Khaan mckennai*, the most posterior transverse processes are T-shaped with lateral tips that are nearly as long anteroposteriorly as the centra.

The neural spines have what is perhaps the only truly typical theropod shape in the entire caudal series: they are dorsoventrally tall on the anterior vertebrae, gradually declining in height posteriorly and becoming absent on the posterior vertebrae.

The chevrons of oviraptorosaurs are variable. In *Caudipteryx*, the anterior chevrons are dorsoventrally tall and anteroposteriorly narrow, while the posterior chevrons are dorsoventrally short with extended ventral anterior and posterior tips (overall, the posterior chevrons of *Caudipteryx* are similar to those of other coelurosaurs). The chevrons of more advanced oviraptorosaurs are bladelike, with haemal spines that are mediolaterally compressed but anteroposteriorly broad and taper to a ventral point. The posterior chevrons of advanced oviraptorosaurs are present between all but the last few caudal vertebrae, and are progressively longer anteroposteriorly than they are tall dorsoventrally. In some oviraptorosaurs the posterior chevrons have a distinctive rectangular shape in lateral view (Balanoff and Norell, 2012).

Many authors have commented that oviraptorosaurs lack a clear caudal "transition point" (e.g., Barsbold et al. 1990; Osmólska et al. 2004). The caudal transition point is the region where the M. caudofemoralis is presumed to have tapered out, and is usually identified by the termination of the transverse process series and by an abrupt shift in the chevron shape (Russell 1972; Gatesy 1990a). In oviraptorosaurs, transverse processes persist until nearly the tip of the tail; however, a transition point is generally recognizable prior to the final vertebrae. In *Nomingia gobiensis* (MPC-D 100/119), the last set of transverse processes is present on caudal vertebra 18; caudal vertebrae 14–17 show a pattern of rapid descent of the transverse processes, and the associated chevrons become markedly shorter and anteroposteriorly longer. In both *Ajancingenia yanshini* and *Khaan mckennai*, the final transverse processes are found on the 25th caudal vertebrae. This leaves six post-transition-point vertebrae in *Nomingia gobiensis*, four in *Ajancingenia yanshini*, and three in *Khaan mckennai*. Nevertheless, it is clear that the M. caudofemoralis of oviraptorosaurs was unique among theropods in that it extended through most of the caudal series.

Oviraptorosaur femora lack a pronounced fourth trochanter, but have marked bone rugosities at the fourth trochanteric positions. This attests to the insertion of large caudofemoral tendons (similar to the conditions in some ornithomimids, including *Gallimimus bullatus* MPC-D 100/52 and *Garudimimus brevipes* MPC-D100/13).

Three new pygostyles and associated caudal material.—MPC-D 102/5, from the Nemegt Formation (Upper Cretaceous) of the Western Sayr of the Nemegt Locality of Mongolia, is a second and previously undescribed specimen of the oviraptorosaur taxon *Nomingia*. MPC-D 102/5 includes a series of five fused terminal caudal vertebrae (Fig. 3; see Supplementary Online Material (SOM 1) at http://app.pan.pl/SOM/app59-Persons_etal_SOM.pdf for details on discovery and preparation). An almost identical fused caudal series was reported by Barsbold et al. (2000a, b) in the type specimen of *Nomingia gobiensis* (MPC-D 100/119) and was identified as a pygostyle. MPC-D 102/5 confirms that the fused vertebrae of MPC-D 100/119 were not the result of an injury or other osteological aberration and that a pygostyle is a typical feature of *Nomingia*.

MPC-D 100/978 is the type specimen of *Citipati osmolskae* from the Djadokhta Formation (Upper Cretaceous) of Ukhaa Tolgod, Mongolia (Clark et al. 2001; see SOM for details on discovery and preparation). The tail is complete, composed of 33 vertebrae. The terminal three (or possibly two) caudal vertebrae are fused into a pygostyle (Fig. 4). Neural spines are only conspicuous in the first twelve vertebrae after which they persist as low longitudinal ridges until approximately the 24th caudal. The base of the neural spine is excavated laterally above the transverse process by a pair of pneumatic excavations (infrapostzygapophyseal and supradiapophyseal) in the first three caudals. The supradiapophyseal excavation is not present in the fourth and subsequent caudals, but the infrapostzygapohyseal pneumatopore persists in the fourth and fifth caudals. On the left side of the fourth caudal, this pneumatic feature is enlarged into a centimeter wide opening that passes through the transverse process, whereas on the right side of the same vertebra the diameter is half the size and opens only into the base of the neural spine. Throughout the tail, the anteroposterior midpoint of each neural spine is at approximately the same level as the anterior margins of the postzygapophyseal facets. The paired postzygapophyses are separated by a posterior, midline notch in each of the first 26 caudals, after which the articular facets disappear in the 27th caudal, and the postzygapophyses merge into a short midline bar positioned between the prezygapophyses of the following vertebra. The postzygapophyseal bar is progressively reduced in the next three caudals, until it

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disappears in the last free caudal before the pygostyle. The prezygapophyses persist as paired structures until the last free caudal, but in the three vertebrae that form the pygostyle they merge into single midline structures arching over the centra of the preceding vertebrae. The ventral side of the base of each transverse process has two pneumatopores (separated by a subdiapophyseal lamina) in each of the first twelve caudals, after which the neural arches appear to have been apneumatic. A single pneumatopore enters each side of the first twenty centra below the neurocentral suture at midlength. The neurocentral sutures are fused but still visible in the first ten caudals, but are obliterated in more posterior caudals. Transverse processes persist until the last free vertebra (#30) before the pygostyle. In MPC-D 100/978, the pygostyle is composed of the last three caudal vertebrae, making it two vertebrae shorter than the pygostyle of *Nomingia*. The contact between the caudals in the pygostyle is continuous along both the intercentral and zygapophyseal surfaces, but only faintly visible. The proximal end of the pygostyle is 4.5 mm wide, and it tapers steadily through its component vertebrae until it is only 1.3 mm wide at the distal end. The longitudinal midline ventral groove is present only on the first of the three vertebrae. There is a minute haemal arch (3.6 mm long) between the 30th caudal vertebra and the pygostyle, but no evidence of a haemal arch between the component vertebrae of the pygostyle. In lateral view (Fig. 4), the ventral margin of the pygostyle behind the suture with the first pygostyle vertebra has a double concavity separated by a convexity, indicating that two vertebrae have been fused into a single unit with no evidence remaining of the contact between them. For this reason, it is uncertain whether three or only two vertebrae have been incorporated into the pygostyle.

MPC-D 100/1275 is an articulated specimen of *Conchoraptor gracilis* (see SOM for details on discovery and preparation). Although the tail of MPC-D 100/1275 is weathered, the terminal three (possibly two) caudal vertebra are fused into a pygostyle (Fig. 5). Like other specimens of *Conchoraptor*, MPC-D 100/1275 probably had a longer tail than either *Nomingia* or *Citipati*. However, no *Conchoraptor* specimen has a complete enough tail to provide confirmation. If it is conservatively assumed that the tail of MPC-D 100/1275 was the same length (33 vertebral units) as that of *Citipati*, then there are many clear differences between the tails of the two animals. If the tail had more than 33 vertebrae, then these differences would become even more obvious. Conspicuous neural spines persist much farther down the tail in *Conchoraptor*, and neural spines of the same relative proportion as the 14th caudal of *Citipati* are still present in the 22nd+ caudal of MPC-D 100/1275, and persist as low ridges until the 30th+ vertebra. The transverse processes of the mid-caudals are flat platelike sheets of bone that are anteroposteriorly longer than they are mediolaterally wide back to the 18th+ caudal, but become small nubbins for the next four vertebrae (19th to 22nd+). These last four caudals with transverse processes have centra that are rounded in cross-section and the transverse processes are close to mid-height on the sides of



Fig. 3. Oviraptorosaur theropod *Nomingia gobiensis* Barsbold, Currie, Myhrvold, Osmólska, Tsogtbaatar, and Watabe, 2000, from the Nemegt Formation of Mongolia. Pygostyle of MPC-D 102/5, in right lateral view , with pygostyle vertebrae (P1–P5) denoted).



Fig. 4. Oviraptorosaur theropod *Citipati osmolskae* Clarke, Norell, and Barsbold, 2000, from the Djadokhta Formation of Mongolia. Pygostyle of MPC-D 100/978, in left lateral view , with pygostyle vertebrae (P1–P3) denoted).

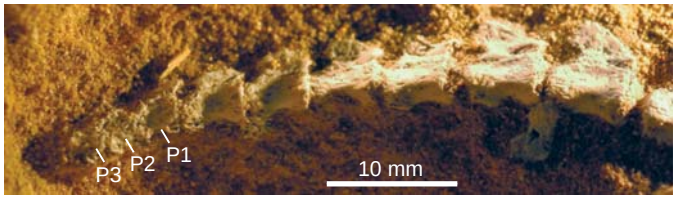


Fig. 5. Oviraptorosaur theropod *Conchoraptor gracilis* Barbsold, 1986, from the Nemegt Formation of Mongolia. Pygostyle and pre-pygostle terminal vertebrae of MPC-D 100/1275, in ventral view, with pygostyle vertebrae (P1–P3) denoted).

the centra. In contrast, the transverse processes of the distal caudals of *Citipati* (MPC-D 100/978) and *Nomingia* (Barsbold et al. 2000a) are ventrolateral in position. The anterior haemal spines are similar to those of *Citipati* in that they are elongate, bladelike bones that extend posteroventrally to a much greater extent than the corresponding neural spines extend posterodorsally. However, whereas these haemal arches transform into "boat-like" keels that are longer anteroposteriorly than they are dorsoventrally high by the 13th vertebral section from the hip of *Citipati*, they are still higher than long and are just starting to change shape in *Conchoraptor* by the 8th segment from the end of the tail. The prezygapophyses of the first vertebra of the pygostyle merge to form an anterodorsally oriented, midline process that overlaps the back of the last free vertebra (30+). In *Citipati*, the same anterodorsal processes can be seen on caudals 29 to 32, and in *Nomingia* on caudals 19 to 24.

The small pygostyle of MPC-D 100/1275 shows that the presence or absence of an oviraptorosaur pygostyle cannot be reliably inferred from anything less than a complete caudal series, and it may reveal the form taken by oviraptorosaur pygostyles early in their evolution. Among oviraptorosaurs, the presence of a pygostyle can be taken as a reasonable indi-

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cator that a tail-feather fan was also present (Barsbold et al. 2000a, b). However, as shown by *Caudipteryx* (which has a tail-feather fan but no pygostyle), the absence of a pygostyle cannot be taken as evidence that a tail-feather fan was also absent.

Muscle reconstruction methodology

Tails should not be mistakenly assumed to have simple or constant muscular configurations that merely taper conically from anterior to posterior. Rather, muscle groups can change in morphology and arrangement along the length of a tail. Nor is the arrangement of tail muscles taxonomically uniform. As with limb or cervical musculature, caudal musculature has been modified and adapted for a variety of functions and shows substantial variation across major clades. In the effort to reconstruct the caudal muscles of dinosaurs, much is owed to a wealth of studies that have documented the tail anatomy of modern reptiles (e.g., Ali 1941; Snyder 1949; Cong et al. 1998) and to several classic works that have applied inferences from the modern taxa to dinosaurs (e.g., Dollo 1883; Romer 1923, 1927; Madsen 1976).

Following the terminology established in Persons and Currie (2011b), dinosaur caudal musculature is divided into four major sets: M. spinalis, M. longissimus, M. ilio-ischiocaudalis, and M. caudofemoralis. In modern sauropsids, some of these four can be subdivided into additional sets. Because of its position predominantly below the axial midline, the M. caudofemoralis is here referred to, along with the M. ilio-ischiocaudalis, as a hypaxial muscle, as in Persons and Currie (2011a, b). However, this reference should not be misinterpreted with regard to the homology of the M. caudofemoralis, which is a posteriorly positioned limb muscle and is not homologues with any of the "true" axial musculature. (For a more complete review of theropod and extant reptile caudal musculature arrangements and insertion patterns see Persons and Currie 2011b).

Using the muscle insertion patterns of modern sauropsids as a guide, basic observation of the caudal skeleton is sufficient to assess the proportions of oviraptorosaur tail muscles in qualitative terms. To quantify the muscle proportions and absolute masses, the digital muscle modeling techniques described in Persons and Currie (2011a, b) were applied to MPC-D 100/30, MPC-D 100/119, and MPC-D 100/1127 using the software Rhinoceros NURBS modeling for Windows 4.0 (McNeel Robert and Associates 2007). First, the caudal and pelvic skeletons of the three oviraptorosaurs were digitally sculpted based on detailed measurements taken on the specimens (SOM 2–4). Then, the caudal muscles were digitally sculpted over the skeletons. All models were created using the digital modeling program Rhinoceros® (McNeel Robert and Associates 2007).

The M. spinalis and M. longissimus were reconstructed together by assuming they were bound medially by the neural arches and neural spines, and ventrally by the transverse processes (Fig. 6). Where the vertebrae lack transverse processes, the reconstructed muscles are limited by a conceptual

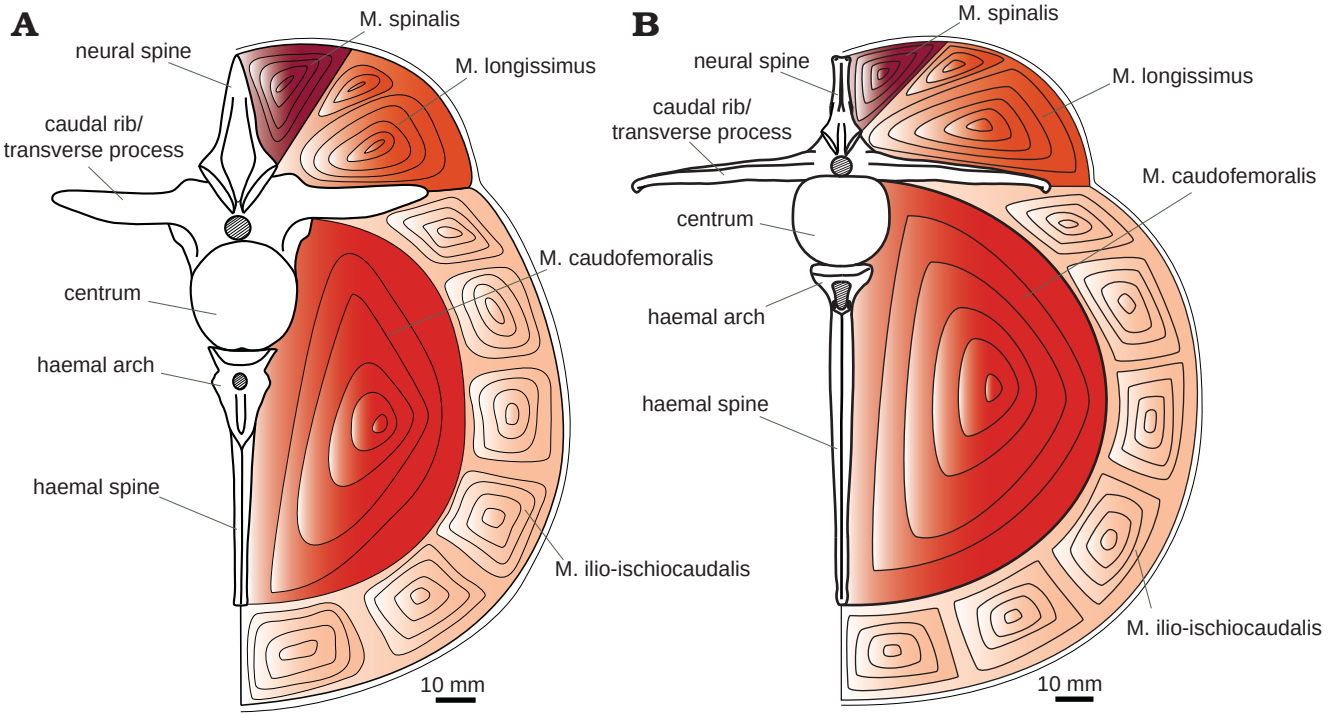


Fig. 6. Explanatory drawing of posterior view of caudal vertebra and chevron with one half of caudal musculature illustrated. **A**. First caudal vertebra of *Nomingia gobiensis* (MPC-D 100/119, type specimen) from the Nemegt Formation of Mongolia. **B**. Second caudal vertebra of *Ajancingenia yanshini* (MPC-D 100/30).

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horizontal plane that is level with the base of the neural arch, and dorsolaterally by a conceptual arch between the dorsal tip of each neural spine and a point level with the dorsal surface of each transverse process or each neural arch base. Later, the M. spinalis and M. longissimus were divided by assuming the septum that separated the two extended at a strong dorsolateral angle and originated roughly in line with the dorsolateral edges of the prezygapophyses.

The M. caudofemoralis was reconstructed by assuming that it tapered out at the caudal transition point. Anteriorly, it was bound medially by the lateral edge of each chevron and the portions of the centra and neural arches below the transverse processes; dorsally by the ventral surfaces of the transverse processes and by the M. ilio-ischiocaudalis, and laterally by a conceptual arch between the most ventral contact between the centra and the transverse process/neural arch and the ventral chevron tips (Fig. 6). Only the m. caudofemoralis longus portion of the M. caudofemoralis was digitally sculpted. Because the m. caudofemoralis brevis is capped by the brevis fossa, the size of the m. caudofemoralis brevis was estimated by directly calculating the volume of the brevis fossa.

Prior to the caudal transition point, the M. ilio-ischiocaudalis was reconstructed by assuming it inserted across and was bound dorsally by the ventral surface of each transverse process and formed a lateral reef around the M. caudofemoralis (Fig. 6). Posterior to the caudal transition point, the M. ilio-ischiocaudalis was reconstructed by assuming it was bound medially by the lateral surfaces of each chevron and centra, dorsally by a conceptual horizontal plane extended from the base of each neural arch, and laterally by a conceptual arch swung from the base of each neural arch to the ventral tip of each chevron.

The volume of each reconstructed muscle was calculated by the Rhinoceros® software, and the calculated volumes of the m. caudofemoralis longus and m. caudofemoralis brevis were combined into a single M. caudofemoralis volume estimation. To obtain estimates of muscle mass, the volume estimates were multiplied by the known standard muscle density of 1.06 g/cm^{-3} (Mendez and Keys 1960). The mass prediction accuracy of these methods has been tested on modern animals and found to be accurate (Persons and Currie 2011b). However, the methods are conservative, are known to consistently slightly underestimate muscle mass (Persons and Currie 2011b), and should, therefore, be interpreted as estimations of the lowest masses that are anatomically reasonable.

Results

The cross-section (Fig. 6) illustrates general muscle proportions and arrangement resolved for the anterior portion of a typical oviraptorosaur tail. The laterally extensive and lobate transverse processes of oviraptorosaurs indicate that the M. ilio-ischiocaudalis and M. longissimus were both greatly expanded. The ventral position of the transverse processes (relative to other non-avian theropods) also implies a large M. longissimus. The only average neural spines heights suggest that the M. spinalis was moderately sized. The distance from the ventral surfaces of the transverse processes to the ventral tips of the chevrons are predictive of the overall size of the M. caudofemoralis, and the depth of the anterior chevrons indicates a large anterior M. caudofemoralis.

The previous results of digital modeling of theropod and modern reptile data from Persons and Currie (2011b) and the mass estimation for each tail muscle of each animal is presented as a percentage of that animal's estimated total tail muscle mass and as a percentage of its estimated total body mass (Fig. 7, Table 2). These percentage results should be

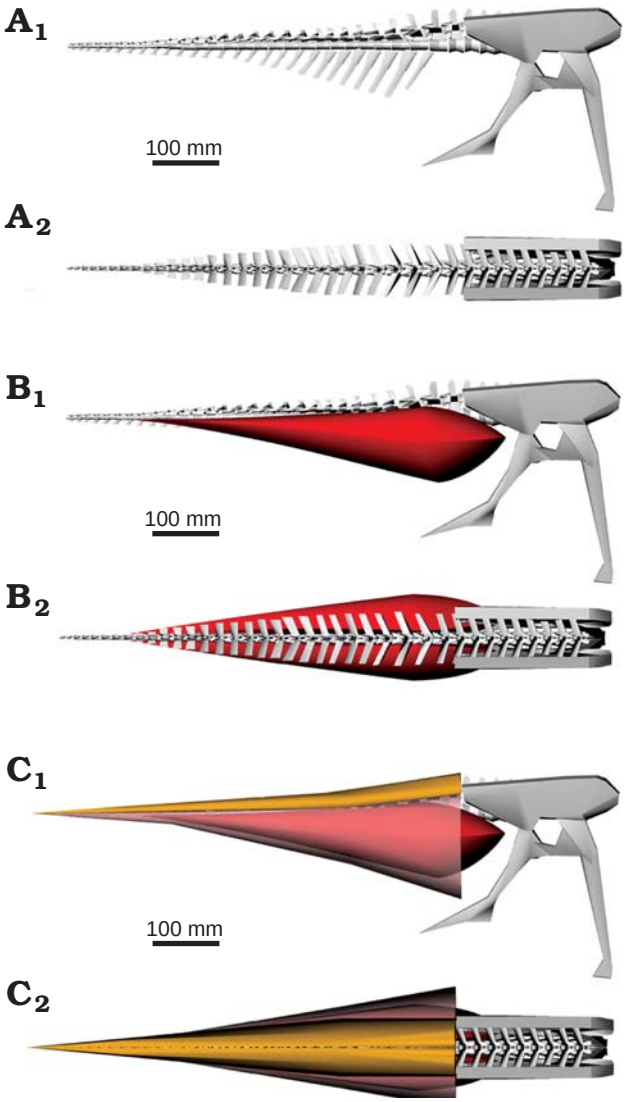


Fig. 7. Digital models of the caudal osteology and musculature of *Khaan mckennai* (MPC-D 100/1127). Three stages of reconstruction are shown in right lateral (A_1–C_1) and dorsal (A_2–C_2) views: the caudal skeleton modeled based on specimen measurements (**A**); the m. caudofemoralis longus modeled over the digital skeleton (**B**); and the full muscle reconstruction with the epaxial M. spinalis/M. longissimus and the hypaxial M. ilio-ischiocaudalis (**C**). Generated from Rhinoceros NURBS modeling for Windows 4.0.

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Table 2. Estimated caudal muscle masses of modern reptiles, non-avian coelurosaurs, and oviratorosaurs. *Gorgosaurus*, *Ornithomimus*, and *Tyrannosaurus* tail muscle estimations are taken from Persons and Currie (2011a). *Velociraptor* tail muscle estimations are taken from Persons and Currie (2012). Total body mass estimations 1 are taken from or, in the case of *Gorgosaurus*, calculated based on data given for similar specimens by Paul (2010a). Total body mass estimations 2 are derived from femur circumference based on Anderson et al. (1985).

	M. spinalis	M. longissimus	M. ilio-ischiocaudalis	M. caudofemoralis
Modern reptiles				
Caiman crocodilus	1.4 g	9.6 g	9 g	13.8 g
total tail muscle mass: 33.8 g	4.10%	28.40%	26.60%	40.80%
total body mass: 578 g	0.20%	1.70%	1.60%	2.40%
Tupinambis merianae	3.9 g	22.5 g	12.2 g	13.3 g
total tail muscle mass: 51.9 g	7.50%	43.40%	23.50%	25.60%
total body mass: 539.3 g	0.72%	4.17%	2.26%	2.47%
Iguana iguana	20.8 g	52.6 g	70 g	49.2 g
total tail muscle mass: 192 g	18.80%	27.30%	36.30%	25.50%
total body mass: 2357.6 g	0.90%	2.20%	3.00%	2.10%
Basiliscus vittatus	0.6 g	2.4 g	3 g	3.4 g
total tail muscle mass: 9.4 g	6.40%	25.50%	31.90%	36.20%
total body mass: 112.6 g	0.50%	2.10%	2.70%	3.00%
Chamaeleo calyptratus	0.2 g	0.6 g	0.8 g	0.6 g
total tail muscle mass: 2.2 g	9.10%	27.30%	36.40%	27.30%
total body mass: 121.15 g	0.20%	0.50%	0.70%	0.50%
Non-avian coelurosaurs				
Gorgosaurus libratus TMP 91.36.500	3900 g	6900 g	10300 g	17300 g
total tail muscle mass: 38300 g	10.20%	18.00%	26.90%	45.20%
total body mass estimation 1: 400000 g	0.98%	1.73%	2.58%	4.33%
total body mass estimation 2: 266000 g	1.47%	2.59%	3.87%	6.50%
Ornithomimus edmontonicus TMP 95.11.001	860 g	2440 g	5050 g	9890 g
total tail muscle mass: 18240g	4.70%	13.40%	27.70%	54.20%
total body mass estimation 1: 150000 g	0.57%	1.63%	3.37%	6.59%
total body mass estimation 2: 85000 g	1.01%	2.87%	5.94%	11.64%
Tyrannosaurus rex BHI 3033	65200 g	154200 g	159400 g	522200 g
total tail muscle mass: 901000 g	7.20%	17.10%	17.70%	58.00%
total body mass estimation 1: 5622000 g	1.16%	2.74%	2.84%	9.29%
total body mass estimation 2: 3838000 g	1.70%	4.02%	4.15%	13.61%
Velociraptor mongoliensis MPC100/986	108 g	210 g	318 g	202.4 g
total tail muscle mass: 838.4 g	12.90%	25.10%	37.90%	24.10%
total body mass estimation 1: 15000 g	0.70%	0.10%	2.12%	1.40%
total body mass estimation 2: 8000 g	1.35%	2.63%	3.98%	2.53%
Oviraptorosaurs				
Ajancingenia yanshini MPC-D 100/30	89 g	660 g	1220 g	1504 g
total tail muscle mass: 3473 g	2.56%	19%	35.10%	43.30%
total body estimation mass 1: 17000 g	0.52%	3.88%	7.18%	8.85%
total body mass estimation 2: 25000 g	0.36%	2.64%	4.88%	6.02%
Khaan mckennai MPC-D 100/1127	25 g	161 g	500 g	569 g
total tail muscle mass: 1255 g	1.99%	12.83%	39.84%	45.34%
total body mass estimation 1: 4500 g	0.55%	3.58%	11.11%	12.64%
Nomingia gobiensis MPC-D 100/119	145 g	541 g	1299 g	2353 g
total tail muscle mass: 4338 g	3.34%	12.47%	29.64%	54.24%
total body mass estimation 1: 20000 g	0.73%	2.71%	6.50%	11.77%
total body mass estimation 2: 25000	0.58%	2.16%	5.20%	9.41%

interpreted carefully, and it should be noted that, as means of comparison, both sets suffer from different weaknesses. The percentages of total tail muscle mass are generated strictly from the data and methods presented here, but do not relate the sizes of the caudal muscles to the total size of the animals; this is particularly a problem when comparing M. caudofemoralis masses (because the M. caudofemoralis is a locomotor muscle). The percentages of body mass are confounded by all the problems associated with attempts at estimating the total mass of an extinct animal (see Paul 1997; Hutchinson et al.

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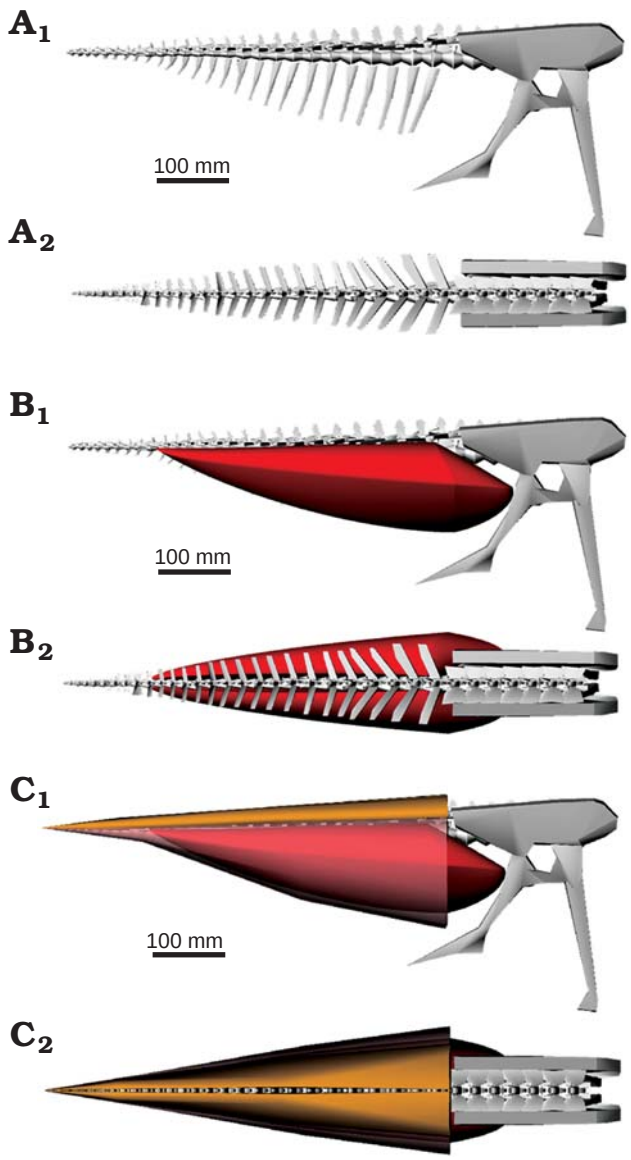


Fig. 8. Digital models of the caudal osteology and musculature of *Ajancingenia yanshini* (MPC-D 100/30). Three stages of reconstruction are shown in right lateral (A_1–C_1) and dorsal (A_2–C_2) views: the caudal skeleton modeled based on specimen measurements (**A**); the m. caudofemoralis longus modeled over the digital skeleton (**B**); and the full muscle reconstruction with the epaxial M. spinalis/M. longissimus and the hypaxial M. ilio-ischiocaudalis (**C**). Generated from Rhinoceros NURBS modeling for Windows 4.0.

2011 [and comments]; Campione and Evans 2012). Two sets of total body mass estimations are used. The first set is taken from the work of Paul (2010a) or from his work on similar specimens and scaled according to femur size. As argued in Persons and Currie (2011b), tail mass is itself a likely source of error in Paul's (2010a) mass estimations, because the tails of the reconstructions used to generate the mass estimations are overly compressed (WSP, PJC, and MAN unpublished calculations suggest, that the impact is modest, affecting total body mass estimates by no more than 5% in the case of *Tyrannosaurus*). Nonetheless, these total mass estimations were chosen because the methods used to generate them have been tested with modern analogs (Paul 1997), and because they are uniquely available for the necessary wide range of theropod genera. This last point is critical, because it insures that, whatever errors or biases may be present in the first set of total-mass estimations, these errors are consistent across all theropod taxa, and the results are, therefore, still useful as a means of comparison. The second set of total body mass estimations were made using the method of Anderson et al. (1985) and the equation: body mass in kg = 0.00016*(femur circumference in mm)$^{2.73}$. In the second set, no calculations were made for *Khaan mckennai* (MPC-D 100/1127), because femur circumference could not be measured. The second set of total body mass estimations should also be interpreted

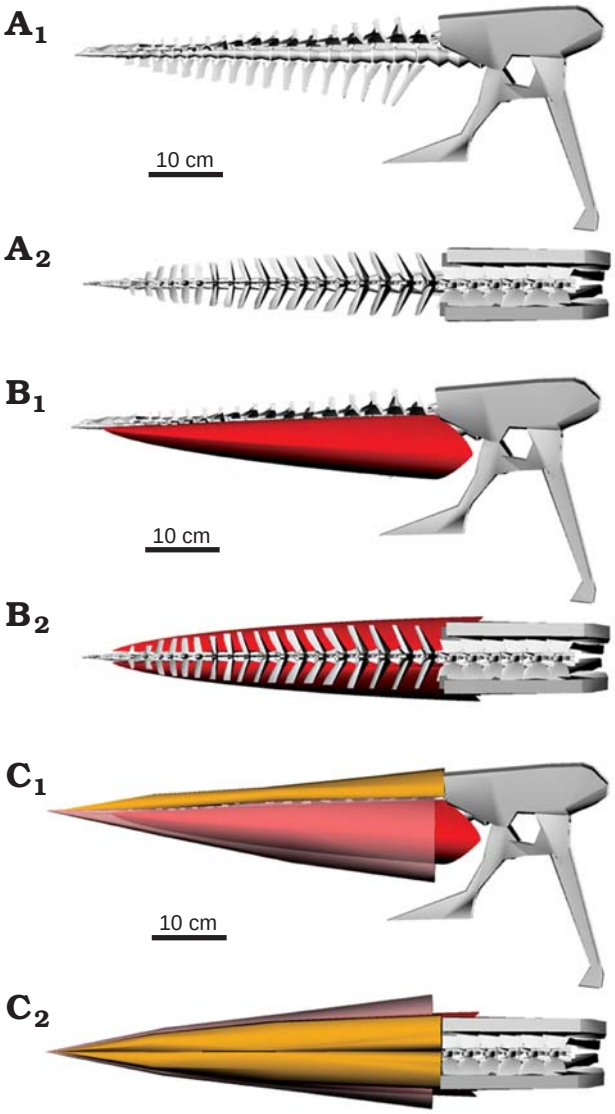


Fig. 9. Digital models of the caudal osteology and musculature of *Nomingia gobiensis* (MPC-D 100/119). Three stages of reconstruction are shown in right lateral (A_1–C_1) and dorsal (A_2–C_2) views: the caudal skeleton modeled based on specimen measurements (**A**); the m. caudofemoralis longus modeled over the digital skeleton (**B**); and the full muscle reconstruction with the epaxial M. spinalis/M. longissimus and the hypaxial M. ilio-ischiocaudalis (**C**). Generated from Rhinoceros NURBS modeling for Windows 4.0.

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cautiously, because they are prone to underestimation and because the reliability of femur circumference as a mass indicator is known to be reduced in animals that weigh less than 30 kg (which, according to the calculations, includes all the considered oviraptorosaurs) (Anderson et al. 1985). Additionally, using femoral circumference to estimate body mass has been criticized because the method does not account for differences in femur shape that may result from differences in posture and locomotion (Blob and Biewener 1999; Rubin and Lanyon 1984) and, in the specific case of Anderson et al. (1985), because the data set used to develop the equation may have been too heavily influenced by certain outliers (Packard et al. 2009) and by an overabundance of data from ungulate mammals (Carrano 2001), but see Campione and Evans (2012) for a response to these criticisms and a new quantitative consideration that (though limited to terrestrial quadrupeds) largely affirms the validity of the Anderson et al. (1985) method.

The results of the digital modeling (Table 2) indicate that none of the three modeled oviraptorosaurs had a M. caudofemoralis that was exceptionally small compared to other non-avian theropods (either in terms of total tail musculature or relative to body size). In the oviraptorosaurs *Ajancingenia yanshini*, *Khaan mckennai* (MPC-D 100/1127), and *Nomingia gobiensis*, robust caudofemoral musculature was supported by proportionally extended chevrons and the postponement of the caudal transition point until near the end of the caudal series. Tail-length reduction appears, therefore, to have been non-uniform across the caudal series and was predominantly limited to the region posterior to the caudal transition point. The digital modeling results also confirm that, despite shortened tail lengths, the M. longissimus and the M. ilio-ischiocaudalis were notably large in oviraptorosaurs. This result is especially striking, given that, unlike the M. caudofemoralis, both the M. longissimus and the M. ilio-ischiocaudalis are continuous down the entire length of the tail, and the relative mass of both is negatively affected by proportionately reduced post transition-point tail lengths.

Overall, oviraptorosaur tails were found to be short but stocky, and it is likely that most oviraptorosaurs had a center of mass that was located only slightly more anteriorly than in most other non-avian theropods.

Discussion

Evolutionary context.—Both oviraptorosaurs and modern birds have caudal series that can be described as "reduced", but citing this general similarity as compelling evidence for close kinship is a substantial oversimplification.

The probable evolutionary sequence leading to the reduced state observed in the tails of modern birds has been previously described (Gatesy 1990b; Gatesy and Dial 1996; Persons and Currie 2012). The general sequence appears to have been: (i) reduction in the total number of caudal vertebrae (accomplished by the loss of distal vertebrae and by the incorporation of anterior vertebrae into the sacrum), considerable elongation of the posterior caudal vertebrae (which, combined with the loss of caudal vertebrae, resulted in only a slight shortening in overall caudal length), reduction in epaxial musculature (as reflected in a reduction in transverse process and neural spine proportions), and substantial reduction in the mass of the hypaxial musculature, particularly the M. caudofemoralis (as indicated by a reduction in chevron height and the total number of transverse process sets). This condition is observed in basal members of the Deinonychosauria, including *Anchiornis*; (ii) continued loss of caudal vertebrae and reduction in caudal musculature—as seen in *Archaeopteryx* and *Jeholornis*; (iii) complete loss of the elongate posterior caudal vertebrae and development of a pygostyle—as seen in *Confuciusornis* and more derived avians (Fig. 10).

Oviraptorosaurs do not fit neatly into any stage of this sequence, and appear to have achieved their reduced tails through reduction in the absolute number of caudal vertebrae and through reduction in vertebral length throughout the caudal series. If oviraptorosaurs are interpreted to have a shared non-avian ancestor that is more closely related to *Archaeopteryx*/*Jeholornis* than the shared non-avian ancestor of Deinonychosauria (as suggested by Kurzanov 1987; Elzanowski 1999), it must be assumed that oviraptorosaurs secondarily lost the elongate morphology of the posterior caudal vertebrae. If oviraptorosaurs are instead interpreted to have a shared avian ancestor between *Confuciusornis* and *Archaeopteryx*/*Jeholornis* (as suggested by Maryańska et al. 2002), then it is necessary to assume that most oviraptorosaur genera secondarily increased the total number of caudal vertebrae. Further, both scenarios require oviraptorosaurs to have re-evolved extended posterior transverse processes and chevrons, along with the corresponding increases in associated muscle mass.

However, it must be noted that this evolutionary sequence and the conclusions drawn from it hinge on the assumption that both or either *Archaeopteryx* and *Jeholornis* have tails representative of the form ancestral to derived members of the Avialae. In a recent cladistic analysis, Xu et al. (2011) found *Archaeopteryx* to be a member of the Deinonychosauria and the Deinonychosauria to be closely related but peripheral to the true avian lineage. This conclusion was not given strong statistical support, and Xu et al. (2011) still retained *Jeholornis* as a member of Avialae.

Nonetheless, caudal similarities between *Jeholornis* and such basal deinonychosaurs as *Anchiornis*, which include plate-like chevrons with dual anterior and posterior prongs (Zhou and Zhang 2002), raise the possibility that *Jeholornis* is as closely tied to the Deinonychosauria as is *Archaeopteryx*. Given that the next most primitive avialans, such as *Confuciusornis* and *Sapeornis*, already have greatly reduced caudal series and large pygostyles, this possibility would leave the tail morphology of basal Avialae unknown, and it would become plausible to consider the oviraptorosaur tail form, with its reduced caudal series, reduced caudal length, and terminal feathers, as ancestral. In the context of this the-

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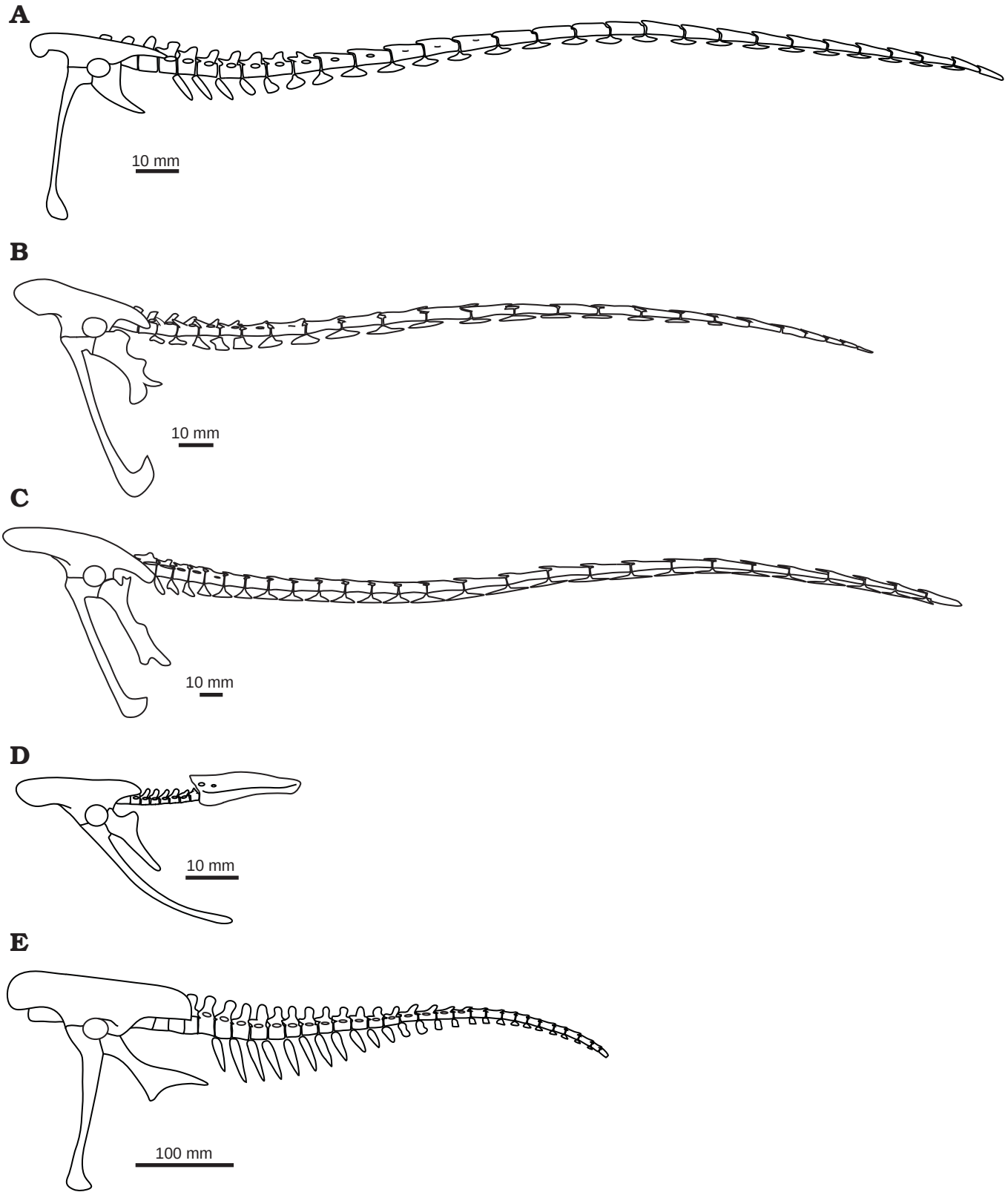


Fig. 10. Comparison of the caudal and pelvic skeletons of *Anchiornis*, LPM-B00169 (**A**), *Archaeopteryx*, Berlin specimen HMN 1880 (**B**), *Jeholornis*, IVPP V 13274 (**C**), *Confuciusornis*, IVPP V 11308 (**D**), and the oviraptorosaur *Khaan*, MPC-D 100/1127 (**E**).

oretical scenario, the shift noted by Gatesy and Dial (1996) in caudal tail feather arrangement from frond-shaped in *Archaeopteryx* and *Jeholornis* to fan-shaped in derived birds would no longer hold, because the fan-shaped arrangement is present in oviraptorosaurs, although it is unknown whether oviraptorosaur tail fans had the muscular specializations

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needed for active opening and closing. It should, however, be reemphasized that the possibility that *Jeholornis* is not a basal member of the Avialae awaits cladistic support.

It is interesting to note that many phylogenetic hypotheses have placed oviraptorosaurs as the sister group to therizinosaurs (for the latest iteration of this view see Turner et al. 2012) and that some therizinosaurs also have a reduced number of caudal vertebrae and possibly pygostyles (Xu et al. 2003). However, given that the basal therizinosaur *Falcarius utahensis* does not have a reduced tail or a pygostyle, these similarities between oviraptorosaurs and therizinosaurs appear to be convergent.

Functional interpretations.—Although it seems parsimonious to assume oviraptorosaurs lack a direct avian relationship, it could be that oviraptorosaurs were secondarily flightless, especially given recent findings of arboreal and potentially gliding and/or flying forms among non-avian Maniraptoriformes (Xu et al. 2002b, 2010a; Zhang et al. 2002, 2008; Xu and Zhang 2005). The reduced caudal series of birds is generally accepted as an adaptation for flight that helped to reduce excess posterior weight (Gatesy 1990a, b) and prevented the action of the power stroke from translating into kinetic tail movements. In particular, the reduction of the M. caudofemoralis was a direct loss of hind-limb locomotive musculature that likely coincided with increased emphasis and reliance on forelimb-powered flight (Persons and Currie 2012). The M. caudofemoralis of pterosaurs was similarly reduced (Persons and Currie 2012). Maryańska et al. (2002) asserted that oviraptorosaurs had greatly reduced caudal masses, a resulting center of mass positioned well anterior to the hips, and a terrestrial locomotor style similar to that of modern ground-running birds that place greater emphasis on knee-flexion than on femoral retraction. The results of the digital muscle reconstructions indicate the opposite.

Instead, the unreduced caudofemoral muscles of *Ajancingenia yanshini*, *Khaan mckennai*, and *Nomingia gobiensis*, despite the overall reduction in tail length, suggest that the mass of the M. caudofemoralis was maintained during oviraptorosaur evolution. This is not consistent with the morphology predicted by the secondarily flightless hypotheses. Our results show that there is no reason to suspect that most oviraptorosaurs diverged from the standard femoral-retraction-dominated locomotor style, or to evoke a flying ancestor as an explanation for the uniqueness of their caudal morphology.

That said, it must be pointed out that the tail of the primitive oviraptorosaur *Caudipteryx* is likely a partial exception, being far more reduced than that of other oviraptorosaurs. While this caudal reduction is very different from the deinonychosaurian condition, and *Caudipteryx* has deep anterior chevrons, the reduction in tail length is so extreme that the size of the M. caudofemoralis must have been affected (although all specimens of *Caudipteryx* are taphonomically flattened and a quantitative muscle reconstruction is impossible). As argued by Jones et al. (2000), the proportions of the hind legs of *Caudipteryx* are also consistent with greater relative emphasis on knee flexion and less emphasis on femoral retraction (but see Christiansen and Bonde [2002] for an alternative interpretation; see also Dyke and Norell [2005] who point out discrepancies in the data of Jones et al. [2000]). It does, therefore, remain a possible alternative that some or all early oviraptorosaurs diverged from an arboreal flying/gliding ancestor, which was not close to the deinonychosaurian lineage and which had only just begun caudofemoral muscle reduction, and, after becoming secondarily terrestrial, later oviraptorosaurs re-enlarged the M. caudofemoralis. The exact phylogenetic position of *Caudipteryx* is not clear, and evaluation of this highly speculative scenario must await additional fossil evidence.

Regardless, the large size of the M. caudofemoralis in most oviraptorosaurs is consistent with their previously inferred cursorial potential. However, the M. longissimus and M. ilio-ischiocaudalis control tail motion, rather than femoral retraction, and the large anterior size of both these muscles still merits functional explanation. Barsbold (1977, 1983) previously recognized the highly muscular nature of oviraptorosaur tails, and speculated that they may have been adapted for aquatic sculling. A swimming explanation is consistent with both a robust M. longissimus and M. ilio-ischiocaudalis, which are responsible for laterally swinging the tail and are large in many modern aquatic reptiles, and with the highly flexible nature of the oviraptorosaur caudal series. However, as later pointed out by Barsbold et al. (1990), the cursorial hind limbs of oviraptorosaurs are inconsistent with an aquatic lifestyle. Moreover, the reduced tail length, un-heightened neural spines, and lack of lateral compression strongly contradict the notion that oviraptorosaur tails were adapted for swimming. Additionally, the majority of oviraptorosaurs are associated with arid to semi-arid environments (Longrich et al. 2010).

An alternative explanation is that in addition to primarily facilitating effective terrestrial locomotion the tails of oviraptorosaurs were also highly specialized to serve as visual display structures. The fans of feathers preserved on the terminal tail tips of the primitive oviraptorosaurs *Caudipteryx* (Ji et al. 1998) and *Similicaudipteryx* (Xu et al. 2010b), combined with the new evidence reported here of pygostyles in advanced oviraptorosaurs, suggests that caudal feather-fans were present throughout the group.

The use of caudal plumage in intraspecific communication and especially courtship rituals is common in modern birds and has been suggested for *Confuciusornis* (Chiappe et al. 1999) and the basal dromaeosaurid *Microraptor* (Li et al. 2012). This function seems probable, as oviraptorosaurs were flightless, and it is worth noting that the tail feathers of *Caudipteryx* are known to have had contrasting bands of pigment (Ji et al. 1998). Short, muscular, and highly-flexible tails would have been well suited to support a distal pygostyle, to maneuver the tail, and to flaunt a feather fan. With a proportionately large M. longissimus and M. ilio-ischiocaudalis, oviraptorosaurs would have been capable of swinging and twisting their tails both mediolaterally and dorsoventral-

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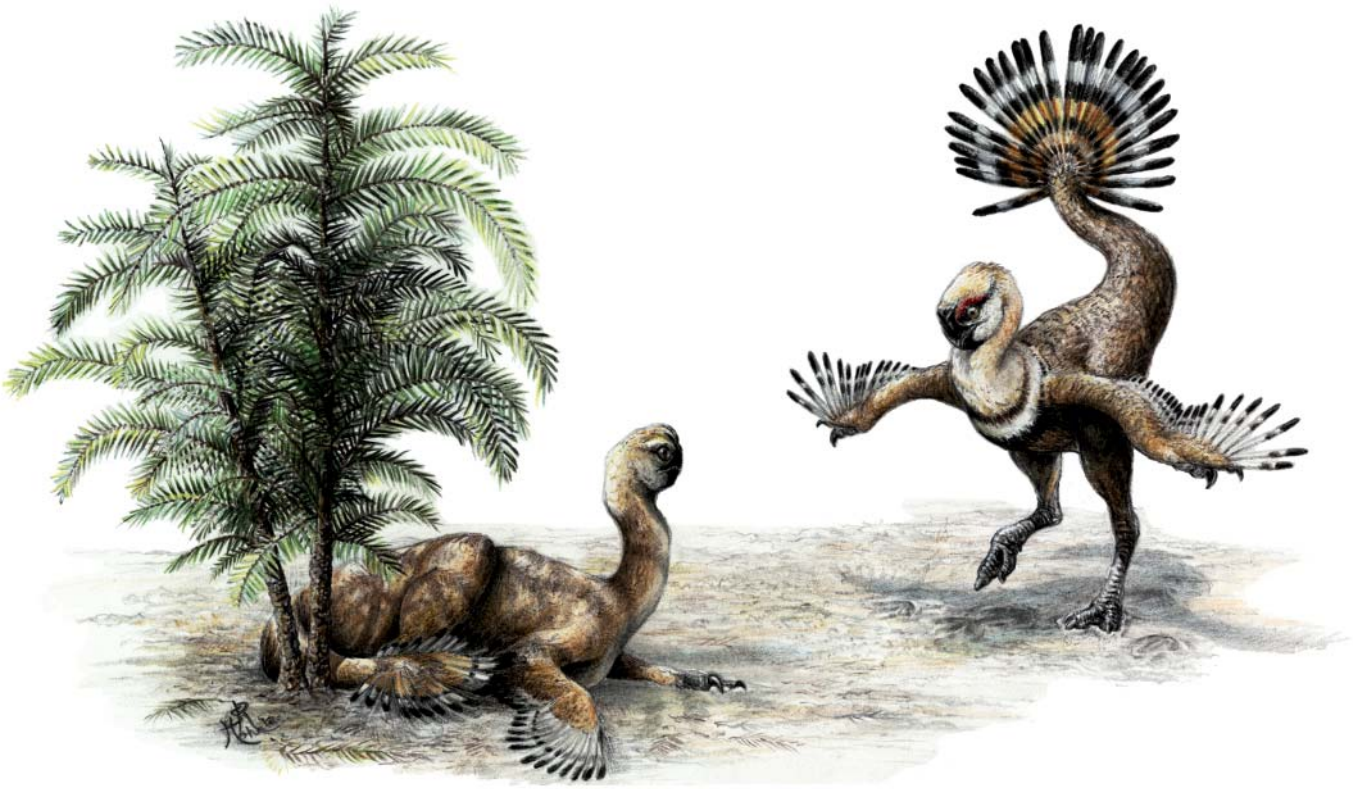


Fig. 11. Life reconstruction of *Ajancingenia yanshini*, depicting a male with a tail-feather fan displaying for an onlooking female. Original painting by Sydney Mohr.

ly with a degree of muscular dexterity beyond that of most other theropods and modern reptiles. Oviraptorosaurs would also have had the muscular control necessary to swiftly strike and hold the tail in desired sinuous or erect poses (Fig. 11).

If this functional hypothesis is true, it follows that the caudal morphology of oviraptorosaurs may prove to be sexually dimorphic, although, at present, the sample size for any oviraptorosaur species is insufficient to test this prediction.

Conclusion

Qualitative anatomical consideration and quantitative digital modeling concur that oviraptorosaurs had muscular, robust tails. Unlike the condition observed in the avian lineage, oviraptorosaurs appear to have maintained large caudofemoral tail muscles, suggesting that the anterior tail region never lost its primary function in terrestrial locomotion. Muscles responsible for controlling tail motion were proportionately larger in oviraptorosaurs than in other theropods, and oviraptorosaur tails were also exceptionally flexible. A terminal tail-feather fan appears to have been a common feature among oviraptorosaurs, and the muscular and flexible tails would have permitted these fans to be flaunted in dynamic displays. This new functional interpretation, combined with the prevalence of cranial crests among the oviraptorosaurs, suggests the group had a propensity for visual exhibition.

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