A NEW CAENAGNATHID (DINOSAURIA: OVISRATOROSAURIA) FROM THE HORSESHOE CANYON FORMATION OF ALBERTA, CANADA, AND A REEVALUATION OF THE RELATIONSHIPS OF CAENAGNATHIDAE

GREGORY F. FUNSTON* and PHILIP J. CURRIE
Department of Biological Sciences, CW 405, Biological Sciences Building, University of Alberta, Edmonton, Alberta, Canada T6G 2E9, funston@ualberta.ca; pjcurrie@ualberta.ca

ABSTRACT—Our understanding of caenagnathids has benefited from recent discoveries, including nearly complete skeletons from the Hell Creek Formation of Montana. However, their phylogenetic relationships remain unclear. A new specimen from the Horseshoe Canyon Formation of Alberta has implications for the phylogeny and paleobiology of these creatures. The partial skeleton is articulated and includes a mandible, a full cervical and dorsal series of vertebrae, a right pectoral girdle and arm, a sternum, gastralia, a partial ilium, and a partial hind limb. The mandible is edentulous and the articular ridge is intermediate in form between Caenagnathus collinsi and Chirostenotes pergracilis. The neck is long and composed of at least 11 well-pneumatized cervical vertebrae with fused cervical ribs. The dorsal ribs have finger-like uncinate processes dissimilar in shape to those of other oviraptorosaurs. The pectoral girdle is large and typically maniraptoran, except that the glenoid of the scapulocoracoid faces laterally instead of posteroventrally. The arm is well muscled and can be interpreted to have been a pennibrachium, as indicated by ulnar papillae on the ulna. The manus is characterized by a short first metacarpal but an elongate phalanx I-1 and oviraptorid-like phalangeal proportions in the second digit. These and other features indicate that the specimen represents a new taxon, Apatoraptor pennatus, gen. et sp. nov. Phylogenetic analysis resolves the complicated relationships of Caenagnathidae and allows the evolution of display features to be traced throughout Oviraptorosauria.

http://zoobank.org/urn:lsid:zoobank.org:pub:122957D7-F65F-4A2C-86AF-386AE8A9F2C4

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Funston, G. F., and P. J. Currie. 2016. A new caenagnathid (Dinosauria: Oviraptorosauria) from the Horseshoe Canyon Formation of Alberta, Canada, and a reevaluation of the relationships of Caenagnathidae. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2016.1160910.

INTRODUCTION

Oviraptorosauria is a clade of maniraptoran theropods from the Cretaceous of Asia and North America. Asian forms are known from numerous complete skeletons, but despite an equally long history of discovery (Gilmore, 1924; Osborn, 1924), North American forms are less well known. Gilmore (1924) described a set of elongate hands from the Upper Cretaceous (Campanian) Dinosaur Park Formation and named them Chirostenotes pergracilis. Subsequent work by C. M. Sternberg (1932, 1934), Parks (1933), and R. M. Sternberg (1940) described feet and a mandible, but only much later would this material be united within Oviraptorosauria as Caenagnathidae (Osmolska, 1976, 1981; Currie, 1989). A partial skeleton (Currie and Russell, 1988) revealed more of the anatomy, and a plethora of mandibular material (Currie et al., 1993) highlighted the diversity within the group. Another partial skeleton (ROM 43250), collected by G. E. Lindblad in 1923 from the Upper Cretaceous (Campanian-Maastrichtian) Horseshoe Canyon Formation and described by Sues (1997), cemented the monophyly of Caenagnathidae but stimulated debate about which specimens were conspecific.

In recent years, a number of new discoveries have clarified our understanding of the anatomy of caenagnathids. Anzu wyliei (Lamanna et al., 2014), represented by three reasonably complete skeletons from the Upper Cretaceous (Maastrichtian) Hell Creek Formation, has a prominent cranial crest and a short tail with modified pygostyle-like distal vertebrae. A frontal of Elmisaurus rarus, a caenagnathid from Mongolia, indicates that this taxon also had a cranial crest, and additional postcranial material improves our knowledge of its anatomy (Currie et al., 2016). More material referable to Leptorhynchos elegans from the Dinosaur Park Formation of Alberta and the Frenchman Formation of Saskatchewan shows close ties to Elmisaurus rarus from Mongolia (Funston et al., 2016). Large isolated postcranial material from the Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, can be referred to Caenagnathus collinsi, based on demonstrably larger size and a number of morphological features that distinguish it from Chirostenotes pergracilis and Leptorhynchos elegans (Funston et al., 2015).

Despite these advances, the taxonomy and phylogenetics of caenagnathids have been debated without resolution, in part because of fragmentary and non-overlapping specimens. Currie (1989) separated material with fused tarsometatarsi and referred it to Elmisaurus elegans based on similarities to the Mongolian Elmisaurus rarus. Sues (1997) argued that material of Elmisaurus elegans was congeneric with Chirostenotes pergracilis and referred ROM 43250 to the latter. Sullivan et al. (2011)
suggested that ROM 43250 was sufficiently distinct to merit its own genus, *Epichirostenotes*, and named *Ojoraptorsaurus* for pubic material from New Mexico. Longrich et al. (2013) grouped mandibles by size and proposed a new genus, *Leptorhynchos*, for material from Texas and Alberta. Within this genus, they erected *Leptorhynchos elegans* for the fused metatarsi referred by Currie (1989) to *Elmisaurus* and small, upturned mandibles from the Dinosaur Park Formation (Longrich et al., 2013). Lamanna et al. (2014) countered this, arguing that without overlapping material to unite mandibles and metatarsi in *Leptorhynchos elegans*, it was more conservative to apply a taxonomic approach using only species with unambiguous mandibular material.

In 1993, an articulated partial skeleton (Fig. 1) was recovered from the Horseshoe Canyon Formation near Drumheller, Alberta (Fig. 2). At that point, the Horseshoe Canyon Formation had produced little noteworthy caenagnathid material, with the exception of ROM 43250, the holotype of *Epichirostenotes curriei*. Preparation on TMP 1993.051.0001 did not begin until 2002, because it was thought to represent a relatively common ornithomimid. When it was determined that no skull was present, the jacket was recapped. In 2008, the jacket was opened again and prepared. After uncovering the mandible, manual unguals, and uncinate processes, the preparators realized that the specimen was not an ornithomimid, but a caenagnathid (Tanke, pers. comm., 2013). Although originally suggested to be the coeval *Epichirostenotes* (Eberth et al., 2013), further examination showed that the specimen represents a new taxon. Computed tomography (CT) scans (available online at http://dx.doi.org/10.6084/m9.figshare.1522639) allow access to the unprepared data and helps resolve a number of taxonomic issues in the Caenagnathidae.

**Institutional Abbreviations—CMN**, Canadian Museum of Nature, Ottawa, Ontario; **ROM**, Royal Ontario Museum, Toronto, Ontario; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; **UAMZ**, University of Alberta Museum of Zoology, Edmonton, Alberta.

**SYSTEMATIC PALEONTOLOGY**

**DINOSAURIA** Owen, 1842  
**SAURISCHIA** Seeley, 1888  
**THEROPODA** Marsh, 1881  
**COELUROSAURIA** Huene, 1914  
**MANIRAPTORA** Gauthier, 1986  
**OVIRAPTOROSAURIA** Barsbold, 1976  
**CAENAGNATHIDAE** Sternberg, 1940

**APATORAPTOR PENNATUS**, gen. et sp. nov.  
(Figs. 1, 3–10, 13)

**Holotype**—TMP 1993.051.0001, articulated partial skeleton with right palatine, nearly complete left and fragmentary right mandibles, left and fragmentary right ceratobranchials, axis and complete postaxial cervical series, complete dorsal series, partial left and complete right pectoral girdle, right sternal plate, right forelimb, partial right ilium, partial right femur, partial right tibia, and partial right fibula.

**Locality and Horizon**—Recovered 3 km west of the Royal Tyrrell Museum of Palaeontology (UTM 12U 374600, 5705950), Horsethief Member (just above coal 7) of the Horseshoe Canyon Formation (sensu Eberth and Braman, 2012).

**Etymology**—*Apatoraptor pennatus*. ‘*Apato*’—from Apatosaurus, an evil spirit released from Pandora’s Box in Greek mythology, used as a personification of deceit, and ‘*raptor*’—from Latin (thief). The intended gender of the name is masculine. The name is appropriate because TMP 1993.051.0001 deceived the collectors, who believed that it was an ornithomimid. The specific name, *pennatus* (Latin: feathered, winged), refers to the feathered or ‘winged’ appearance of the arms. The name means ‘deceptive feathered thief.’

**Diagnosis**—Small elmisaur theropod diagnosed by the following autapomorphies: ventral flange of angular underlying posteroventral ramus of the dentary; anterior constriction of external mandibular fenestra by posteroventral ramus of the dentary; medial fossa anterior to articular region of mandible; articular region of mandible with low articular ridge offset from dorsal margin of articular-surangular-coronoid complex; metacarpal I less than half as long as metacarpal II; manual I-1 longest phalanx of hand; and manual phalanx II-1 longer than II-2.

Also distinguished by the unique combination of the following characters: thin retroarticular process of mandible oriented posterolaterally; cervical vertebrae with infradiaphyseal fossae in addition to infrapre- and infrapostzygapophyseal fossae; fusion of cervical ribs to vertebrae; finger-like uncinate processes on dorsal ribs; glenoëd of scapulocoracoid directed laterally; enlarged coracoid with relatively straight posteroventral process; manual ungual I-2 lacking transverse groove between proximal articular surface and flexor tubercle; anterior margin of preacetabular portion of ilium rounded; and tibia with expanded cnemial crest.

**DESCRIPTION**

**Cranial Skeleton**

**Palatine**—A right palatine (Fig. 3) was revealed by CT scans, situated below the ceratobranchial and medial to the mandible. The palatine fragment is a quadrangular plate of bone about 25 mm long, with a long anterior process that contacted the maxilla and a long posterior pterygoid process. The bone is overall similar in shape to that of *Epichirostenotes curriei* (e.g., Sues, 1997), although the vomerine process is longer, and the anteromedial process is less offset from the body of the palatine.

**Dentary**—The left mandible (Fig. 4) is approximately 165 mm long (Table 1) and is preserved with the ventral and lateral sides exposed. The left dentary is relatively long and shallow, and the lateral surface has a deep mandibular fossa perforated by a pneumatopore. The postero dorsal ramus of the dentary contacts the articular-surangular-coronoid complex in an interlocking dentary-surangular suture. In *Apatoraptor pennatus*, the dentary-surangular suture (Fig. 3C) does not extend posteriorly to the coronoid process, whereas it does in *Anzu wyliei* (CM 78000), *Caenagnathus collinsi* (CMN 8776), and *Chirostenotes pergracilis* (TMP 2001.012.0012). The posteroventral ramus of the dentary contacts the angular and forms the ventral border of the external mandibular fenestra.

**Angular**—The angular is medial to the posteroventral ramus of the dentary, but it has a ventral flange underlying the posteroventral ramus of the dentary (Fig. 4). This ventral flange is unique to *Apatoraptor pennatus*. Together, the angular and dentary bow ventrally beneath the external mandibular fenestra, similar to *Anzu wyliei* (CM 78000) and *Chirostenotes pergracilis* (TMP 2001.012.0012), but unlike *Caenagnathus collinsi* (CMN 8776).

**Prearticular**—The prearticular (Fig. 3C) is a thin, plate-like bone medial to the angular and can be seen in CT scans. It becomes transversely thick posteriorly where it meets the articular and forms the medial part of the retroarticular process.

**Articular-Surangular-Coronoid (ASC) Complex**—The ASC complex is fused without a suture, as in other caenagnathids (Currie et al., 1993). There is a lateral flange on the surangular at the dorsal margin of the external mandibular fenestra, which extends from the coronoid process posteriorly to the end of the external mandibular fenestra. In CT scans it can be seen that where the ASC complex meets the angular just anterior to the articular region, there is a deep fossa on the medial surface of

**Funston and Currie—A new caenagnathid from Alberta (e1160910-2)**
the mandible (Fig. 3C). The articular region was revealed by CT scans (Fig. 4C). There is a convex articular ridge, as in all caenagnathids, and well-developed medial and lateral glenoids. The articular ridge is not as well developed as in *Chirostenotes per gracilis* (TMP 2001.012.0012) (Funston and Currie, 2014) and is more similar to that of *Caenagnathus collinsi*; however, it is more offset from the dorsal margin of the surangular than it is in the latter genus. The retroarticular process is formed of the
articulart laterally and the prearticular medially. It is directed posterolaterally and has a narrow hatchet-shaped distal end in dorsal view. The external mandibular fenestra is anteroposteriorly elongate (51 mm), as in other caenagnathids, but it is constricted anteriorly by the posteroventral ramus of the dentary.

Hyoid—The left ceratobranchial of the hyoid apparatus (Fig. 4A, B) is thin and rod-like, with slightly expanded anterior and posterior ends. It is 68.4 mm long, roughly 41% the length of the mandible; the maximum shaft diameter (2.0 mm) is 3% of its length. Parts of the hyoid apparatus have been previously reported in three

---

**FIGURE 2.** Locality information for *Apatoraptor pennatus* (TMP 1993.051.0001). **A**, stratigraphic section of the Horseshoe Canyon Formation, modified from Eberth and Braman (2012). Star indicates stratigraphic level of TMP 1993.051.0001; **B**, region surrounding Midland Provincial Park, Alberta. Pointer indicates locality where TMP 1993.051.0001 was recovered.
Oviraptorosaurs: *Caudipteryx zoui*, *Citipati osmolskae*, and *Khaan mckennai* (Ji et al., 1998; Clark et al., 2002; Balanoff and Norell, 2012). In *Caudipteryx zoui* and *Khaan mckennai*, the ceratobranchial is straight, but in *Citipati osmolskae* it bows laterally. The ceratobranchial (Table 2) of TMP 1993.051.0001 is straight, but appears to be relatively longer (41%) compared with the mandible than in *Caudipteryx zoui* (~20%), and more gracile compared with its length than in *Khaan mckennai*, where the ceratobranchial is more robust and has a more pronounced anterior expansion. There are no muscle scars on the ceratobranchial of TMP 1993.051.0001, so no inferences about the strength of the lingual apparatus can be made.

**Axial Skeleton**

**Vertebrae**—There would have been 12 cervical vertebrae in life (Figs. 1, 5), but only 11 are preserved. These 11 cervical vertebrae include the axis but not the atlas, which is not preserved, and exclude the cervicodorsal, of which at least two are present. The neck is 680 mm long, and the longest centrum in the neck is the ninth cervical, which is 61.5 mm long. The centra of the anterior cervical vertebrae are elongate, but the aspect ratio (length: height) decreases posteriorly. On the lateral side of the centrum, there is a pneumatic depression. The cervical ribs obscure the anterolateral parts of the centra, but CT scans reveal the presence of the pleurocoels described by Sues (1997) and Lamanna et al. (2014). Unlike in *Caenagnathus martinsoni* (e.g., Sues and Averianov, 2015), there are no pleurocoels on the lateral surfaces of the centra posterior to the parapophyses. As in *Epichirostenotes curriei* (e.g., Sues, 1997), the parapophyses extend anteroventrally and a lateral ridge extends on the ventral surface of the centrum posteriorly from each parapophysis. The articular surfaces of the anterior cervical vertebrae face anteroventrally. Posterior cervical vertebrae have anterior articular surfaces that are perpendicular to the longitudinal axis of each vertebra. The neurocentral sutures are closed, as in *Epichirostenotes curriei*, suggesting that both specimens represent relatively mature individuals (Brochu, 1996; Sues, 1997). There are three pneumatic fossae delimited by the laminae of the neural arches: infraprezygapophyseal, infrapostzygapophyseal, and infradiapophyseal (Fig. 5C). An infradiapophyseal fossa is not present in ROM 43250, but is present in *Elmisaurus rarus* from Mongolia (Currie et al., in press). The infraprezygapophyseal fossa is deep in TMP 1993.051.0001, unlike ROM 43250. The transverse processes of the anterior cervical vertebrae are small, in contrast to...
with the large, wing-like transverse processes of ROM 43250. The neural spines are low and anteroposteriorly elongate, as in most oviraptorosaurs. Starting with the third or fourth postaxial vertebra, the posterior cervical ribs are fused to the centra as in *Anzu wyliei*, *Avimimus portentosus*, and *Khaan mckennai* (Kurzanov, 1981; Balanoff and Norell, 2012; Lamanna et al., 2014), but unlike ROM 43250 (Sues, 1997).

There are nine dorsal vertebrae, including the cervicodorsals (Fig. 1). The dorsal vertebrae of TMP 1993.051.0001 are not exposed and were not accessible through CT scanning, because the jacket was too wide for the CT scanner gantry. This prevents a proper description, except for the first cervicodorsal and the neural spines of the posterior dorsals. The first cervicodorsal has a reduced rib and a prominent hypapophysis. Unlike *Anzu wyliei*, the hypapophyses are triangular in lateral view, not rounded. The transverse process and the neural spine of the first cervicodorsal are triangular in lateral view and the neural spine is dorsoventrally tall. The infraprezygapophyseal fossa is deep. The neural spines of the posterior vertebrae are quadrangular in shape and become progressively taller posteriorly.

**Ribs**—There are nine dorsal ribs per side (Fig. 1) and at least three sets of sternal ribs. There is a foramen piercing the lamina that connects the capitulum and tuberculum in each rib, suggesting that the ribs are pneumatized. On dorsal ribs 5, 6, and 7, there are finger-like uncinate processes (Fig. 1) that are attached but not fused to the posterior surfaces of the rib shafts. These uncinate processes are slightly wider at the base, curve dorsally, and taper to points distally. Uncinate processes have been reported in *Caudipteryx* (Zhou and Wang, 2000) and *Citipati* (Clark et al., 1999), where they are wide and plate-like proximally and taper distally into rounded ends. The uncinate processes of *Apatoraptor pennatus* are unlike those of *Caudipteryx* and *Citipati* and more similar in shape to...
TABLE 2. Proportions of the ceratobranchial of the hyoid apparatus in oviraptorosaurs.

| Taxon             | Mandible length (mm) | Ceratobranchial length (mm) | Percent (mean) |
|-------------------|----------------------|----------------------------|----------------|
| Apatoraptor pennatus | 165c                | 68.4                       | 41%            |
| TMP 1993.051.0001  |                      |                            |                |
| Caudipteryx zoai    | 75                   | 15c                        | 20%            |
| NGMC 97-9-A         |                      |                            |                |
| Citipati osmolskiae | 151                  | 74                         | 49%            |
| IGM 100/978        |                      |                            |                |
| Conchoraptor sp.    | 40.0                 |                            | 108            |
| UALVP 49393        | 139                  | 81                         | 37%            |
| UALVP 49394        | 99.8                 | 44                         |                |
| Khaan mckennai      | 108                  | 40                         |                |
| IGM 100/1127       |                      |                            |                |

e, estimated measurement

those of Velociraptor mongoliensis (Norell and Makovicky, 1999).

Appendicular Skeleton

Pectoral Girdle—The coracoid (Fig. 6) of Apatoraptor pennatus is relatively larger (96 mm across the widest breadth) than that of Chirostenotes pergracilis (66 mm), despite the similarly sized manus. The manus of TMP 1993.051.0001 and TMP 1979.020.0001 are close in length, based on the length of digit II excluding the metacarpal (203 vs. 213 mm, respectively). The posteroventral process of the coracoid is large, and its posterior margin is strongly concave, but it is straighter than that of Chirostenotes pergracilis. The coracoid tubercle is relatively closer to the glenoid in Apatoraptor pennatus than in Chirostenotes pergracilis, which would shorten the lever arm for adduction of the humerus. The glenoid faces laterally, as in Elmisaurs rarus, rather than posteroventrally as in most theropods. The two bones of the scapulocoracoid are unfused but tightly sutured. The right scapula (Fig. 6) is long (215 mm in a straight line to the glenoid) and strap-like (22 mm midshaft diameter), without a pronounced distal expansion. The acromion process is directed dorsolaterally but mostly remains obscured by matrix.

Humerus—The head of the humerus (Fig. 8) is rectangular and has a poorly developed articulation similar to those of Anzu wyliei and Khaan mckennai (Lamanna et al., 2014). The deltopectoral crest is expanded to one-third the length of the humerus (206 mm), and occupies more than one-third the length of the humeral shaft. This is similar to Falcarius utahensis and Khaan mckennai, in which the deltopectoral crest is expanded to one-third the length of the humerus. In therizinosaurs, expansion of the deltopectoral crest compared with basal coelurosaur is tied to greater tensile loads in adduction of the arm (Zanno, 2006). As in other maniraptorans, the humerus twists midshaft, and as in Anzu wyliei (Lamanna et al., 2014), the humerus bows laterally.

Ulna and Radius—Near the proximal end, the shaft of the ulna (Fig. 8) is straight, but distally it bows posteriorly for most of its length (167 mm). The olecranon and coronoid processes are weakly developed and form a shallow trochlear notch for the humerus. Our CT scanning revealed seven small, evenly spaced depressions on the posterolateral surface of the ulna (Fig. 8C). The position and size of these depressions is consistent with ulnar papillae (quill marks) in Velociraptor mongoliensis, Ornithomimus edmontonicus,

FIGURE 5. Apatoraptor pennatus (TMP 1993.051.0001). A, cervical series in right lateral view; B, illustration of cervical series in right lateral view; C, detail of cervical vertebra cervical 10 in right lateral view; D, illustration of cervical 10 in right lateral view. Abbreviations: ?Ax, possible axis; C3-C11, cervical vertebrae C3 through C11; cr, cervical rib; crtb, ceratobranchial; for, foramen; infdpzf, infradiaphysal fossa; infozf, infrapostzygapophyseal fossa; mand, mandible.
Conchavenator corcovatus (Turner et al., 2007; Ortega et al., 2010; Zelenitsky et al., 2012), and the modern Great Blue Heron Ardea herodius (UAMZ B6969). On the exposed (flexor) side of the ulna, there are four small, donut-shaped depressions that are likely ulnar papillae from the anconal series (sensu Edington and Miller, 1942). The depressed donut shape of these marks is nearly identical to those described in the male White Stork (Ciconia alba) by Edington and Miller (1942). Based on the spacing between the ulnar papillae (5 mm) in Apatoraptor and the proportion of the ulna occupied by secondary feathers in modern birds, there would be room for about 16–18 secondary feathers in Apatoraptor. This is consistent with its relatively large size, and the presence of a similar number in modern birds with similarly sized ulnae. Based on ulnar measurements from Wang et al. (2011), these include Bubo scandiaca, with a 169 mm ulna and 16 secondaries (Solheim, 2012); Ardea purpurea with a 159 mm ulna and 16 secondaries (G.F., pers. observ.); Bubo bubo with a 183 mm ulna and 15–16 secondaries (Solheim, 2011); Branta canadensis with a 161 mm ulna and 16 secondaries (G.F., pers. observ.); and Larus marinus with a 170 mm ulna and 24 secondaries (Ingolfsson, 1970).

The radius (Fig. 8) is straighter than the ulna, but has a slight anterior curve at its midpoint. The proximal end of the radius is square in outline, and the distal end is expanded, with a large medial flange for the ulnar notch, a small styloid process, and a concave facet for the carpals. The radius is narrower in diameter than the ulna but is equal to it in length.

Carpals and Manus—The preservation of the carpal region (Fig. 9) is poor, and neither of the two potential carpals can be positively identified. There may be a semilunate carpal overlying the proximal ends of the first and second metacarpals. There may also be a radiale, but this could be the compressed proximal end of metacarpal I. In Hagryphus giganteus Zanno and Sampson, 2005, four carpals are preserved—the semilunate, radiale, and two smaller carpals (likely homologous with the intermedium and ulnare). It is likely that Apatoraptor pennatus possessed all four of these carpals in life, but they have not been preserved.

All of the phalanges of the manus (Fig. 9), except ungual III-4, are preserved to some degree. Digit II (metacarpal II plus phalanges II-1, II-2, and II-3) is the longest digit, and digit III is longer than digit I, as in other caenagnathids (Fig. 9C). The second metacarpal is the longest (105 mm) and most robust of the three, and metacarpal III (75 mm) is longer than metacarpal I (52 mm), but more gracile (Table 3). Unlike the condition in other caenagnathids, metacarpal I is less than half the length of metacarpal II. Digits I and II are complete, including unguals,
but digit III is missing most of phalanx III-1, and the ungual (III-4). The phalanges are elongate and gracile, as in all caenagnathids, and the unguals are long and sharply curved. Phalanx I-1 is the longest phalanx of the hand (82.4 mm) and bows dorsally at the midshaft. This is unlike all other caenagnathids, in which phalanx I-1 is shorter than or subequal to phalanx II-1. Phalanx I-2 has a pronounced flexor tubercle and proximodorsal lip, both characteristics of caenagnathids. Phalanx I-2 measures 39 mm in a straight line from the middle of the proximal articular surface to the tip, and 47 mm around the outside curve. This ungual is similar in shape to those of *Elmisaurus rarus* (Osmólska, 1981; Currie et al., 2016), although it is shorter proximodistally (57 mm) than I-2, but is less strongly curved (65.5 mm around the outside curve). There is a well-developed proximodorsal lip, but the flexor tubercle is not as pronounced as in I-2. Most of phalanx III-1 is missing, but its distal end is preserved near the proximal end of III-2. Phalanx III-2 is complete, and much smaller than phalanges of the other digits (32 mm in length). Phalanx III-3 is at least as long as III-2, but the distal end is absent. Ungual III-4 is not present, but in other caenagnathids this ungual is similar in morphology to I-2 but smaller (Gilmore, 1924; Currie and Russell, 1988).

**Ilium**—Only the preacetabular blade of the ilium (Fig. 1) is preserved. The anterior edge of the preacetabular blade is dorsoventrally tall, smooth, and rounded. The anteroventral portion of the preacetabular blade has been broken so that it lies below the lateral surface of the ilium. This suggests that there was at least a shallow cuppedicus fossa, as in *Nomingia gobiensis* (Barsbold et al., 2000). From the location of the break, it is clear that the anteroventral portion of the preacetabular blade extended...
ventrally past the cuppedicus fossa and was possibly level with the pubic peduncle. The shape of the anteroventral process of the preacetabular blade cannot be determined, but in *Anzu wyliei* Lamanna et al., 2014 and probably *Chirostenotes pergracilis* (Currie and Russell, 1988), the anterior margin of the preacetabular blade is straight. This is also true for *Khaan mckennai* (e.g., Balanoff and Norell, 2012); however, *Ingenia yanshini* (MPC-D 102/11, MPC-D 102/12) and *Nomingia gobiensis* Barsbold et al., 2000 have downturned, rounded preacetabular blades.

**Femur**—The exposed portion of the femur (Fig. 10) is 220 mm long, with an anteroposterior midshaft diameter of 31.8 mm. Using other oviraptorosaurs for comparison, femoral length can be estimated based on humerus length and femoral midshaft diameter. In both cases, these produce estimates of 345 mm in TMP 1993.051.0001. *Chirostenotes pergracilis* (TMP 1979.020.0001) has a complete femur 304 mm long, relatively shorter than *Apatoraptor pennatus*, despite similarly sized manus. A ‘V’-shaped ridge on the posterolateral surface of the shaft of the femur in TMP 1993.051.0001 represents the insertion of M. caudofemoralis.

**Tibia and Fibula**—The tibia (Fig. 10) has an anteriorly enlarged anterior cnemial crest for anchoring the quadriceps femoralis, like in *Anzu wyliei* Lamanna et al., 2014 and *Elmisaurus rarus* (e.g., Currie et al., 2016). In both of those taxa, the tibia is elongate, suggesting that most caenagnathids were relatively fast runners. The cnemial crest of *Apatoraptor pennatus* extends at least 35 mm anterior to the fibular condyle, more than that of *Elmisaurus rarus* (25 mm; MPC-D 102/7), despite being similar in size.

The exposed portion of the fibula (Fig. 10) is 54 mm long proximodistally and covers the lateral surface of the tibia. At its proximal end, the fibula is 45.7 mm wide anteroposteriorly, and it tapers distally to 21.2 mm wide. The presence of a medial fossa, present in other caenagnathids (but not oviraptorids), cannot be determined without disarticulating the specimen, but the convex lateral surface of the proximal end is consistent with a medial fossa.

**DISCUSSION**

**Comparison with Other Caenagnathid Taxa**

*Epichirostenotes currii*—The close temporal and geographic proximity of *Apatoraptor* and *Epichirostenotes* necessitates a comparison of the two taxa. Despite relatively little overlapping material between ROM 43250 and TMP 1993.051.0001, some
important observations can be made. Comparison of the preserved cervical vertebrae of ROM 43250 with the complete axial series of TMP 1993.051.0001 allows their positions to be determined. The anterior-most cervical of ROM 43250 is distinguished by greatly enlarged posterolaterally directed lateral processes and an anteroposteriorly short centrum with inclined articular faces. The neural spine is a short triangular process that does not extend as far dorsally as the prezygapophyses, which are large, finger-like, and directed anterodorsally. The postzygapophyses are small, and their articular facets are nearly vertical. The centrum has a sigmoidal ventral margin and is pierced by a single pneumatic foramen just ventral to the large transverse process on the left side. The cervical ribs are reduced and fused to the centrum and transverse processes, producing a single wing-like lateral process on either side of the vertebra. Based on its size relative to the other cervicals and the short, sigmoidal centrum, it is likely that this vertebra represents the anterior-most postaxial cervical (C3). Two other preserved cervicals of ROM 43250 are less distinctive, and it is therefore more difficult to determine their exact positions. Based on the height-to-length ratio of the centra, they appear to represent postaxial cervicals 4 and 5 (i.e., C6 and C7). This is supported by the large, wide transverse processes that descend close to the parapophyses, the low neural spines, and the flat ventral margins. The presence of

| Measurement (mm) | Apatoraptor pennatus TMP 1993.051.0001 | Chirostenotes pergracilis CMN 2367 | Chirostenotes pergracilis TMP 1979.020.0001 | Elmisaurus rarus MgD-I/98 | Hagryphus giganteus UMNH VP 12756 |
|-----------------|--------------------------------------|----------------------------------|------------------------------------------|--------------------------|----------------------------------|
| Metacarpal I, length | 52 | ? | ? | 43.4 | 66 |
| Metacarpal II, length | 105 | ? | ? | ? | 122 |
| Metacarpal III, length | 75 | ? | ? | ? | 87 |
| Phalanx I-1, length | 82.4 | 62.1 | 65.4 | 62.6 | 87 |
| Ungual I-2, length | 50 | 56.8 | 48e | 62 | 94 |
| Phalanx II-1, length | 74 | 63.5 | 71.9 | 64 | 95 |
| Phalanx II-2, length | 68.5 | 67.9 | 75.8 | 62 | 99 |
| Ungual II-3, length | 70 | 73.4 | 83 | ? | ? |
| Phalanx III-1, length | ? | ? | ? | ? | 29.7 |
| Phalanx III-2, length | 32 | ? | 30.3 | 27 | 45 |
| Phalanx III-3, length | >32 | 44 | 39.3 | 40.2 | 60 |
| Ungual III-4, length | ? | ? | ? | ? | ? |

*e*, estimated measurement

**FIGURE 10.** Apatoraptor pennatus (TMP 1993.051.0001). **A**, right femur, tibia, and fibula in right lateral view; **B**, illustration of right femur, tibia, and fibula in right lateral view. Dashed line indicates anterior margin of fibula. **Abbreviations:** cn, cnemial crest; Ifr, lateral femoral ridge.
laminae connecting the transverse processes to the postzygapophyses—absent in the posterior cervical vertebrae of Apatoraptor pennatus—is also evidence that these vertebrae are from the anterior part of the neck. The largest and best preserved cervical of ROM 43250 is probably more posterior than the other vertebrae, as noted by Sues (1997). It is likely the sixth postaxial vertebra (C8), but could be from further posterior. Its similarity in size (85 mm ventral length) compared with C7 (81 mm in ventral length) suggests that the two vertebrae are either consecutive in the cervical series or separated by only a single vertebra.

With the approximate positions of the cervical vertebrae in ROM 43250, better comparisons can be drawn between Apatoraptor pennatus and Epichirostenotes curriei. The first postaxial vertebra of Apatoraptor has unfused cervical ribs, as do most oviraptorosaurs, and lacks the wing-like transverse processes of Epichirostenotes. The laminae connecting the neural spine to the transverse processes of C6 and C7 are not as well developed in Apatoraptor as in Epichirostenotes, especially in their posterior extent. The sixth cervical of Epichirostenotes has a lamina that connects the transverse process to the postzygapophysis, which appears to be absent in Apatoraptor. In ventral view, the parapophyses of Apatoraptor, especially on C6 and C7, extend much further anteriorly and are separated by a deeper depression than in Epichirostenotes. The ambiguous C8 of Epichirostenotes has a much more dorsally displaced transverse process, indicating that the cervical rib in this position has a larger dorsal process than in Apatoraptor. Alternatively, this could be evidence that this cervical is in fact from further posterior. In any case, the lack of infra-diapophyseal fossae on this vertebra distinguishes it from Apatoraptor, in which all vertebrae posterior to C4 have infra-diapophyseal fossae.

Comparisons can also be made between the ribs of Apatoraptor pennatus and Epichirostenotes curriei. In Apatoraptor, the tubercula of the ribs decrease in size posteriorly, as does the degree of proximal expansion of the shaft. The preserved dorsal rib of Epichirostenotes has a large tuberculum and a proximally expanded shaft, which indicates, as suggested by Sues (1997), that it comes from the mid-dorsum. In Apatoraptor, all but the posterior three ribs have a lamina of bone that connects the tuberculum to the capitulum and encloses a pneumatic opening. Both the opening and the lamina appear to be absent in Epichirostenotes, as are the uncinate processes that mark the ribs of Apatoraptor pennatus. However, with only a single complete rib preserved from Epichirostenotes, the absence of these structures is uncertain.

Based on the lengths of the seventh cervical vertebrae of ROM 43250 (81 mm) and TMP 1993.051.0001 (53.2 mm), Epichirostenotes would have been 52% larger than Apatoraptor. Both specimens have closed neurocentral sutures in the cervical vertebrae, which tentatively indicates that they represent relatively mature individuals (Brochu, 1996). The obliteration of sutures in the braincase in ROM 43250 and the fusion of cervical ribs to the centra in TMP 1993.051.0001 support this assertion.

Other Caenagnathids—Apatoraptor pennatus has several features that distinguish it from all other known caenagnathid species. The angular has a ventral flange that underlies the posteroventral ramus of the dentary, which, itself, constricts the external mandibular fenestra anteriorly. The dentary-surangular suture does not extend posteriorly to the coronoid process, which is unlike all other known mandibles. Apatoraptor differs from Anzu in several features of the postcranium. Apatoraptor lacks the foramen that pierces the postero-lateral region of the sternum in Anzu, and also lacks the fusion between the scapula and the coracoid. Phalanx II-2 of Apatoraptor lacks the distinctive ventral groove of Anzu, and the unguals of Apatoraptor do not have a transverse groove between the flexor tubercle and the articular surface. In Apatoraptor pennatus, manual phalanx II-2 is distinctly shorter in length than I-1 and I-1, which contrasts Chirostenotes pergracilis, and phalanx I-1 is the longest of the hand, unlike all other caenagnathids. Apatoraptor pennatus is similar to Elmisaurus rarus in the presence of the infradiapophyseal fossa in the cervical vertebrae, the lateral orientation of the glenoid of the scapulocoracoid, and the expanded cnemial crest of the tibia. Based on these features and the close relationship of Elmisaurus and Leptorhynchos (Currie et al., 2016; Funston et al., 2016), Apatoraptor, Elmisaurus, and Leptorhynchos can be grouped into an informal ‘elmisaur’ clade. This is supported by the suite of unique mandibular and manual features in Apatoraptor, which, although not known unambiguously in other elmisaurids, are dissimilar to other caenagnathids. Apatoraptor pennatus is the first record of an elmisaur in the Horseshoe Canyon Formation and fills a stratigraphic gap in the elmisaur fossil record. The larger size of Epichirostenotes suggests that, like other elmisaurids, Apatoraptor pennatus can be distinguished from contemporaneous caenagnathids by its smaller size at maturity. Elliptical regression estimate (ELLR-anteposterior) of femoral circumference from Bradley et al. (2015) produces a circumference estimate of 107.1 mm for the femur of Apatoraptor. The body mass of Apatoraptor can be estimated using the technique of Campione et al. (2014), where \( \log_{10}(BM_{\text{biped}}) = 2.754 \times \log_{10}(C_{\text{tibia}}) - 0.683 \). This produces an estimate of 80.8 kg (lower limit: 60.6 kg; upper limit: 101.0 kg) for Apatoraptor.

**Mandibular Morphology**—The mandible of TMP 1993.051.0001 is incomplete anteriorly, but has several features that allow inference of the shape of the beak. Comparison with Anzu wyliei, Caenagnathus collinsi, Chirostenotes pergracilis, and Leptorhynchos elegans (senus Longrich et al., 2013), all of which have relatively complete mandibles, reveals a suite of characters that suggest a deep-beaked morphology for Apatoraptor pennatus. The dentary of Apatoraptor (Fig. 4), Chirostenotes, and Leptorhynchos all have deep mandibular fossae on their lateral sides, in contrast to the shallow mandibular fossae of Anzu and Caenagnathus. Similarly, the mandibles of Apatoraptor and Chirostenotes have only one apex on the dorsal margin of the mandible (Fig. 4), whereas Anzu and Caenagnathus have two: one anterior to the external mandibular fenestra and one directly above the midpoint of the external mandibular fenestra. The articular ridge of Apatoraptor is low compared with Chirostenotes, but is well offset from the dorsal margin of the surangular, contrasting both Anzu and Caenagnathus, in which the articular ridge is confluent with the surangular. Other features better developed in Apatoraptor and Chirostenotes than in Anzu and Caenagnathus—such as a well-developed lateral surangular flange and the strong ventral bow of the angular and dentary below the external mandibular fenestra—support this interpretation.

**Phylogenetic Position of Apatoraptor pennatus**

A cladistic analysis was performed in TNT version 1.1 (Goloboff et al., 2008), using a character matrix updated (Appendix 1 in Supplementary Data) from Lamanna et al. (2014) of 250 characters and 41 taxa. This matrix differed from previous analyses (Longrich et al., 2013; Lamanna et al., 2014) in several ways. First, Caenagnathus sternbergi, Chirostenotes pergracilis, and ‘Macrocephalia’ canadensis were combined, as were ‘Alberta dentary morph 3’ and Leptorhynchos elegans, to follow Longrich et al. (2013). Second, Ojoraptorsaurus boerei was excluded from the analysis, because it could be coded for only 1% of the characters in the matrix. Third, Caenagnathus collinsi, Caenagnathasia martinsoni, Elmisaurus rarus, and Leptorhynchos elegans were updated based on the additional material described by Funston et al. (2015), Sues and Averianov (2015), Currie et al. (2016), and Funston et al. (2016), respectively. One character state (150)
for *Chirostenotes per gracilis* was changed (150:0 to 150:1) from Stues and Averianov (2015), based on further examination of TMP 1979.020.0001. Lastly, the ordering of certain mandibular and manual characters (Appendix 1) was removed, due to the variable nature of those characters in caenagnathids. Until the degree of individual and ontogenetic variation in caenagnathids can be qualified, it is more conservative to allow free movement between character states. Two analyses were run: the first included all 41 taxa, and the second excluded *Leptorhynchos gaddisi*, for which only mandibular material is unambiguously known. Nexus (.nex) files of each analysis are available upon request.

Tree searches were run with 1000 replications of Wagner trees followed by tree bisection-reconnection (TBR) branch swapping, holding up to 10 trees each replication. A final round of TBR branch swapping was used on the resulting trees to find additional most parsimonious trees. Strict consensus trees were created in TNT (Goloboff et al., 2008) and then exported to Mesquite version 2.75 (Maddison and Maddison, 2009) for figure creation. Bremer support values were calculated for the strict consensus trees using the 'Bremer.run' script provided with TNT (Goloboff et al., 2008). The first analysis produced 15 most parsimonious trees of 577 steps (consistency index [CI]: 0.47; retention index [RI]: 0.66). The strict consensus tree (Fig. 11A) finds microsauroid trees of 577 steps (consistency index [CI]: 0.47; retention index [RI]: 0.66). The strict consensus tree (Fig. 11A) finds *Microvenator celer*, *Gigantoraptor erlianensis*, and *Hagryphus giganteus* as successive basal caenagnathids, and two groups of derived caenagnathids. The most basal of these two caenagnathid groups is composed of *Anzu wyliei* and *Epichroristoneosaurus curriei* as sister taxa. *Caenagnathus collinsi* is found in the other group of caenagnathids despite the similarity of its mandibular morphology to *Anzu wyliei*. The other caenagnathid group contains the elmisauroid *Apatoraptor pennatus*, *Elmisaurus rarus*, and *Leptorhynchos elegans* in a polytomy with *Chirostenotes per gracilis*, *Caenagnathasia martinsoni*, and *Leptorhynchos gaddisi*.

When *Leptorhynchos gaddisi* was removed from the character matrix, three most parsimonious trees of 577 steps were found (CI: 0.49; RI: 0.68). The strict consensus tree (Fig. 11B) has drastically improved resolution for the more derived group of caenagnathids. *Caenagnathus collinsi*, *Caenagnathasia martinsoni*, and *Chirostenotes per gracilis* are recovered as successive outgroups to a group of elmisauroids in which *Leptorhynchos elegans* is sister to the sister taxa *Apatoraptor pennatus* and *Elmisaurus rarus*. This result strongly supports the interpretation of *Apatoraptor pennatus* as an elmisaur.

**Paleobiological Implications of *Apatoraptor pennatus***

**Ulnar Papillae**—In modern birds, the presence of ulnar papillae is highly variable and does not appear to be tied to flight style or performance (Hieronymus, 2015). Ulnar papillae are produced by an exostosis at the attachment site of the follicular ligament to the ulna, and their relative development is linked to feather musculature (Edington and Miller, 1942). In modern birds, feather movement is controlled by networks of integumentary muscles and ligaments, the complexity and size of which reflect feather function (Stettenheim, 2000). These muscles and ligaments work in tandem with hydrostatic pressure (Homberger and de Silva, 2000). Feather arrector muscles contract to raise the feathers, and upon relaxation, subcutaneous fat and the elasticity of the skin move the calamus back into resting position (Homberger and de Silva, 2000). The secondaries of modern birds are muscularized by two main muscles, the flexor sublimis digitorum and the flexor carpi ulnaris, which connect to a network of follicular ligaments (Lowe, 1942). The morphology of ulnar papillae in the pennibrachia of feathered theropods, therefore, is probably linked to the development of these muscles or their homologues.

Although well-preserved ulnae are known from many oviraptorid taxa (e.g., *Citipati, Conchoraptor, Ingenia*, and *Klaan*), none shows any trace of ulnar papillae. The presence of complex branched feathers and a pennibrachium in basal oviraptorosauras such as *Caudipteryx*, however, suggests that pennibrachia were present throughout oviraptorosaurs. The presence of ulnar papillae in *Apatoraptor*, therefore, likely reflects a relative increase in the development of feather arrector musculature in *Apatoraptor*, rather than a lack of pennibrachia in oviraptorids. Multiple oviraptorid skeletons have been found in brooding posture (Dong and Currie, 1996; Clark et al., 1999; Hopp and Orson, 2004; Fanti et al., 2012), with their arms over their nests. The position of the arms in these specimens is congruent with the use of remiges for insulation or protection of the eggs (Hopp and Orson, 2004). The consistent lack of ulnar papillae on oviraptorids, despite excellent preservation, suggests that brooding behavior was not impeded by relatively poorly developed feather arrector musculature. Ulnar papillae, therefore, are unlikely to reflect an adaptation for brooding behavior, although it is likely that *Apatoraptor* did engage in brooding behavior. Pennibrachia are unlikely to contribute significantly to insulation, or to have aided with foraging. Even if either were true, it is difficult to conceive an associated adaptive pressure that would promote the development of arm feather musculature. Because the large size of *Apatoraptor* precludes it from flight, the increased feather musculature must be explained in another manner.

One possible explanation is that this structure was used for display (Foth et al., 2014; Koschowitz et al., 2014). The late ontogenetic development of pennibrachia (and therefore the associated arrector musculature) in *Ornithomimus* led Zelenitsky et al. (2012) to suggest that pennibrachia were used for sexual display in that taxon. Although the ontogenetic timing of pennibrachium development in *Apatoraptor* is unknown, the presence of a well-muscled pennibrachium could be reasonably explained as a secondary sex characteristic. Further support for increased feather musculature in conjunction with display comes from feather musculature patterns in modern birds. Lowe (1942) notes that in the male Gould’s Manakin (*Manacus vitellinus*), which uses its wings in an elaborate courtship display, the flexor sublimis digitorum and the flexor carpi ulnaris are greatly hypertrophied. Similarly, Stettenheim (2000) notes that, especially in males, feather musculature is larger in display feathers than in non-display feathers.

**Sexual Display**—Sexual display in oviraptorosaurs has been examined by several authors, although most studies have focused on the tail and its associated feathers (Ji et al., 1998; Barsbold et al., 2000; Pittman et al., 2013; Persons et al., 2014). Oviraptorids, which frequently develop fused pygostyles or cranial crests (Fig. 12), may have used those structures for display instead of pennibrachia. Thus, the presence of a pennibrachium potentially associated with sexual display in *Apatoraptor* (Fig. 13) expands on the known display structures of oviraptorosaurs. There is now evidence for three types of display in oviraptorosaurs: tail display (Persons et al., 2014), cranial crests (Clark et al., 2002), and pennibrachia (Fig. 13). The widespread presence and frequent convergence of sexual display features in oviraptorosaurs (Fig. 12) suggests that sexual display was an important factor in the evolution of this group. This has important ramifications for cladistic analysis of oviraptorosaurs, because several features cited as taxonomic differences may, in fact, be homoplastic, ontogenetic, or sexually dimorphic. For example, as recovered in these analyses, the development of a cranial crest has evolved at least three separate times, and cranial crests have been lost once (Fig. 12). Furthermore, the fusion of the distal caudals into a pygostyle—associated with a fan of feathers for display—appears to be
independent of phylogeny, with differing morphology even in closely related taxa (e.g., MPC-D 100/42 and Citipati osmolskae). Indeed, the most parsimonious explanation for the evolution of pygostyles requires at least five separate convergent events (Fig. 12). It is likely that the presence or absence of a pygostyle is controlled by ontogeny and possibly sexual dimorphism, rather than taxonomy. At the moment, however, there is not a sufficient sample size in the literature to examine this possibility. Although these sexual display features are homoplastic, when removed from the matrix their impact on the consistency index of the consensus tree—raised from 0.47 to 0.48—is negligible. Thus, it may be that low consistency indices in oviraptorosaur cladistic analyses are not solely the result of characters linked to display. As ontogeny and individual variation in oviraptorosaurs become better known, it may be necessary to reevaluate the use of certain characters in cladistic analyses and their impact on our understanding of oviraptorosaur relationships.

CONCLUSIONS

In addition to being the first articulated skeleton of the group, TMP 1993.051.0001 provides a wealth of anatomical
FIGURE 12. Time-calibrated phylogeny of 38 taxa (36 oviraptorosaurs) and 250 characters, based on strict consensus of three most parsimonious trees of 577 steps. Anatomical features potentially related to sexual display are indicated (legend bottom right). Black bars indicate stratigraphic ranges of taxa (see Table S1 for sources).

FIGURE 13. Life reconstruction of *Apatoraptor pennatus*, showing plumage potentially related to sexual display. Original artwork by Sydney Mohr.
information previously unknown in Albertan caenagnathids. A number of autapomorphic features of the mandible and manus suggest that TMP 1993.051.0001 represents a new taxon, Apatoraptor pennatus, and this is supported by a unique combination of diagnostic features. Apatoraptor pennatus can be distinguished from the coeval *Epichirostenotes curriei* by size and by features of the cervical vertebrae and ribs. Feather scars on the ulna are the first good evidence of a muscularized pennibrachium in oviraptorosaurs and expand upon known display structures in oviraptorosaurs.

**ACKNOWLEDGMENTS**

The specimen was expertly prepared by K. Aulenback and D. Tanke. Quill marks on the exposed surface of the ulna were identified by D. Macleod. We thank the Royal Tyrrell Museum of Palaeontology, especially B. Strilisky and D. Brinkman, for access to the specimen. We thank S. Mohr for the beautiful life restoration in Figure 13. CT scanning was conducted by E. Sonnax at the Alberta Cardiovascular and Stroke Research Centre (ABACUS) CT Facility in the University of Alberta Hospitals Mazzankowski Centre. TNT version 1.1 was provided by the Will Hennig Society. G.F.F. is funded by NSERC, Alberta Innovates, the Dinosaur Research Institute, the Alberta Lottery Fund, and the Alberta Historical Resources Foundation. P.J.C. is funded by NSERC Discovery Grant (no. 203091-2011). The manuscript was drastically improved by the helpful suggestions of A. Turner, H.-D. Sues, and L. Zanno.

**LITERATURE CITED**

Balannof, A. M., and M. A. Norell. 2012. Osteology of *Khaan mckennai* (Oviraptorosauria: Theropoda). Bulletin of the American Museum of Natural History 372:1–77.

Barsbold, R. 1976. [On a new Late Cretaceous family of small theropods (Oviraptoridae fam. n.] of Mongolia]. Transactions of the Joint Soviet-Mongolian Geological Expedition 3:68–75. [Russian]

Barsbold, R., H. Osmolska, M. Watabe, P. J. Currie, and K. Tsogtbaatar. 2000. A new oviraptorosaur (Dinosaur, Theropoda) from Mongolia: the first dinosaur with a pygostyle. Acta Palaeontologica Polonica 45:97–106.

Bell, P. R., P. J. Currie, and D. A. Russell. 2015. Large caenagnathids (Dinosauria, Oviraptorosauria) from the uppermost Cretaceous of western Canada. Cretaceous Research 52:101–107.

Bradley, G. J., M. E. Burns, and P. J. Currie. 2015. Missing data estimation in tyrannosaur dinosaurs: can diameter take the place of circumference? Cretaceous Research 55:200–209.

Brochu, C. A. 1996. The closure of neurocentral sutures during crocodile ontogeny: implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16:49–62.

Campione, N. E., D. C. Evans, C. M. Brown, and M. T. Carrano. 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. Methods in Ecology and Evolution 5:913–923.

Clark, J. M., M. A. Norell, and L. M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Khakha Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. American Museum Novitates 3265:1–36.

Clark, J. M., M. A. Norell, and T. Rowe. 2002. Cranial anatomy of *Citipati osmolskayi* (Theropoda, Oviraptorosauria), and a reinterpretation of the holotype of *Oviraptor philoceratops*. American Museum Novitates 3361:1–24.

Currie, P. J. 1989. The first records of *Elmisaurus* (Saurischia, Theropoda) from North America. Canadian Journal of Earth Sciences 26:1319–1324.

Currie, P. J., and D. A. Russell. 1988. Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. Canadian Journal of Earth Sciences 25:972–986.

Currie, P. J., S. J. Godfrey, and L. Nesson. 1993. New caenagnathid (Dinosauria: Theropoda) specimens from the Upper Cretaceous of North America and Asia. Canadian Journal of Earth Sciences 30:2255–2272.

Currie, P. J., G. F. Funston, and H. Osmolska. 2016. New specimens of the crested theropod dinosaur *Elmisaurus rarus* from Mongolia. Acta Palaeontologica Polonica 61:143–157. doi: 10.4202/app.00130.2014.

Dong, Z.-M., and P. J. Currie. 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People’s Republic of China. Canadian Journal of Earth Sciences 33:631–636.

Eberth, D. A., and D. R. Braman. 2012. A revised stratigraphy and depositional history of the Horseshoe Canyon Formation (Upper Cretaceous), southern Alberta plains. Canadian Journal of Earth Sciences 49:1053–1086.

Eberth, D. A., D. C. Evans, D. B. Brinkman, F. Thérrien, D. H. Tanke, and L. S. Russell. 2013. Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. Canadian Journal of Earth Sciences 50:701–726.

Edington, G. H., and A. E. Miller. 1942. XII—The avian ulna: its quill-knobs. Proceedings of the Royal Society of Edinburgh. Section B. 61:138–148.

Faniti, P. J. Currie, and D. Badamgarav. 2012. New specimens of *Nemegtomaia* from the Baruungoyot and Nemegt Formations (Late Cretaceous) of Mongolia. PLoS ONE 7:e31330. doi: 10.1371/journal.pone.0031330.

Funston, G. F., P. J. Currie, and M. E. Burns. 2016. New elmisaur specimens from Alberta, Canada, and their relationship to the Mongolian *Elmisaurus rarus*. Acta Palaeontologica Polonica 61:143–157. doi: 10.4202/app.00129.2014.

Funston, G. F., W. S. Persons IV, G. J. Bradley, and P. J. Currie. 2015. New material of the large-bodied caenagnathid *Caenagnathus col- linsi* from the Dinosaur Park Formation of Alberta, Canada. Cretaceous Research 54:179–187.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds; pp. 1–55 in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. Memoirs of the California Academy of Sciences 8. California Academy of Sciences, San Francisco, California.

Gierlinski, G., and M. Lockley. 2013. A trackmaker for *Saurexalopus*: ichnological evidence for oviraptorosaurian tracks from the Upper Cretaceous of western North America; pp 526–529 in A. L. Titus and M. A. Loewen (eds.), *At the Top of the Grand Staircase:* The Late Cretaceous of Southern Utah. Indiana University Press, Bloomington, Indiana.

Gilmore, C. W. 1924. Contributions of vertebrate palaeontology. Geological Survey of Canada, Bulletin 38:1–89.

Goloboff, P., J. Farris, and C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Hieronymus, T. L. 2015. Qualitative skeletal correlates of wing shape in extant birds (Aves: Neornithes). BioMed Central Evolutionary Biology 15:30. doi: 10.1186/s12862-015-0303-7.

Holtz, T. P., and M. J. Orson. 2004. Dinosaur brooding behaviour and the origin of flight feathers; pp 234–250 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright (eds.), Feathered Draconic Studies on the Transition from Dinosaurs to Birds. Indiana University Press, Bloomington, Indiana.

Huene, F. von 1914. The dinosaurs not a natural order. American Jour- nal of Science (Series 4) 38:145–146.

Ingolfsson, A. 1970. Moulting of remiges and rectrices in Great Black-Backed *Larus marinus* and Glaucous Gulls *L. hyperboreus* in Iceland. Ibis 112:83–92.

Kirkland, J. I., L. E. Zanno, S. D. Sampson, J. M. Clark, and D. D. DeBlieux. 2005. A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. Nature 435:84–87.

Kobayashi, Y., J.-C. Lu, Z.-M. Dong, R. Barsbold, Y. Azuma, and Y. Tomida. 1999. Herbivorous diet in an ornithomimid dinosaur. Nature 402:480–481.

Koschowitz, M. C., M. C. Fischer, and M. Sander. 2014. Beyond the rainbow. Science 346:416–418.

Kurzanov, S. M. 1981. *An unusual theropod from the Upper Cretaceous of Mongolia*. Joint Soviet-Mongolian Paleontological Expedition 15:39–49. [Russian]
Funston and Currie—A new caenagnathid from Alberta (e1160910-18)

Lamanna, M. C., H.-D. Sues, E. R. Schachner, and T. R. Lyson. 2014. A new large-bodied oviraptorosaurian theropod dinosaur from the latest Cretaceous of western North America. PLoS ONE 9:e92022. doi: 10.1371/journal.pone.0092022.

Longrich, N. R., K. Barnes, S. Clark, and L. Milner. 2013. Caenagnathidae from the Upper Campanian Agujia Formation of West Texas, and a revision of the Caenagnathinae. Bulletin of the Peabody Museum of Natural History 54:23–49.

Lowe, P. L. 1942. The anatomy of Gould’s Manakin (Anasus electricus) in relation to its display, with special reference to an undescribed pterylar tract and the attachments of the flexor carpi ulnaris and flexor sublimis digitorum muscles to the secondary wing-feathers. Ibis 84:50–83

Maddison, W. P., and D. R. Maddison. 2009. Mesquite: A Modular System For Evolutionary Analysis, version 2.75 (built 564). Available at http://mesquiteproject.org. Accessed January 1, 2015.

Marsh, O. C. 1881. Classification of the Dinosauria. American Journal of Science 23:81–86.

Norell, M. A., and P. J. Makovicky. 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of Velociraptor mongoliensis. American Museum Novitates 3823:1–45.

Ortega, F., F. Escaso, and J. L. Sanz. 2010. A bizarre, humped Carcharodontosaurus (Theropoda) from the Lower Cretaceous of Spain. Nature 467:203–206.

Osmolska, H. 1976. New light on the skull anatomy and systematic position of Oviraptor. Nature 262:683–684.

Osborn, H. F. 1924. Three new Theropoda, Protoceratops Zone, Central Mongolia. American Museum Novitates 1441:1–12.

Osmolska, H. 1981. Coosified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. Palaeontologia Polonica 42:79–95.

Owen, R. 1842. Report on British fossil reptiles. Part II. Report of the British Association for the Advancement of Science 11:60–204.

Parks, W. A. 1933. New species of dinosaurs and turtles from the Upper Cretaceous formations of Alberta. University of Toronto Studies, Geological Series 34:1–33.

Persons, W. S., IV, P. J. Currie, and M. A. Norell. 2014. Oviraptorosaur tail forms and functions. Acta Palaeontologica Polonica 59:553–567.

Pittman, M., S. M. Gatesy, P. Upchurch, A. Goswami, and J. R. Hutchinson. 2014. Shake a tail feather: the evolution of the theropod tail into a stiff aerodynamic surface. PLoS ONE 8:e63115. doi: 10.1371/journal.pone.0063115.

Ji, Q., P. J. Currie, M. A. Norell, and S. A. Ji. 1998. Two feathered dinosaurs from northeastern China. Nature 393:753–761.

Senter, P., and J. M. Parrish. 2005. Functional analysis of the hands of the theropod dinosaur Chirostenotes pergracilis: evidence for an unusual paleoecological role. Paleobios 25(2):9–19.

Solheim, R. 2012. Wing feather moult and age determination of Snowy Owls Bubo scandiacus. Ornis Norvegica 35:48–67.

Sternberg, C. M. 1932. Notes on certain recently described dinosaurs. Canadian Field Naturalist 48:7–8.

Sternberg, R. M. 1940. A toothless bird from the Cretaceous of Alberta. American Museum Novitates 1940:1–45.

Sternberg, C. M. 1934. Notes on certain recently described dinosaurs. Proceedings of the Royal Society of London 141:363–370.

Sternberg, C. M. 1935. Notes on certain recently described dinosaurs. Bulletin of the American Museum of Natural History 71:309–356.

Sternberg, C. M. 1940. A toothless bird from the Cretaceous of Alberta. Journal of Vertebrate Paleontology 15:81–125.

Sues, H.-D. 1988. On Chirostenotes, a Late Cretaceous Oviraptorosaur (Dinosauria: Theropoda) from western North America. Journal of Vertebrate Paleontology 18:698–716.

Sues, H.-D., and A. Averianov. 2015. New material of Caenagnathus martinsoni (Dinosauria: Theropoda: Oviraptorosauria) from the Biszekky Formation (Upper Cretaceous: Turonian) of Uzbekistan. Cretaceous Research 54:50–59.

Sullivan, R. M., S. E. Jasinski, and M. P. A. van Tomme. 2011. A new caenagnathid Oviraptorosaur boerii n. gen., n. sp. (Dinosauria, Oviraptoraurosauroidea), from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member), San Juan Basin, New Mexico. Fossil Record 3, New Mexico Museum of Natural History and Science Bulletin 53:418–428.

Turner, A. H., P. J. Makovicky, and M. A. Norell. 2007. Feather quill knobs in the dinosaur Velociraptor. Science 317:1721.

Varricchio, D. J., 2001. Late Cretaceous oviraptorosaur (Theropoda) dinosaurs from Montana; pp. 42–57 in D. Tanke and K. Carpenter (eds.), Mesozoic Vertebrate Life. Indiana University Press, Bloomington, Indiana.

Wang, X., A. J. McGowan, and G. J. Dyke. 2011. Avian wing proportions and flight styles: first step towards predicting the flight modes of Mesozoic birds. PLoS ONE 6:e28672. doi: 10.1371/journal.pone.0028672.

Xu, X., Q. Tan, J. Wang, X. Zhao, and L. Tan. 2007. A gigantic bird-like dinosaur from the Late Cretaceous of China. Nature 447:844–847.

Zanno, L. E. 2006. The pectoral girdle and forelimb of the primitive therizinosauroid Falcarius utahensis (Theropoda, Maniraptora): analyzing evolutionary trends within Therizinosauroidae. Journal of Vertebrate Paleontology 26:636–650.

Zanno, L. E., and S. D. Sampson. 2005. A new oviraptorosaur (Theropoda, Maniraptora) from the Late Cretaceous (Campanian) of Utah. Journal of Vertebrate Paleontology 25:897–904.

Zelenitsky, D. K., F. Thirrien, G. M. Erickson, C. L. DeBuhr, Y. Kobayashi, D. A. Eberth, and F. Hadfield. 2012. Feathered non-avian dinosaurs from North America provide insight into wing origins. Science 338:510–514.

Zhou, Z.-H., and X.-L. Wang. 2000. A new species of Caudipteryx from the Yixian Formation of Liaoning, Northeast China. Vertebrata PalAsiatica 38:111–127.

Submitted February 23, 2015; revisions received December 7, 2015; accepted February 9, 2016.

Handling editor: Alan Turner.