

JOURNAL OF VERTEBRATE PALEONTOLOGY

A new caenagnathid (Dinosauria: Oviraptorosauria) from the Horseshoe Canyon
Formation of Alberta, Canada, and a reevaluation of the relationships of Caenagnathidae

GREGORY F. FUNSTON*, 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

SUPPLEMENTARY DATA 1

CHARACTERS MODIFIED FROM LAMANNA ET AL. (2014)

78. Dentary: (0) elongate; (1) proportionally short and deep, with maximum depth of dentary between 25% and 50% of dentary length (with length measured from the tip of the jaw to the end of the posterodorsal process); (2) extremely short and deep, with maximum depth 50% or more of dentary length. [ORDERED]

Modification—Removed [ORDERED]

Justification—Mandibular variation through ontogeny in has not been qualified in oviraptorosaurs, nor has the degree of intraspecific variation. This character in particular is correlated with size in caenagnathids, such that larger specimens tend show state 0, and smaller specimens tend to show state 2, with a smooth gradient between.

84. Anterodorsal margin of dentary in lateral view: (0) straight; (1) concave; (2) broadly concave. [ORDERED]

Modification—Removed [ORDERED]

Justification—As above, though the opposite correlation to size is shown: large specimens tend to show state 2, and small specimens tend to show state 0.

176. Manual phalanx II-2: (0) longer than II-1; (1) subequal to or slightly shorter than II-1; (2) distinctly shorter than II-1. [ORDERED]

Modification—Removed [ORDERED]

Justification—Caenagnathid manual proportions are highly variable, with a number of apparent reversals within clades. For example, *Hagryphus giganteus*, scored as character state 1 for this character, is consistently recovered as a basal caenagnathid, but within more derived caenagnathids, all three character states for this character are present, indicating that the character state can move both directions.

189. Dentary, symphyseal ridges inside the tip of the beak: (0) absent; (1) present, but weakly developed; (2) present and well developed. [ORDERED]

Modification—Removed [ORDERED]

Justification—Caenagnathid mandibular variation has not been well quantified, leading to problems distinguishing between character states 1 and 2, which are subjective. Furthermore, the development of these ridges may be ontogenetically controlled, or related to dietary adaptations, which likely varied between closely related species.

200. Manual phalanx I-1: (0) longer than II-2; (1) subequal to II-2; (2) shorter than II-2. [ORDERED]

Modification—Removed [ORDERED]

Justification—As above, caenagnathid manual proportions are highly variable, with all three character states present in derived caenagnathids and apparent reversals.

CHARACTERS ADDED TO MATRIX OF LAMANNA ET AL. (2014)

231. Frontal: divided anteriorly by slot for nasal and possibly lacrimal: (0) absent; (1) present

In *Elmisaurus*, the frontal is divided anteriorly by a slot for the contact with the nasal and possibly lacrimal. This indicates a high nasal crest in this taxon. In other oviraptorosaurs, even those with high nasal crests, the frontal is undivided and meets the nasal in a simple contact. The presence of this feature in other caenagnathids is unknown, but it may be a feature shared by crested taxa within the group.

232. Infradiapophyseal, infraprezygapophyseal and infrapostzygapophyseal fossae on cervical and dorsocervical vertebrae: (0) one or more absent; (1) all three present

Some caenagnathids, including *Elmisaurus rarus* and *Apatoraptor pennatus* have infradiapophyseal fossae on the cervical vertebrae, in addition to infrapost- and infraprezygapophyseal fossae.

233. Ratio of minimum shaft diameter of manual phalanx II-1 to minimum shaft diameter of metacarpal II: (0) >1 (1) <1

The hands of caenagnathids tend to be elongate and gracile, with manual phalanx II-1 thinner mediolaterally than metacarpal II. The exception is *Hagryphus giganteus* (Zanno and Sampson 2005), which has a manus that is relatively robust for a caenagnathid. In oviraptorids, the hands are robust and manual phalanx II-1 is wider mediolaterally than metacarpal II.

234. Ratio of minimum shaft diameter to length of manual phalanx II-2: (0) >0.10 (1) <0.10

Another measure of manual robusticity, manual phalanx II-2 tends to be very gracile in caenagnathids, with a mediolateral width less than 10% of its length. The variation of this character within oviraptorids has not yet been assessed.

235. Ratio of the length of the metatarsus to the length of the tibia: (0) <0.5 (1) >0.5

Caenagnathids, especially elmisaurines, have metatarsi that are long compared to the tibia. In this group, the metatarsus is more than half the length of the tibia. This is not true in oviraptorids, which have shorter metatarsi compared to their tibiae.

236. Tibia: ratio of the transverse width of the distal condyles to the length: (0) 0.20 or greater (1) less than 0.20

A measure of robusticity of the tibia, oviraptorids tend to have tibiae that are shorter and more robust than those of caenagnathids are. The transverse width of the distal condyles compared to the length seems to accurately track this difference, whereas shaft circumference is interfered with by crushing and different cross-sections.

237. Ratio of minimum transverse width to length of tarsometatarsus: (0) greater than 0.20 (1) less than 0.20

Oviraptorosaurs in general tend to have tarsometatarsi that are at least 20% as wide as they are long. The exception is elmisaurines, which have elongate metatarsi that are mediolaterally pinched midlength.

238. Fusion of distal tarsals III and IV at maturity: (0) absent; (1) present

In elmisaurines, distal tarsals III and IV fuse in mature individuals. This appears to be a synapomorphy of the group, as it has not been documented in other oviraptorosaurs, and is only found convergently in *Avimimus* and *Avisaurus*, which have dissimilar metatarsal structure.

239. ‘Hook-like’ posterodorsal process of distal tarsal IV: (0) absent; (1) present

In elmisaurines, distal tarsal IV is expanded posterodorsally into a hook-like process that articulates with and sometimes fuses to metatarsal V. This process is unique to elmisaurines, and may have biomechanical implications for the mobility of the foot.

240. Posterior protuberance on proximal end of tarsometatarsus caused by coossification of distal tarsals III and IV, plus MT II, III and IV: (0) absent; (1) present

In *Elmisaurus rarus*, the coossification of the distal tarsals and proximal metatarsals creates a subrectangular protuberance of bone that projects posteriorly. Although the function of this protuberance is unknown, it is distinctive enough that it can be used to distinguish *Elmisaurus rarus* from *Leptorhynchus elegans*

241. Anterior margin of Metatarsal V in lateral view: (0) straight or slightly curved; (1) tightly curved

Most oviraptorosaurs have a fifth metatarsal that is straight or slightly curved in lateral view. Caenagnathines, like *Chirostenotes*, however, have fifth metatarsals that are moon-shaped and tightly curved anteriorly. The functional significance of this difference is unknown.

242. Concavity on posterior surface of tarsometatarsus in cross section: (0) absent or shallow; (1) prominent and deep

Caenagnathids can be distinguished from other theropods by the flatness of metatarsal III, which does not protrude posteriorly between metatarsals II and IV. The result is a concave profile to the posterior surface of foot in cross section. In elmisaurines especially, this concavity is deep. The biomechanical importance of this feature is not yet known, but its consistency within the caenagnathids suggests that they had different locomotory constraints than their relatives.

243. Sharp “Cruciate” ridges on posterior surface of metatarsal III: (0) only one sharp longitudinal ridge or no ridges; (1) sharp medial longitudinal ridge continuous with lateral postcondylar ridge, and sharp lateral longitudinal ridge continuous with medial

postcondylar ridge, forming a chiasmata. Ridges are separated from each other by longitudinal sulcus

In elmisaurines, the posterior surface of metatarsal III is marked by two longitudinal ridges that cross each other distally to continue as postcondylar ridges. Although caenagnathines have similar ridges, they are not as pronounced, and the medial ridge is often rounded or hump-like instead of sharp. Isolated elmisaurine third metatarsals can be identified on the basis of these ridges, which are subequal in height and sharp along their lengths. They are separated by a well-defined longitudinal sulcus, which is variably present in caenagnathines, but not to the same extent as in elmisaurines.

244. Posteromedial and posterolateral ridges of MT II and IV, respectively: (0) weakly developed, do not extend past posterior extent of distal condyle; (1) well developed, extend posteriorly past distal condyle

The posterior concavity of the foot in caenagnathids is created in part by posteromedial and posterolateral ridges on the shafts metatarsals II and IV, respectively. In elmisaurines, these ridges are better developed, and extend past the posterior extent of the distal condyles. In addition, they are often rugose or faceted at their apices. Caenagnathines do not have posteromedial or posterolateral ridges that are as well developed, and they extend less than or equal to the posterior extent of the distal condyles. The development of these ridges contributes to a relatively deeper posterior concavity of the foot in elmisaurines.

245. Distal ends of shafts of metatarsals II and IV: (0) both straight; (1) Metatarsal II medially deflected, metatarsal IV straight; (2) Metatarsal II straight, metatarsal IV laterally deflected

In oviraptorids and most caenagnathines, the shafts of metatarsals II and IV are straight, and do not accommodate a wide distal metatarsal III. In *Leptorhynchos elegans* and possibly *Chiostenotes pergracilis* (isolated second metatarsi at the TMP attributed to *Chiostenotes*) the distal width of metatarsal III is accommodated for by a medial deflection of the shaft of metatarsal II. This is often accompanied by an anterior deflection of the shaft, but this feature is variable, perhaps ontogenetically. Metatarsal IV is straight in this taxon, with only a minor lateral deflection of the distal condyle. In *Elmisaurus rarus*, the opposite is true: metatarsal II is straight, and metatarsal IV is laterally deflected to accommodate the wide distal shaft of metatarsal III. This feature can be used to identify isolated metatarsals to either taxon.

246. Ratio of transverse width to anteroposterior length of distal condyle of metatarsal III: (0) <1; (1) >1

In *Leptorhynchos elegans*, the distal condyles of metatarsal III are longer anteroposteriorly than wide transversely. This appears to be an autapomorphy of this taxon, and is not shared by the otherwise similar *Elmisaurus rarus*. This character can be

used to identify isolated distal condyles, as caenagnathines have distal condyles that are wider transversely than anteroposteriorly.

247. External mandibular fenestra: (0) expanded anteriorly; (1) anteriorly constricted by posteroventral ramus of dentary

In *Apatoraptor pennatus* and *Leptorhynchus elegans*, a bulge in the dorsal margin of the posteroventral ramus of the dentary constricts the external mandibular fenestra anteriorly. This constriction is not present in other caenagnathine mandibles, though no other certain elmsaurine mandibles are known.

248. Articular ridge of mandible: (0) low, less than 25% as tall dorsoventrally as long anteroposteriorly; (1) high, more than 25% as tall as long.

The articular ridge of caenagnathids is variable in height and can be used to distinguish morphotypes where the rest of the mandible is missing. *Anzu wyliei* and *Caenagnathus collinsi* have low articular ridges, and *Chirostenotes pergracilis* has a high articular ridge. The height of the articular ridge is measured as a straight line between the apex of the articular ridge and the dorsal surface of the medial glenoid at that position.

249. Transverse groove between flexor tubercle and proximal articular surface of manual ungual I-2: (0) absent; (1) present.

Recent work by Bell et al. (2015) and Funston et al. (2015) has shown that transverse grooves between the flexor tubercles and the proximal articular surfaces are variable in caenagnathids and probably useful diagnostically. In *Chirostenotes pergracilis* and *Elmsaurus rarus*, manual ungual I-2 has a transverse groove, and in *Caenagnathus collinsi* and *Anzu wyliei*, it does not. Where this groove is absent, usually manual ungual II-3 has a groove in this position, though manual ungual I-2 is better represented among articulated caenagnathid hands.

250. Cnemial crest of tibia greatly enlarged such that the proximal articular surface of the tibia is longer anteroposteriorly than wide mediolaterally: (0) absent; (1) present

In *Elmsaurus rarus*, *Leptorhynchus elegans*, and *Apatoraptor pennatus*, the cnemial crest of the tibia is greatly expanded, and in proximal view the tibia is longer anteroposteriorly than wide mediolaterally. This distinguishes them from *Anzu wyliei* and *Chirostenotes pergracilis*, where the cnemial crest is not so large.

STRATIGRAPHIC INFORMATION

TABLE S1: Sources for stratigraphic data for phylogenetic analysis

Taxon	Stratigraphic interval	Age Source
<i>Velociraptor</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Archaeopteryx</i>	Early Tithonian	Elzanowski, 2002
<i>Protarchaeopteryx</i>	Early Aptian	Chang et al. 2009
<i>Similicaudipteryx</i>	Early Aptian	Chang et al. 2009
<i>Caudipteryx</i>	Early Aptian	Chang et al. 2009
<i>Incisivosaurus</i>	Early Aptian	Chang et al. 2009
<i>Luoyanggia</i>	Early Aptian	Chang et al. 2009
<i>Ningyuansaurus</i>	Early Aptian	Chang et al. 2009
<i>Avimimus</i>	Campanian-Maastrichtian	Averianov and Sues, 2012
<i>Microvenator</i>	Middle to Late Albian	O’Emic and Britt, 2008
<i>Gigantoraptor</i>	Santonian	Averianov and Sues, 2012
<i>Hagryphus</i>	Campanian	Zanno and Sampson 2005
<i>Anzu</i>	Maastrichtian	Lamanna et al. 2014
<i>Epichirostenotes</i>	Campanian	Eberth et al. 2013
<i>Caenagnathus</i>	Campanian	Eberth 2005
<i>Caenagnathasia</i>	Turonian	Sues and Averianov, 2015
<i>Chirostenotes</i>	Campanian	Eberth 2005
<i>Leptorhynchos</i>	Campanian	Eberth 2005
<i>Apatoraptor</i>	Campanian	Eberth et al. 2013
<i>Elmisaurus</i>	Campanian-Maastrichtian	Averianov and Sues, 2012
<i>Nankangia</i>	Campanian-Maastrichtian	Wang et al. 2013
<i>Ganzhousaurus</i>	Campanian-Maastrichtian	Wang et al. 2013
<i>Nomingia</i>	Maastrichtian	Averianov and Sues, 2012
<i>Yulong</i>	Campanian-Maastrichtian	Wang et al. 2013
<i>Oviraptor</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Rinchenia</i>	Maastrichtian	Averianov and Sues, 2012
MPC-D 100/42	Early to Middle Campanian	Averianov and Sues, 2012
<i>Citipati</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Banji</i>	Campanian-Maastrichtian	Wang et al. 2013
<i>Wulatelong</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Shixinggia</i>	Maastrichtian	Clyde et al. 2010
<i>Khaan</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Conchoraptor</i>	Middle to Late Campanian	Averianov and Sues, 2012
<i>Machairasaurus</i>	Early to Middle Campanian	Averianov and Sues, 2012
<i>Jiangxisaurus</i>	Campanian-Maastrichtian	Wang et al. 2013
<i>Nemegtomaia</i>	Maastrichtian	Averianov and Sues, 2012
<i>Heyuannia</i>	Maastrichtian	Fanti et al. 2012
<i>Ingenia</i>	Maastrichtian	Averianov and Sues, 2012

LITERATURE CITED

- Averianov, A., and H.-D. Sues. 2012. Correlation of Late Cretaceous continental vertebrate assemblages in Middle and Central Asia. *Journal of Stratigraphy* 36:462–485.
- 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.
- Chang, S.-C., H. Zhang, P. R. Renne, and Y. Fang. 2009. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280:94–104.
- Clyde, W. C., S. Ting, K. E. Snell, G. J. Bowen, Y. Tong, P. L. Koch, Q. Li, and Y. Wang. 2010. New paleomagnetic and stable-isotope results from the Nanxiong Basin, China: implications for the K/T boundary and the timing of Paleocene mammalian turnover. *The Journal of Geology* 118:131–143.
- D'Emic, M., and B. Britt. 2008. Reevaluation of the phylogenetic affinities and age of a basal titanosauriform (Sauropoda: Dinosauria) from the Early Cretaceous Cloverly Formation of North America. *Journal of Vertebrate Paleontology* 28:68A.
- Eberth, D. A. 2005. The Geology; pp 55–82 in P. J. Currie and E. B. Koppelhus (ed.), *Dinosaur Provincial Park a Spectacular Ancient Ecosystem Revealed*. Indiana University Press, Bloomington, Indiana.
- Eberth, D. A., D. C. Evans, D. B. Brinkman, F. Therrien, 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.
- Elzanowski, A. 2002. Archaeopterygidae (Upper Jurassic of Germany); pp. 129–159 in L. M. Chiappe and L. M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley.
- Fanti, F., 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.
- Funston, G. F., W. S. Persons, IV, G. J. Bradley, and P. J. Currie. 2015. New material of the large-bodied caenagnathid *Caenagnathus collinsi* from the Dinosaur Park Formation of Alberta, Canada. *Cretaceous Research* 54:179–187.
- 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(3): e92022. doi:10.1371/journal.pone.0092022.
- Sues, H.-D. and A. Averianov. 2015. New material of *Caenagnathasia martinsoni* (Dinosauria: Theropoda: Oviraptorosauria) from the Bissekty Formation (Upper Cretaceous: Turonian) of Uzbekistan. *Cretaceous Research* 54:50–59.
- Wang, S., C. Sun, C. Sullivan, and X. Xu. 2013. A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of southern China. *Zootaxa* 3640:242–257.
- 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.