VOLUMINA JURASSICA, 2016, XIV: 159–164
DOI:

A review of the basal tyrannosauroids (Saurischia: Theropoda) of the Jurassic Period

Changyu YUN

Key words: tyrannosauroid, Saurischia, theropod, Jurassic

Abstract. The well supported clade Tyrannosauroidea represents one of the most basal coelurosaurian theropods. Given that current fossil records of earliest coelurosaur theropods are extremely scarce, basal-most tyrannosauroid materials are key to understanding the origin and diversification of coelurosaurs. Here, I present a brief overview of currently known basal tyrannosauroids of Jurassic age, discussing their systematics and distribution. The currently oldest known Jurassic tyrannosauroids are from Europe continent, possibly suggesting the European origin of the superfamily.

INTRODUCTION

The Coelurosauria is the only dinosaurian clade which survives today as birds, and it is one of the most diverse theropod clades comprising many herbivorous and carnivorous taxa. Therefore, the diversification of the Coelurosauria is one of the most interesting subject of the evolutionary history of the dinosaurs. Unfortunately, most of the oldest known coelurosaurian fossils are largely fragmentary so it is currently very dificult to understand the clade's diversification. One putative record from the Early Jurassic of China might be the oldest known therizinosaurian (Zhao, Xu, 1998; Barrett, 2009) but its exact age and taxonomic status are controversial (Kirkland, Wolfe, 2001; Kirkland *et al.*, 2005).

The Tyrannosauroidea is considered as a basal-most clade of Coelurosauria by a majority of recent phylogenetic analyses (*e.g.* Loewen *et al.*, 2013; Brusatte *et al.*, 2014) but some analyses found them to be more derived than the Compsognathidae (*e.g.* Rauhut *et al.*, 2010; Novas *et al.*, 2013). What is clear is that the tyrannosauroids represent a clade close to the origin of the Coelurosauria. Therefore the oldest tyrannosauroid material plays an important role in understanding coelurosaurian origin and diversification.

This paper aims to present a review of the currently known Jurassic tyrannosauroids, and a general description of each taxon or subclade. My hope is that this paper will be a helpful guide to understanding tyrannosauroid or coelurosaurian origin and/or distribution.

POSSIBLE CASES

Iliosuchus incognitus (Huene, 1932)

Age: Middle Bathonian, Middle Jurassic

Occurrence: Stonesfield Slate, England

Comments: Only 3 small ilia are the currently known material of this taxon. Though this material is very small in size (being 9 to 10 cm long), a vertical iliac ridge is clearly present similar to other tyrannosauroids. So this taxon was traditionally allied with the tyrannosauroids (Galton, 1976), though the fact that some other theropods belonging to the

[1] Vertebrate Paleontological Institute of Incheon, Incheon 21974, Republic of Korea, Biological Sciences, Inha University, Incheon 22212, Republic of Korea; e-mail: changyu1015@naver.com.

Tetanurae such as *Megalosaurus* or *Piatnitzkysaurus* have similar feature makes this referral uncertain (Benson, 2009). Recent studies have considered *Iliosuchus* to be an indeterminate avetheropod or a juvenile *Megalosaurus* (Benson, 2009; Carrano *et al.*, 2012) but such fragmentary material is not enough for accurate classification.

If *Iliosuchus* is indeed a tyrannosauroid, it would be the earliest genus in the clade or maybe even in the whole Coelurosauria itself (Rauhut, 2003).

Coeluridae (Marsh, 1881)

Definition: The most inclusive clade containing *Coelurus fragilis* but not *Proceratosaurus bradleyi*, *Tyrannosaurus rex*, *Allosaurus fragilis*, *Compsognathus longipes*, *Ornithomimus edmontonicus* and *Deinonychus antirrhopus* (Hendrickx *et al*., 2015)

Comments: Whether or not this clade is monophyletic is controversial, and some taxon or whole members of the clade might not belong to the Tyrannosauroidea at all (Choiniere *et al*., 2014). Many of the recent analyses found that this clade belongs to the basal tyrannosauroids (*e.g.* Senter, 2007; Brusatte *et al*., 2014). There are currently two genera in this clade, which are *Coelurus* and *Tanycolagreus*. This clade comprises small carnivorous coelurosaurs which are likely have hunted small prey.

Coelurus fragilis (Marsh, 1879)

Age: Middle, Late Kimmeridgian, Late Jurassic

Occurrence: Morrison Formation, Wyoming, USA

Comments: The exact position of this taxon's theropoda phylogenetical tree is uncertain. Some consider *Coelurus* as more derived than the tyrannosauroids (Turner *et al.*, 2007), or even than the basal maniraptoran (Zanno, 2010). If this taxon indeed forms a clade Coeluridae and belongs to the tyrannosauroid, it is probably close to the base (Senter, 2007). This taxon had a relatively long neck and trunk, and a long slender hindlimb. This suggests it was a small, gracile theropod with great speed ability.

Tanycolagreus topwilsoni (Carpenter *et al.*, 2005)

Age: Middle, Late Kimmeridgian, Late Jurassic

Occurrence: Morrison Formation, Wyoming, USA

Comments: This taxon could be synonymous with the tyrannosauroid *Stokesosaurus clevelandi*, since they are similar sized coelurosaurs from the same geological formation. However, the ilium of *Tanycolagreus* is currently unknown so the direct comparison of the taxa is currently impossible (the distinctive bones of *Stokesosaurus* being the ilia). If this taxon indeed forms the clade Coeluridae and belongs to the tyrannosauroid, it is probably close to the base (Senter, 2007). The taxon had a large, enlongated skull and long legs, and gracile general morphology.

CERTAIN CASES

Proceratosauridae (Averianov *et al.*, 2010)

Definition: A node based taxon including *Proceratosaurus bradleyi* and *Kileskus aristotocus*, their most recent common ancestor and all its decendants (Averianov *et al*., 2010).

Comments: Rauhut *et al.* (2010) first suggested the definition for the Proceratosauridae as "all theropods that are more closely related to *Proceratosaurus* than to *Tyrannosaurus*, *Allosaurus*, *Compsognathus*, *Coelurus*, *Ornithomimus*, or *Deinonychus*". Averianov *et al.* (2010) pointed out that this definition suggested by Rauhut *et al.* (2010) does not meet ICZN's requirements, so their "Proceratosauridae" is a *nomen nudum*. There are currently 5 valid taxa belong to this clade, based on the parsimony analysis of Brusatte, Carr (2016) and 3 of them are from the Jurassic period.

This clade comprises small to large basal tyrannosauroids (Brusatte, Carr, 2016) characterized by crests on their head. Since the crests of these dinosaurs are thin, they might have served as display organs.

Guanlong wucaii (Xu *et al*., 2006)

Age: Oxfordian, Late Jurassic

Occurrence: Shishugou Formation, Xinjiang, China

Comments: This is a taxon famous for its highly distinctive crest on its skull (Fig. 1A). Carr (2006) suggested that this taxon is actually a Carnosauria sister to *Monolophosaurus* or even possibly synonymous with it. This was supported by Paul (2010) as he described this taxon as *Monolophosaurus wucaii*. However, no other analyses have found them as closely related (*e.g.* Loewen *et al*., 2013; Brusatte, Carr, 2016). As this taxon had long forelimbs with a large manus and a small skull with small teeth, it is likely that its forelimbs played an important role in hunting unlike the more derived tyrannosauroids, as their forelimbs are very shortened.

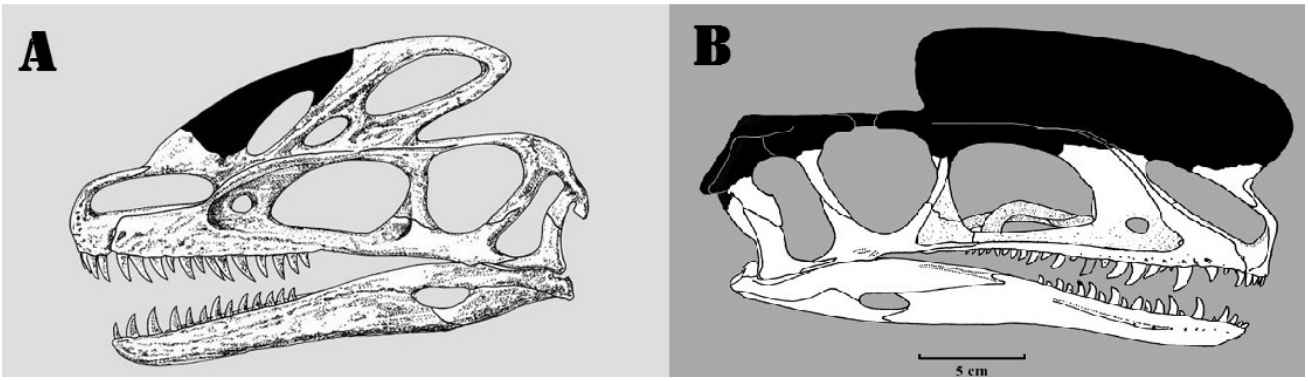

Fig. 1. Skull reconstructions of the two Jurassic proceratosaurids

A. *Guanlong*. **B.** *Proceratosaurus*. Reconstructions by Tracy Ford

Proceratosaurus bradleyi (Woodward, 1910; Huene, 1926)

Age: Middle Bathonian, Middle Jurassic

Occurrence: Great Oolite, England

Comments: Once considered as a taxon closely related to *Ceratosaurus* (Huene, 1926), this is now considered as the currently oldest definite tyrannosauroid and coelurosaur of all time (Rauhut *et al.*, 2010). The currently only known skull has a small "horn" on the end of its snout, but this is probably the trace of a broken delicate crest similar that present in *Guanlong* (Rauhut *et al*., 2010; Fig. 1B). It had a small, subrectangular head and it probably had a similar lifestyle to *Guanlong*.

Kileskus aristotocus (Averianov *et al*., 2010)

Age: Bathonian, Middle Jurassic

Occurrence: Itat Formation, Russia

Comments: This is only known from very fragmentary cranial material, but this is very similar to *Proceratosaurus*. This is one of the most basal coelurosaur and tyrannosauroid genera, and one of the oldest records of these clades. This taxon probably hunted small vertebrates such as fishes, salamanders, turtles or lizards which are widely known in the Itat Formation (Averianov *et al*., 2010).

Primitive **Tyrannosauroidea**

Comments: These genera are placed in between the Proceratosauridae and the Tyrannosauridae. It is still possible that some taxa belong to primitive clades like Proceratosauridae or Coeluridae. There are currently 3 taxa known from the Jurassic Period (Brusatte, Carr, 2016).

Aviatyrannis jurassica (Rauhut, 2003)

Age: Early Kimmeridgian, Late Jurassic

Occurrence: Alcobaca Formation, Portugal

Comments: This is one of the oldest tyrannosauroids ever found. The holotype ilium was once originally referred to *Stokesosaurus*, though later study described it as a new genus (Rauhut, 2003). However, it is probable that this genus is in fact a Portuguese species of *Stokesosaurus*. Some material such as an ilium (now lost) and an isolated tooth from the North American Morrison Formation were once referred to *Stokesosaurus*, but might actually belong to *Aviatyrannis* (Rauhut, 2003). These findings, and the cases of Portuguese *Allosaurus* or *Torvosaurus* (Mateus *et al.*, 2006), support the Kimmeridgian land connections between North America and Europe.

Juratyrant langhami (Benson, 2008; Brusatte, Benson, 2013)

Age: Early Tithonian, Late Jurassic

Occurrence: Kimmeridge Clay, England

Comments: Once thought to be a species of *Stokesosaurus*, later study found this taxon to be a new genus of tyrannosauroid. A 2013 analysis found the taxon to be closely related to *Eotyrannus* (Brusatte, Benson, 2013) but later analyses support a close relationship with *Stokesosaurus* (*e.g.* Loewen *et al.*, 2013). *Juratyrant* and *Stokesosaurus* once thought to be as derived Proceratosauridae (Loewen *et al.*, 2013) but later analyses found no support for this classification (*e.g.* Brusatte, Carr, 2016). This taxon was quite larger than *Stokesosaurus*, as the preserved ilium was more than twice as big as the *Stokesosaurus* holotype (Fig. 2A).

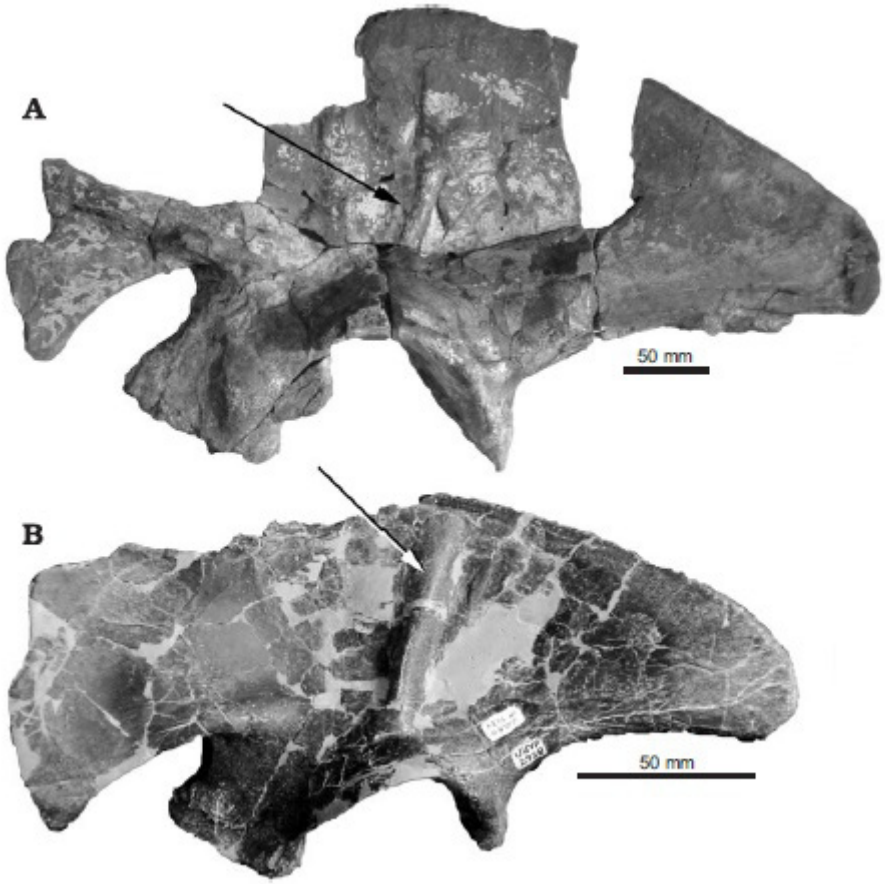

Fig. 2. Comparison of the two ilia of different Jurassic tyrannosauroids

A. *Stokesosaurus*. **B.** *Juratyrant*. Modified from Brusatte, Benson (2013)

Stokesosaurus clevelandi (Madsen, 1974)

Age: Middle, Late Kimmeridgian, Late Jurassic

Occurrence: Morrison Formation, South Dakota, USA

Comments: Even though material belonging to several specimens has been referred to this taxon, the only certain material is the holotype ilium (Fig. 2B). Some material referred to this taxon may be *Aviatyrannis*. The genus once had an English species *Stokesosaurus langhami*, but this taxon was recently described as the new genus *Juratyrant* (Brusatte, Benson, 2013). *Stokesosaurus* and *Juratyrant* once thought to be derived Proceratosauridae (Loewen *et al*., 2013) but later analyses found no support for this classification (*e.g.* Brusatte, Carr, 2016).

DISCUSSION

There are currently 6 certain cases of Jurassic tyrannosauroids, and this becomes 9 when possible cases are included. At least 3 taxa are from the European continent, this being about 50% of the current diversity. When possible cases are included, 4 taxa are from Europe and this is approximately 44% of current cases. This strongly suggests the European origin of the tyrannosauroids, and the currently known oldest tyrannosauroid taxa (*Proceratosaurus*, possibly *Iliosuchus*) are found in Europe. The fact that North America and Europe were connected in the Late Jurassic further supports this hypothesis. However, with the current state of the lack of enough tyrannosauroid material from the Jurassic, this is still not certain. But the abundance of basal, Jurassic tyrannosauroid material from Eurasia indicates they are originated at least in Eurasia.

The question of where and when the clade Coelurosauria originated, and diversified remains uncertain. *Eshanosaurus* from the Lufeng Formation of China is Early Jurassic in age, and the possibility that *Eshanosaurus* might be a derived therizinosaurian could suggest that the coelurosaurs might have originated and diversified long before that (Xu *et al.*, 2001). However, this taxon still could be a basal Sauropodomorpha convergent with the therizinosaurs (Kirkland, Wolfe, 2001) so this is yet to be certain.

Given the fact that the tyrannosauroids are largely considered as the basal-most coelurosaurian clade (*e.g.* Loewen *et al.*, 2013; Brusatte *et al.*, 2014), the diversification or the origin of the coelurosaurs could be inferred from Jurassic tyrannosauroids. *Proceratosaurus* is the definite oldest coelurosaur known as today (Rauhut *et al*., 2010), so it is possible that the whole Coelurosauria clade originated in Europe, or at least Eurasia. However later, detailed studies of the exact age and systematic position of *Eshanosaurus*, or future discoveries of basal coelurosaurs, will make this issue clear.

Acknowledgements. I thank Thomas Holtz, and Thomas Carr for kindly discussing the evolutionary history of the tyrannosauroids with me. Discussions with J.Y. Park, Y.W. Lee, B.H. Ji about coelurosaur radiation were also helpful. I thank all these people. My special thank goes to Mickey Mortimer, whose excellent database of theropod information helped this study a lot. I am particularly thankful of Tracy Ford for allowing me to use his skull reconstructions.

REFERENCES

AVERIANOV A.O., KRASNOLUTSKII S.A., IVANTSOV S.V., 2010 — A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute*. **314**, 1: 42–57.

BARRETT P.M., 2009 — The affinities of the enigmatic dinosaur *Eshanosaurus deguchiianus* from the Early Jurassic of Yunnan Province, People's Republic of China. *Palaeontology*, **52**, 4: 681–688.

BENSON R.B.J., 2009 — An assessment of variability in theropod dinosaur remains from the Bathonian (Middle Jurassic) of Stonesfield and New Park Quarry, UK and taxonomic implications for *Megalosaurus bucklandii* and *Iliosuchus incognitus*. *Palaeontology*, **52**: 857–877.

BRUSATTE S.L., BENSON R.B.J., 2013 — The systematics of Late Jurassic tyrannosauroids (Dinosauria: Theropoda) from Europe and North America. *Acta Palaeontologica Polonica*, **58**, 1: 47–54.

BRUSATTE S.L., CARR T.D., 2016 — The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Scientific Reports*, **6**, 20252.

BRUSATTE S.L., LLOYD G.T., WANG S.C., NORELL M.A., 2014 — Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology*, **24**, 20: 2386–2392.

CARPENTER K., MILES C., CLOWARD K., 2005 — New small theropod from the Upper Jurassic Morrison Formation of Wyoming. *In*: The Carnivorous Dinosaurs (ed. K. Carpenter): 23–48. Indiana University Press, Bloomington.

CARR T., 2006 — Is *Guanlong* a tyrannosauroid or a subadult *Monolophosaurus*? *Journal of Vertebrate Paleontology*. **26**: 48A.

CARRANO M.T., BENSON R.B.J., SAMPSON S.D., 2012 — The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **10**, 2: 211–300.

CHOINIERE J.N., CLARK J.M., FORSTER C.A., NORELL M.A., EBERTH D.A., ERICKSON G.M., CHU H., XU X., 2014 — A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle-Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. *Journal of Systematic Palaeontology*, **12**, 2: 177–215.

GALTON P.M., 1976 — *Iliosuchus*, a Jurassic dinosaur from Oxfordshire and Utah. *Palaeontology*, **19**, 3: 587–589.

HENDRICKX C., HARTMAN S.A., MATEUS O., 2015 — An overview of non-avian theropod discoveries and classification. *PalArch's Journal of Vertebrate Palaeontology*, **12**, 1: 1–73.

HUENE F.V., 1926 — On several known and unknown reptiles of the order Saurischia from England and France. *Annals and Magazine of Natural History*, **9.17**, 101: 473–489.

HUENE F.V., 1932 — Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie*, serie 1, **4**, 1/2: 1–361.

KIRKLAND J.I., WOLFE D.G., 2001 — First definitive therizinosaurid (Dinosauria: Theropoda) from North America. *Journal of Vertebrate Paleontology*, **21**, 3: 410–414.

KIRKLAND J.I., ZANNO L.E., SAMPSON S.D., CLARK J.M., DEBLIEUX D.D., 2005 — A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature*, **435**, 7038: 84–87.

LOEWEN M.A., IRMIS R.B., SERTICH J.J.W., CURRIE P.J., SAMPSON S.D., 2013 — Tyrant Dinosaur Evolution Tracks the Rise and Fall of Late Cretaceous Oceans. *PLoS ONE*, **8**, 11: e79420.

MARSH O.C., 1879 — Notice of new Jurassic reptiles. *American Journal Science*, **18**: 501–505.

MARSH O.C., 1881 — A new order of extinct Jurassic reptiles (Coeluria). *American Journal Science*, **21**: 339–341.

MADSEN J.H., 1974 — A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of Paleontology*, **48**: 27–31.

MATEUS O, WALEN A, ANTUNES M.T., 2006 — The large theropod fauna of the Lourinha Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of a new species of *Allosaurus*. *In*: Paleontology and Geology of the Upper Jurassic Morrison Formation (eds J.R. Foster, S.G. Lucas): 123–129. New Mexico Museum of Natural History and Science Bulletin, **36**. Albuquerque, New Mexico.

NOVAS F.E., AGNOLIN F.L., EZCURRA M.D., PORFIRI J., CANALE J.I., 2013 — Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research*, **45**: 174–215.

PAUL G.S., 2010 — The Princeton Field Guide to Dinosaurs. Princeton University Press. 320 pp.

RAUHUT O.W.M., 2003 — A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology*, **46**, 5: 903–910.

RAUHUT O.W.M., MILNER A.C., MOORE-FAY S., 2010 — Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society*, **158**: 155–195.

SENTER P., 2007 — A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Paleontology*, **5**, 4: 429–463.

TURNER A.H., POL D., CLARKE J.A., ERICKSON G.M., NORELL M.A., 2007 — A basal dromaeosaurid and size evolution preceding avian flight. *Science*, **317**: 1378–1381.

WOODWARD A.S., 1910 — On a skull of *Megalosaurus* from the Great Oolite of Minchinhampton (Gloucestershire). *Quarterly Journal of the Geological Society*. **66**: 111–115.

XU X., ZHAO X., CLARK J.M., 2001 — A new therizinosaur from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. *Journal of Vertebrate Paleontology*, **21**, 3: 477–483.

XU X., CLARK J.M., FORSTER C.A., NORELL M.A., ERICKSON G.M., EBERTH D.A., JIA C., ZHAO Q., 2006 — A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature*, **439**, 7077: 715–718.

ZANNO L.E., 2010 — A taxonomic and phylogenetic review of Therizinosauria. *Journal of Systematic Palaeontology*, **8**: 503–543.

ZHAO X., XU X., 1998 — The oldest coelurosaurian. *Nature*, **394**, 6690: 234–235.