TESTING THE HYPOTHESES OF THE ORIGIN OF TYRANNOSAURUS REX: IMMIGRANT SPECIES, OR NATIVE SPECIES?

Chan-gyu Yun

Vertebrate Paleontological Institute of Incheon, Incheon 21974, Republic of Korea
& Biological Sciences, Inha University, Incheon 22212, Republic of Korea
changyu1015@naver.com

Abstract: It is an undoubtable fact that Tyrannosaurus rex is the most iconic dinosaur species of all time. However, it is currently debatable whether this species has a North American origin or Asian origin. In this paper, I test these two hypotheses based on current fossil records and former phylogenetic analyses. Phylogenetic and fossil evidence, such as derived tyrannosaurine fossils of Asia, suggests that the hypothesis of an Asian origin of Tyrannosaurus rex is the most plausible one, but this is yet to be certain due to the scarcity of fossil records.

INTRODUCTION

The most famous and iconic dinosaur of all time, Tyrannosaurus rex, is only known from upper Maastrichtian geological formations in Western North America (e.g. Carr and Williamson, 2004; Larson, 2008). However, older relatives of Tyrannosaurus rex (e.g. Daspletosaurus, Tarbosaurus) are known from both Asia and North America. This leads to an evolutionary question: is the origin of Tyrannosaurus rex from Asia, or North America?

About six of the currently valid tyrannosaurine taxa were described in the twenty-first century (based on parsimony analysis of Brusatte and Carr, 2016), with new species which are being described (Sebastian Dalman, Pers. Comm., 2016; Thomas Carr, Pers. Comm., 2016). It can be said that "now" is the "golden age" for studying tyrannosaurine evolution.

Currie et al. (2003) suggested there was two lineages of tyrannosaurines, an Asian lineage, including Daspletosaurus, Alioramus and Tarbosaurus, and a North American lineage, including Tyrannosaurus and Nanotyrannus. The analysis by Loewen et al. (2013) recovered a very different phylogenetic tree from Currie et al. (2003). In addition, they found a northern Laramidian origin for Tarbosaurus and Tyrannosaurus, and concluded that Tarbosaurus and Zhuchengtyrannus represent a dispersal to Asia (Fig. 1A). In contrast, Brusatte and Carr (2016) found Tyrannosaurus rex as nested within the Asian clade consisting Tarbosaurus and Zhuchengtyrannus, and suggested an Asian origin of the taxon (Fig. 1B). Dalman and Lucas (2016) disputed this based on the absence of Tyrannosaurus rex in Asia.

In this paper, I test these two hypotheses about the origin of Tyrannosaurus rex based on the recent phylogenetic analyses and current fossil records of tyrannosaurines.

REVIEW OF THE PHYLOGENETIC ANALYSES OF THE 21TH CENTURY

Currie et al. (2003) found Tyrannosaurus rex as sister to Nanotyrannus, and this North American clade as sister to clade comprising Daspletosaurus, Tarbosaurus and Alioramus. However, this is problematic since Nanotyrannus is very likely a juvenile Tyrannosaurus rex (Brusatte et al., 2016; Carr, 1999; Carr and Williamson, 2004; Yun, 2015; but see Larson, 2013). Many more recently named genera were missing in the Currie al (2003) analysis.

Loewen et al. (2013) presented a phylogenetic tree containing large number of species of tyrannosauroidea and coelurosauria, and using more anatomical characters. The authors found Tyrannosaurus rex just outside the clade of Asian tyrannosaurines comprising Tarbosaurus and Zhuchengtyrannus, and this conclusion was supported by Fiorillo and Tykoski (2014). However, Brusatte and Carr (2016) criticized the phylogenetic characters used by Loewen et al. (2013) since many of their characters are related to overall skull proportions and it might have caused a 'longirostrine problem' which causes distantly related crocodylomorphs to artifactually group together.

Both parsimony and Bayesian analyses presented by Brusatte and Carr (2016) places Tyrannosaurus rex as sister to the Asian Tarbosaurus, and just more derived than the Asian Zhuchengtyrannus (Fig. 1B). This places Tyrannosaurus rex within the Asian clade of tyrannosaurines. Based on the comments and criticisms of Brusatte and Carr (2016) of previous analyses it is safe to say that most recent phylogenetic analyses support the Asian origin of Tyrannosaurus rex.

REVIEW OF THE FOSSIL RECORDS OF TYRANNOSAURINAE

The closest relatives of Tyrannosaurus rex are Tarbosaurus and Zhuchengtyrannus based on the recent phylogenetic analyses (Loewen et al., 2013; Brusatte and Carr, 2016). They are geologically older than Tyrannosaurus, and from the Asian continent. However, given that these are only scientifically named examples it is necessary to review the distribution of Tyrannosaurus-like tyrannosaurine in order to determine the origin of Tyrannosaurus rex.

Daspletosaurus is closely related to Tyrannosaurus rex, and includes many species. Horner et al. (1992) proposed a Two Medicine Formation species of Daspletosaurus from Montana as transitional between Daspletosaurus torosus and Tyrannosaurus rex, based on an antorbital fenestra that is high rather than long, enlarged ventral foramina of basisphenoid, and occipital condyle pointing ventrally. However, Holtz (2001) found it in three possible positions: as a basal tyrannosaurine, as sister to Daspletosaurus torosus, or as sister to both Tyrannosaurus rex and Tarbosaurus. Carr and Varricchio (2014) found it as sister to Daspletosaurus torosus. Thomas Carr

(pers. com.) and is preparing a monograph to describe the taxon in detail. At present, Daspletosaurus appears to have no direct lineage to Tyrannosaurus.

Stein and Triebold (2013) preliminarily described a new tyrannosaurine skeleton from Judith River Formation of Montana, and concluded it is similar to Daspletosaurus in position of lacrimal horn, but more similar to Tyrannosaurus rex in tooth count, dentary proportion, lacrimal proportion, body proportion and robustness. This unnamed taxon might be close to origin of Tyrannosaurus rex, or represent a new genus or species of tyrannosaurine close to Daspletosaurus.

Urban and Lamanna (2007) reported an isolated tyrannosaurid lacrimal CM 9401 possibly from Judith River Formation of Montana. The lacrimal is similar to that of Tyrannosaurus rex in its large size, lack of a horn, small lacrimal foramen and top of it is inflated. However, it differs from that of Tyrannosaurus rex in its more slender jugal process and an oblique ridge on the medial surface is stouter and robust (Urban and Lamanna, 2007; Fig. 2A). A Tyrannosaurus-sized tooth is also known from the Campanian (Tracy Ford, Pers. Comm., 2014). The lacrimal and tooth suggest that there is a large, as yet unnamed tyrannosaurine from the Campanian of North America. However, Thomas Carr pointed out that some portions of CM 9401 are reconstructed, and may not be different from Tyrannosaurus rex (Thomas Carr, Pers. Comm., 2014). In fairness to Urban and Lamanna (2007), they did mention that this specimen might not come from the Campanian.

Southern regions of North America have yielded fragmentary remains of a large tyrannosaurid, often referred to Tyrannosaurus rex (e.g. Jasinski et al., 2011; Fig. 2B). However, it is possible that these southern geological formations are actually early Maastrichtian in age, several million years older than Tyrannosaurus rex (Sebastian Dalman, Pers. Comm., 2016). It is therefore possible that these materials might actually belong to older species of Tyrannosaurus, or an entirely new genus. Unfortunately, the lack of adequate material makes this hypothesis difficult to test. Also, the most recent age estimates for the Naashoibito Member of Ojo Alamo Formation suggests late Maastrichtian age (Williamson et al., 2014), which is the same for the Hell Creek Formation, where Tyrannosaurus rex is from. So currently there are no definite case of large sized tyrannosaurine close to Tyrannosaurus, Tarbosaurus and Zhuchengtyrannus.

In contrast, Asia has yielded various large tyrannosaurine materials. The Udurchukan Formation of the Tsagayan group in Russia is late Maastrichtian in age, and it has yield a metacarpal I similar in size to that of Tyrannosaurus rex (Bolotsky, 2013).

An incomplete dentary of a large tyrannosaurid, IZK 33/MP-61 was found in Almaty Province in Eastern Kazakhstan; it is Santonian-Early Campanian in age (Fig. 2C). This is some of the oldest tyrannosaurid material known to date, and its large size (approximately 49 cm) and reduced first dentary alveolus, suggest the material is close to Tyrannosaurus, Tarbosaurus and Zhuchengtyrannus (Averianov et al., 2012).

Various fragmentary materials of large tyrannosaurine have reported in China and Mongolia, and some of them are Campanian in age (e.g. Sullivan et al., 2012; Mo and Xu, 2015). These

are contemporaneous with Zhuchengtyrannus, but slightly older than Tarbosaurus which is early Maastrichtian in age. The abundance of definite, large tyrannosaurine materials, which are older than Tyrannosaurus rex, favors the hypothesis of Tyrannosaurus rex as the descendant of immigrant species from Asia. This hypothesis might also explain why Tyrannosaurus rex was, oddly, the only tyrannosaurid species of North America at that time, and how it is closely related to older, Asian taxa. Dalman and Lucas (2016) disputed the hypothesis of Tyrannosaurus rex as immigrant species of Asia as no fossil records of the species are known in that continent. It is, however, possible that the direct ancestors of Tyrannosaurus rex, not the species itself, dispersed into North America from Asia. Also, the geological formations, which are producing tyrannosaurs in Asia, are not the same age as North American Formations as they are Campanian or late Maastrichtian in age. However, given the fact that most materials of both Asia and North America are fragmentary or undescribed, this hypothesis remains tentative.

CONCLUSIONS

The hypothesis of Asian origin for the direct ancestor of *Tyrannosaurus rex* most easily explains why it is the sole species of that time and region and most closely related to Asian *Tarbosaurus* and *Zhuchengtyrannus*, not taxa from North America such as *Daspletosaurus* or *Lythronax*. The most recent phylogenetic analyses, definite fossil records from Asia support this hypothesis. Future studies of dispersal of dinosaurs between North America and Asia may help understanding tyrannosaurid diversity and evolution more than we know now.

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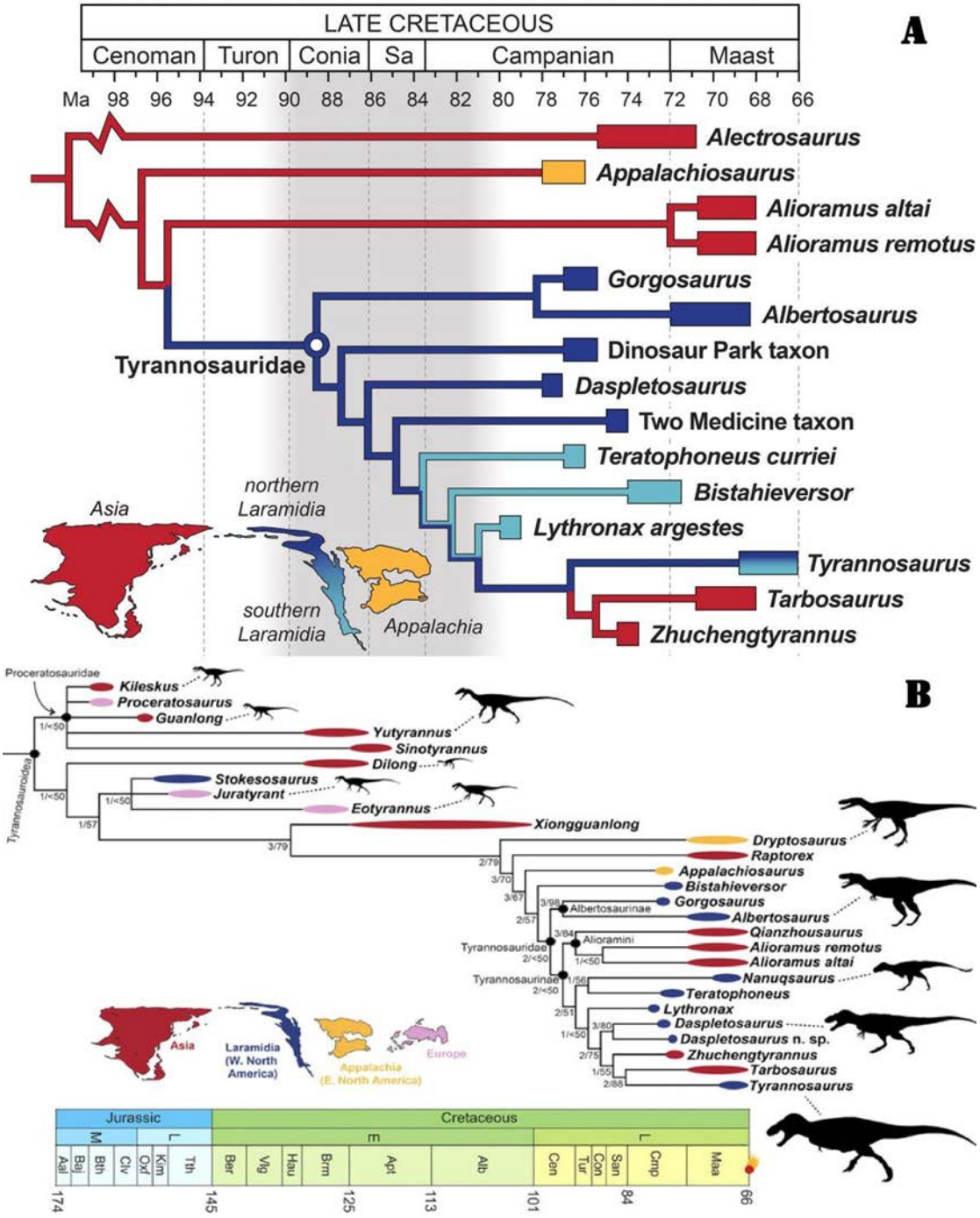

Figure 1. The most recent phylogenetic trees of tyrannosauroid dinosaurs. (A) is from Loewen et al. (2013). Permission to use figure granted through PLoS ONE Open Access under the terms of the Creative Commons Attribution License. Original figure appears in: Loewen, M.A., Irmis, R.B., Sertich, J.J.W., Currie, P.J., and Sampson, S.D. (2013). Tyrant Dinosaur Evolution Tracks the Rise and Fall of Late Cretaceous Oceans. PLoS ONE. 8(11), e79420. (B) is from parsimony analysis of Brusatte and Carr (2016). Permission to use figure granted through Nature Publishing Group under the terms of the Creative Commons Attribution License and from Thomas Carr. Original figure appears in: Brusatte, S.L., and Carr, T.D. (2016). The phylogeny and evolutionary history of tyrannosauroid dinosaurs.

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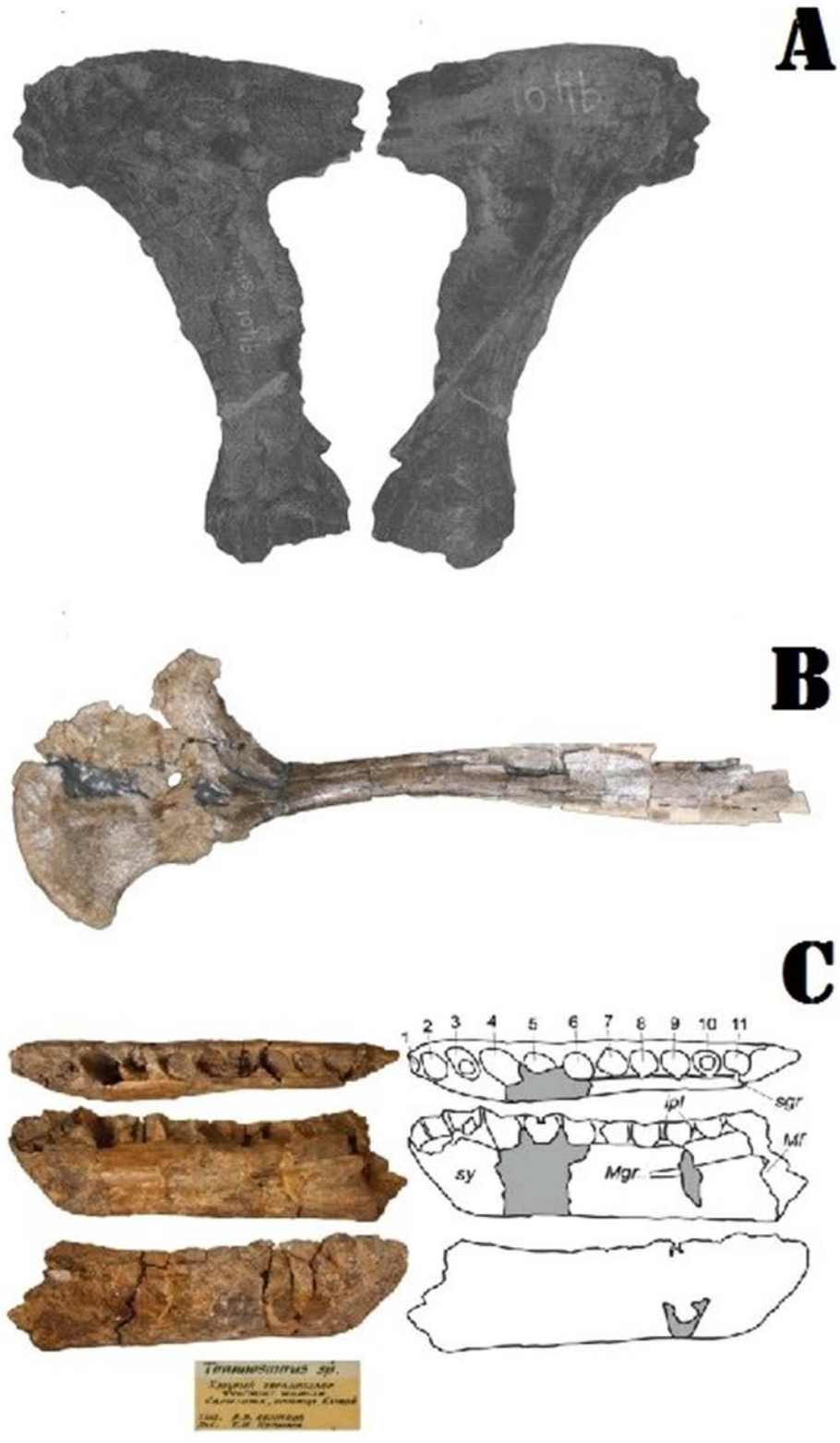

Figure 2. Materials of derived tyrannosaurines from North America and Asia, which are known as older than Tyrannosaurus rex. (A) lacrimal specimen CM 9401, reported as from Judith River Formation but possibly just a mix-up specimen actually from late Maastrichtian. Used with Permission from Carnegie Museum of Natural History. (B) Tyrannosaurus scapula from Naashoibito Member of Ojo Alamo Formation. Used with permission from Spencer G. Lucas. (C) Tyrannosaurid dentary from eastern Kazakhstan, which is Santonian-Early Campanian in age. Used with permission from Alexander O. Averianov. (A) is modified from Urban and Lamanna (2007), (B) is modified from Jasinski et al. (2011), (C) is modified from Averianov et al. (2012).