

An enigmatic theropod *Cryolophosaurus*: Reviews and comments on its paleobiology

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Abstract. *Cryolophosaurus* is a genus of theropod dinosaur that is characterized by its distinctive crest formed by dorsally expanded lacrimals. Although its fossils are rare, currently recognized materials suggest this taxon was the largest predator in the Early Jurassic times in Antarctica, indicating it was the apex predator in its ecosystem. The skeleton of *Cryolophosaurus* bears both advanced and basal characteristics of theropods, making its position within theropod phylogenetic tree controversial. Its unusual anatomical features, size, and the habitat located close to the Jurassic polar circle all differ from other Early Jurassic theropods, indicating it was one of the most ecologically significant taxon of all theropods.

INTRODUCTION

Cryolophosaurus ellioti Hammer & Hickerson, 1994 is the most significant dinosaur ever discovered in Antarctica. It was discovered in 1991 by Ohio State University geologist David Elliot, after whom the species is named. The discovery locality is Mt. Kirkpatrick in the Beardmore Glacier area, Queen Alexandra Range, Transantarctic Mountains (Smith *et al.*, 2007a). Although its body fossils are rare and several important specimens are not formally described, its unusual morphology with distinctive crest above its eyes, large size, and the mixture of both basal and advanced anatomical characteristics mark the taxon out as divergent from the typical morphology and body plan of all other Early Jurassic theropod dinosaurs (Fig. 1). In the literature, the taxon's stratigraphic and paleogeographic distribution is limited to the lower Jurassic, Sinemurian to Pliensbachian aged Hanson Formation that is located in southern Antarctica (Hammer, Hickerson, 1994, 1999). As indicated by its name (*Cryolophosaurus* in Greek means “Frozen Crested Reptile”), *Cryolophosaurus* is also important in regards to representing one of the first cases of theropod dinosaurs that lived and adapted to relatively cooler circum-polar environments, and one of the first cases of theropods were the top predators in their ecosystems. Here the author reviews the taxonomy and paleobiology of *Cryolophosaurus* and comments on its ecological role in the Jurassic Antarctica ecosystem.

TAXONOMY AND SYSTEMATIC POSITION OF *CRYLOPHOSAURUS*

The phylogenetic position of *Cryolophosaurus* has been varied in many different phylogenetic analyses, due to its unusual combination of characters and very limited number of known skeletal materials. The skull of *Cryolophosaurus* shows de-

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Fig. 1. The holotype (FMNH PR 1821) skull of *Cryolophosaurus ellioti* in lateral view. Photo Credit: Jonathan Chen.
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rived features that is similar to tetanurans such as *Allosaurus*, *Yangchuanosaurus* or *Piatnitzkysaurus*, but its postcranial skeleton more closely resembles relatively basal theropods like *Dilophosaurus* or ceratosaurs (Hammer, Hickerson, 1994). In the first description of this taxon, the original authors had suspected three possible positions: one within Ceratosauria with derived cranial features that is convergent with tetanurans, second is an early abelisaur, and the third is primitive tetanuran (Hammer, Hickerson, 1994) but subsequent analyses have been found greatly variable position of *Cryolophosaurus* within theropod phylogenetic tree. Sereno *et al.* (1994) placed *Cryolophosaurus* as Allosauridae based on morphologies of quadrate, surangular and mandibular fenestra. Smith *et al.* (2005) recovered it as very basal tetanuran, but subsequent, more complete studies of the same authors found a less derived position, forming a clade with *Dilophosaurus*, *Dracovenator*, and “*Dilophosaurus*” *sinensis* (regarded as synonymous with *Sinosaurus triassicus* by Xing *et al.*, 2013) that is sister to *Averostra* (Smith *et al.*, 2007a, b; Fig. 2). Nesbitt *et al.* (2009) found a position that is more basal than dilophosaurids and averostrans, and Carrano *et al.* (2012) considered it as basal tetanuran that is closely related to *Sinosaurus*. Lastly, Hendrickx *et al.* (2015) agreed with previous studies that regarded *Cryolophosaurus* as basal tetanuran.

Such confusing, ununiform hypotheses of systematic position and taxonomy is in part, due to the limited number of *Cryolophosaurus* specimens that have been formally described. Until now, only the holotype specimen (Field Museum of Natu-

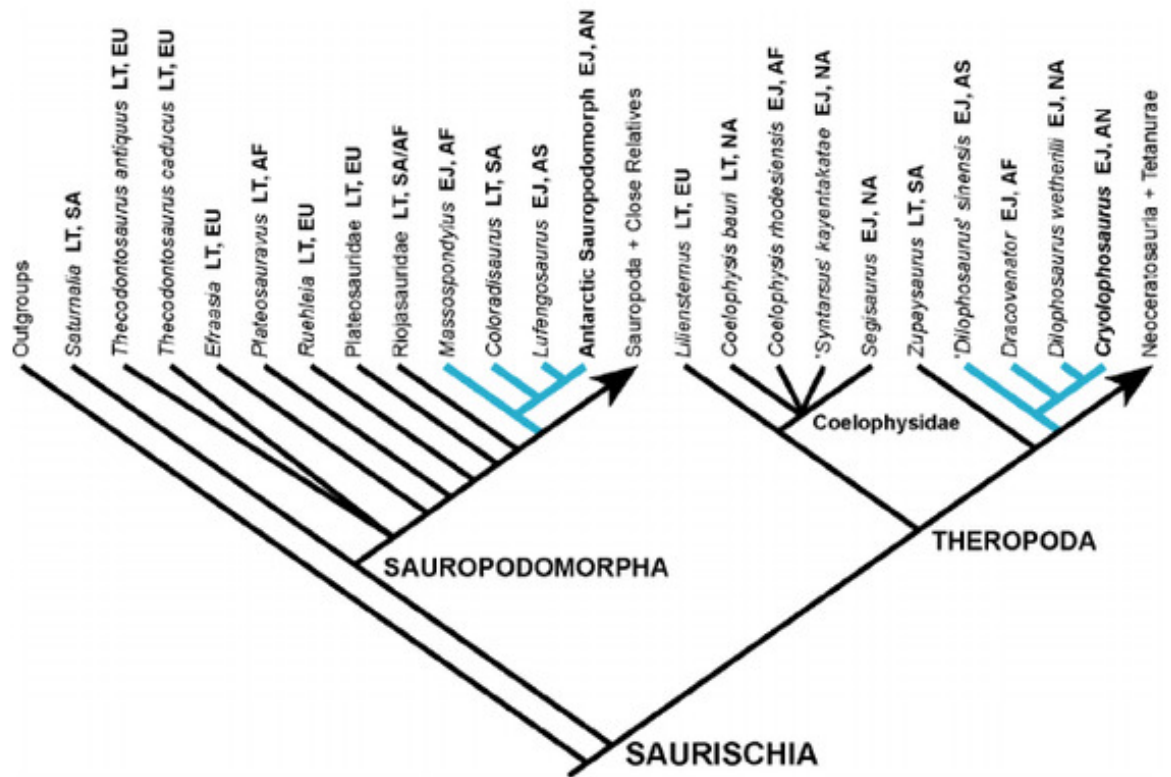


Fig. 2. The position of *Cryolophosaurus* within Saurischia and Theropoda by Smith *et al.* (2007a, b). Modified from Smith *et al.* (2007b)

ral History PR1821) has been received formal description and monographic treatment (*e.g.* Smith *et al.*, 2007a) although undescribed specimens are indeed present (Crandall, 2012; Smith *et al.*, 2012). These specimens have been only appeared in the literature in an abstract form and most informations about them are currently unavailable for more detailed phylogenetic analyses or extract characters for it. Clearly, monographic treatments for these undescribed specimens will reveal more about the systematic position of this theropod with uncertain position. Therefore, it is best to consider *Cryolophosaurus* as Neotheropoda *incertae sedis* at current status, although this uncertain placement will be likely to change depending on future studies or discoveries.

ANATOMY OF *CRYLOPHOSAURUS*

According to Smith *et al.* (2007a), *Cryolophosaurus ellioti* can be distinguished from all other theropods by the presence of a large, anterodorsally curving midline crest with fluted rostral and caudal surfaces formed by dorsal expansions of the lacrimals, a complete constriction across the infratemporal fenestra formed by the squamosal and jugal, and extremely elongate cranial processes on the cervical ribs. However, given that the holotype specimen of *Cryolophosaurus ellioti* is not fully grown individual and only the holotype was formally described, some of its purported autapomorphies could be individually or ontogenetically variable.

In addition to the autapomorphic features listed above that define *Cryolophosaurus*, several other anatomical features or combination of them do mark out *Cryolophosaurus* from the other Early Jurassic theropods. Although the overall morphology of *Cryolophosaurus* cranium is similar to tetanurans like allosaurids or metriacanthosaurids (Hammer, Hickerson, 1994), the braincase and endocranial anatomy was actually more similar to basal theropods and significantly differed from derived tetanurans (Meidinger-Chin, 2013). The vertebral column anatomy of *Cryolophosaurus* is also similar to those of

basal theropods like *Dilophosaurus* rather than derived tetanurans: its vertebrae centra are platycoelous, unlike the condition in larger derived theropods which have opisthocoelous centra (Crandall, 2012). Appendicular skeletons also bear combinations of unusual morphological features: forelimbs most similar to theropods like *Dilophosaurus* in its relatively gracile morphology, while hindlimbs show fusion of tibia, astragalus and calcaneum similar to several ceratosaurians (Smith *et al.*, 2007a). It is possible that many of these unusual features are related to ecology, and this possibility will be discussed at below.

BEHAVIOR, ECOLOGY AND PALEOBIOLOGY OF *CRYOLOPHOSAURUS*

Currently, studies of *Cryolophosaurus* have been concentrated on its position within evolutionary history of Theropoda rather than its paleoecology. In this section, the author comments and speculate on its ecology and biology based on its anatomy and geographical distribution.

Cryolophosaurus is currently one of the largest recognized Early Jurassic theropod that is known to dinosaur paleontology (Hendrickx *et al.*, 2015), indicating it could hunt down larger prey than other theropods at the same period of time. Indeed, large sauropodomorphs or sauropod remains have been yielded in the same geological quarry as *Cryolophosaurus* in Hanson Formation (Smith *et al.*, 2007b), indicating this theropod could have preyed on these large herbivores. If *Cryolophosaurus* was a basal neotheropod or Dilophosauridae that converged with tetanurans as suggested by previous authors, it is possible that such tetanuran-like modifications of the cranium and large body size may be adaptive features that is suited to hunt large prey. Indeed, the robust skull morphology of *Cryolophosaurus* dramatically differs from that of *Dilophosaurus*, and the latter was found to have weak bite force and probably hunted small prey (Therrien *et al.*, 2005). Taphonomic evidence suggest a generalist role of *Cryolophosaurus* as a predator: the holotype's stomach contents included a tooth of a tritylodont cynodont (Stilwell, Long, 2011). Fossils of *Cryolophosaurus* also show evidence of cannibalistic behavior: the holotype of *Cryolophosaurus* was found disarticulated and scattered, and several shed theropod teeth were found nearby. These shed teeth were attributed to juvenile *Cryolophosaurus* (Rich *et al.*, 1997). Evidence for cannibalism are found in numerous clades of theropods, including abelisaurids (Rogers *et al.*, 2007), tyrannosaurids (Longrich *et al.*, 2010) and possibly dromaeosaurids (Roach, Brinkman, 2007) and given that cannibalistic behavior is surprisingly common in mammalian or reptilian predators (Roach, Brinkman, 2007) it is reasonable to assume that *Cryolophosaurus* occasionally consumed its own kind by opportunistic carrion scavenging or necessary predation at harsh seasons.

One of the autapomorphic feature in *Cryolophosaurus* is the elongate cranial processes of cervical ribs. According to a study in 2013 (Preuschoft, Klein, 2013), "cervical ribs" of archosaurs are actually ossified tendons, which implies that the condition in *Cryolophosaurus* indicate this taxon had long tendons in its neck which probably limited its flexibility. This contrasts with the condition in large tetanuran *Allosaurus*, which used its flexible neck to powerful ventroflexion to easily take down large prey like sauropods (Bakker, 1998; Snively *et al.*, 2013). Moreover, the platycoelous condition of cervical vertebrae in *Cryolophosaurus* also strongly differs from the condition in *Allosaurus*, which is opisthocoelous (Snively *et al.*, 2013). Collectively, this suite of features in cervical vertebrae suggests a different mode of prey capture and processing from *Allosaurus* in *Cryolophosaurus*. Platycoelous cervical vertebrae are also known in abelisaurid theropods (e.g. *Carnotaurus*), and considering that such morphology is more suitable to lateral movement than vertical, it is possible that bite-and-hold behavior using neck retraction or low-motion headbutting behavior may have been present in *Cryolophosaurus*, as suggested for

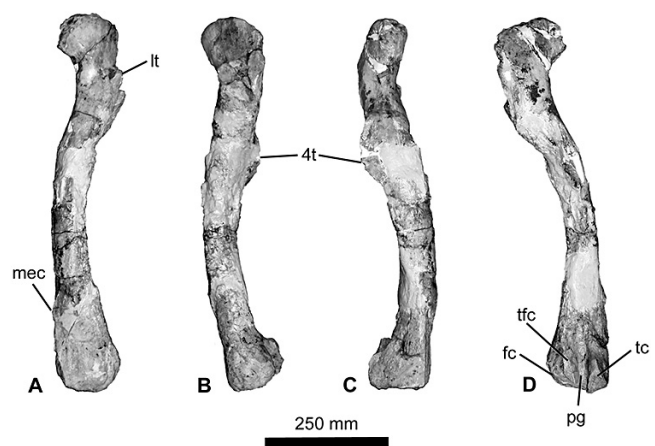


Fig. 3. The left femur of *Cryolophosaurus* holotype (FMNH PR 1821). Notice the prominent fourth trochanter. From Smith *et al.* (2007a)

4t – fourth trochanter; fc – fibular condyle; lt – lesser trochanter; mec – medial epicondylar crest; pg – posterior intercondylar groove; tc – tibial condyle; tfc – tibiofibular crest

abelisauroids (Delcourt, 2018). However, given the paucity of currently known materials and lack of craniofacial soft tissue inference in *Cryolophosaurus*, this possibility should be considered as tentative.

Cryolophosaurus is known to have coossified astragalocalcaneum in its hindlimbs (Smith *et al.*, 2007a). According to Coombs (1978), hinge-like joints in foot is a cursorial character so the fused astragalocalcaneum character in *Cryolophosaurus* may indicate this animal was capable of high-speed running or fast movements. Moreover, the fourth trochanter of the femur in *Cryolophosaurus* is well developed for theropods of its age (it is even more prominent than later tetanuran *Allosaurus*; Smith *et al.*, 2007a; Fig. 3) and caudal ribs are elevated, which suggest it had large caudofemoralis muscle. Given that caudofemoralis muscle is crucial in terms of overall cursoriality, balance and turning agility (Persons, Currie, 2011), it is probable that *Cryolophosaurus* was an agile predator that achieved faster speed than its potential prey items. Combination of hindlimb and tail anatomy suggest a possible predatory model for *Cryolophosaurus*: seize down their prey by chasing after them like modern canids or hyaenids (Holtz, 2008). However, the absolute speed of *Cryolophosaurus* is hard to determine due to lack of trackway records or biomechanical analyses (such test is hard to conduct at present status as the holotype of *Cryolophosaurus* lacks most of tibiae and pes) so the future new discoveries and studies are crucial for test this hypothesis.

The most distinctive feature of *Cryolophosaurus* is the prominent crest that is located above its eyes (Fig. 1). Distinctive cranial crests are known in basal tetanuran *Monolophosaurus* (Zhao, Currie, 1993), proceratosaurid tyrannosauroids (Xu *et al.*, 2006; Yun, 2016) and basal neotheropod dilophosaurids like *Dilophosaurus* and *Sinosaurus* but the crest of *Cryolophosaurus* strongly differs from these theropods in having thin, highly furrowed, pompadour-like morphology. Oddly, the crest of *Cryolophosaurus* actually received little commentary despite its unusual morphology. It is highly unlikely that this crest was used for intraspecific combat, given its thin, fragile structure. It is similar in relatively small relative to the whole body size and situated close to above the eyes as those present in other large theropods (Hone *et al.*, 2012). Such exaggerated cranial or postcranial structures in dinosaurs have been considered as “species recognition” role (Padian, Horner, 2011) but this hypothesis is disputed due to lack of evidence (Hone, Naish, 2013). Applying such model to *Cryolophosaurus* is also problematic as this taxon is the only currently recognized large theropod in Early Jurassic of Antarctica and actually a single body fossil record of any Early Jurassic theropod of that size, with no sympatric relatives. In the absence of compelling counter-evidence, it is best to consider the cranial crest of *Cryolophosaurus* was functioned as socio-sexual display structure (Hone *et al.*, 2012), in other words social-dominance display role or sexually selected character (Fig. 4). Although the cranial crest of *Cryolophosaurus* is prominent, it is relatively small compared to long, large paired crests in its possible relatives *Dilophosaurus* or *Sinosaurus*. According to Hone *et al.* (2012), relatively small size of the cranial crest in theropods could be a sign of trade-off between socio-sexual signaling and to avoid warning prey of their presence so maybe the role of cranial crest as display structure in *Cryolophosaurus* was limited than other dilophosaurs.

Cryolophosaurus is important in being the firstly reported theropod in Antarctica, and the earliest theropod that occurred in Antarctica as well (Hendrickx *et al.*, 2015). Although the Antarctica of the early Jurassic period was considerably warmer and located farther north than what it is now today, it was still cooler than any other places at its time with occasional cold, dark winters (Paul, 2016). Modern vertebrate animals that live in cold, arctic environments show behavioral, physiological or phenotypical changes than related forms in lower latitudes (Fiorillo, Tykoski, 2014) so it is not surprising that *Cryolophosaurus* also show acquisitions that are related to lifestyle in ancient circum-polar ecosystem. *Cryolophosaurus* is considerably larger than any other theropods of its time (Hendrickx *et al.*, 2015), and given that large body size is advantageous in high-latitude environments (e.g. having a lower surface area to volume; Fiorillo, 2008) this feature is perhaps an adaptive or advantageous for *Cryolophosaurus*. However, footprints of large Early Jurassic theropods have been reported from the lowermost Hettangian strata in Poland (Gierliński *et al.*, 2001, 2004; Niedzwiedzki, 2011) indicating that large theropods roamed Pangea since the very beginning of Jurassic in a warm, mid-latitude climate conditions, so it is equally possible that the size of *Cryolophosaurus* has no relation to its circum-polar habitat.



Fig. 4. Life reconstruction of *Cryolophosaurus* exhibiting a speculative courtship display to attract mate. Drawing by Jun-Hyeok Jang, used with permission

The orbit size seems to be relatively larger in *Cryolophosaurus* than its possible relative *Dilophosaurus*, a taxon which is characterized by its small orbits (Holtz, 2008). Considering that eye functions as a photon-catching device and larger eyes are advantageous for circum-polar predators in providing more access to prey items in the low-light conditions (Fiorillo, Tykoski, 2014), this could be adaptive or advantageous feature for *Cryolophosaurus* as well. However, skull in the holotype of *Cryolophosaurus* is incomplete in lacking a rostrum so it is hard to estimate relative eye size compared to other theropods and all dilophosaurids are relatively larger than other contemporaneous theropods (Holtz, 2012; Hendrickx *et al.*, 2015) so it is equally plausible that these features were just potential synapomorphies that were present in the dilophosaurids or basal neotheropods. Obviously, discoveries or descriptions of new *Cryolophosaurus* material are crucial for more detailed understanding lifestyle of this large theropod in ancient, Early Jurassic circum-polar ecosystem – and in other Jurassic climatic zones.

CONCLUSIONS

The large Early Jurassic theropod *Cryolophosaurus ellioti* is important in studying the evolution of early theropods as it represents a dilophosaurid neotheropod or basal tetanuran, both of which are poorly understood. Despite being the most complete theropod known from the Antarctica, the limited amount of fossils prohibits the detailed research on this theropod. However, ecomorphological evidence suggest an active predatory role of *Cryolophosaurus* in the ancient Gondwana-Antarctic ecosystem. Although large Early Jurassic theropod footprints distributed over Pangea point to existence of theropods much larger than *Dilophosaurus* during this epoch, *Cryolophosaurus ellioti* provides the only known and well-preserved bone record of such a big Early Jurassic theropod. Clearly, new discoveries and description of undescribed materials will provide better understanding of this enigmatic, but intriguing theropod in the near future.

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