

# Comments on the ecology of Jurassic theropod dinosaur *Ceratosaurus* (Dinosauria: Theropoda) with critical reevaluation for supposed semiaquatic lifestyle

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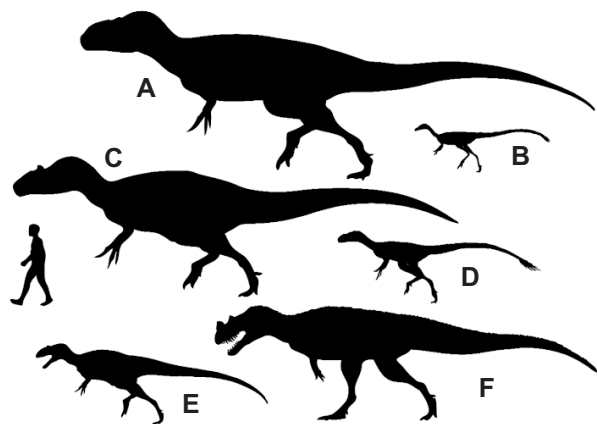
## BACKGROUND

*Ceratosaurus* is a genus of carnivorous theropod that is characterized by distinctive horns located midline of its nasal and above of its eyes. The type species of this genus, *Ceratosaurus nasicornis*, was described from a nearly complete articulated skeleton of the upper Jurassic Morrison Formation that is exposed in Colorado, USA (Marsh, 1884; Gilmore, 1920). Although it is known for a well-preserved skeleton, the taxon had been long remained as enigmatic as the skull was heavily distorted by taphonomic processes (Gilmore, 1920) but subsequent discoveries including well-preserved specimens have greatly improved our understanding of anatomy of this genus (Madsen, Welles, 2000; Rauhut, 2003). Still, their remains are relatively rare in the Morrison Formation (Foster, Chure, 2006) so the paleobiological research on this theropod has not received much attention by now so the ecology and lifestyle of *Ceratosaurus* has been poorly understood.

The paleobiota of Morrison Formation which *Ceratosaurus* lived, is unusual for consisting numerous genera of carnivorous theropods in the same ecosystem (Fig. 1). These include small-sized theropods about the size of cat-sized troodontid *Koparion*, tetanuran *Fosterovenator*, lynx to puma-sized basal coelurosaurs *Coelurus*, *Ornitholestes* and *Tanycolagreus*, leopard-sized basal tyrannosauroid *Stokesosaurus*, lion-sized *Marshosaurus*, polar-bear sized *Ceratosaurus* and multi-ton giants *Allosaurus*, *Saurophaganax* and *Torvosaurus* (Madsen, 1976; Chure, 1994; Foster, 2007; Paul, 2010; Dalman, 2014; Yun, 2016, 2019). Exactly how these multiple large-sized carnivores were capable of co-existing currently remains unclear. Bakker and Bir (2004) suggested a possible divergent ecological role of *Ceratosaurus* from other theropods. They suggested that tall, vertical neural spines and chevrons in caudal vertebrae, and lack of stiffening in the torso and the tail of *Ceratosaurus* are similar to those of crocodylians and they are specialized in feeding on aquatic preys than terrestrial ones. Based on this tail morphology, Bakker and Bir (2004) considered *Ceratosaurus* as semiaquatic animal. Paul (2010) admitted this possibility and noted that deep tail of *Ceratosaurus* may have been used as sculling organ while swimming.

However, Mesozoic dinosaurs were predominantly terrestrial, and most of the known taxa all lack any adaptations for semiaquatic lifestyle (Sampson, 2009). Spinosaurid theropods have been long recognized as piscivorous animals that likely spent considerable time in or around water, and several skeletal features of some taxa have been reported as adaptations for semiaquatic lifestyle (e.g. Ibrahim *et al.*, 2014; Arden *et al.*, 2018) which has been also supported by oxygen isotope analysis (Amiot *et al.*, 2010), although these claims have been disputed due to insufficiency of current data and possible alternative explanations (Hone, Holtz, 2017, 2019). Therefore, the hypothesis of *Ceratosaurus* as semiaquatic animal needs to be seriously reevaluated whether the current evidence are sufficient enough to support this hypothesis, or alternative explanations

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**Fig. 1. Size distribution of the Morrison Formation theropod dinosaur fauna**

**A** – *Torvosaurus*; **B** – *Coelurus*; **C** – *Allosaurus*; **D** – *Stokesosaurus*; **E** – *Marshosaurus*; **F** – *Ceratosaurus*. Modified from Sampson (2009)

style referred here by the author is in the sense of an animal with crocodylian-like habits.

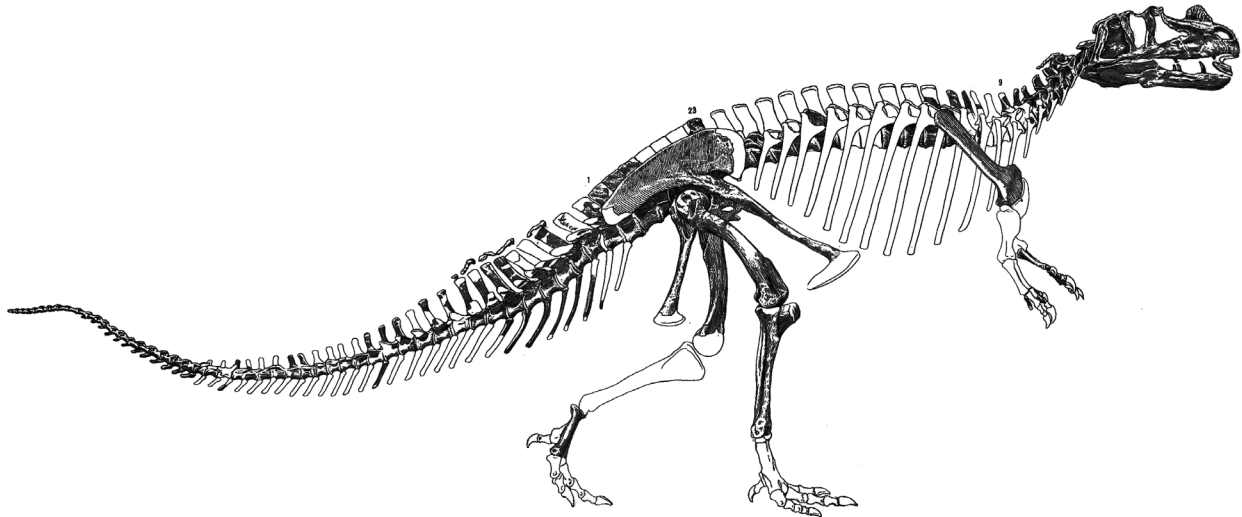
The anatomical features described by Bakker and Bir (2004) as adaptations for increased swimming ability in tail of *Ceratosaurus* include: 1. More resemblance to crocodylian tail than other theropods in having very tall, vertical neural spines in the anterior caudal vertebrae; 2. Very deep chevrons; 3. More flexible tail than allosaurids like *Allosaurus*. However, the author finds problems with each of these suggestions.

1. In holotype of *Ceratosaurus nasicornis* (USNM 4735: Smithsonian National Museum of Natural History specimen), the preserved neural spines of the proximal tail are similar in size or lower than to those of sacral series, so in height they are not as distinctive compared to more anterior parts of the vertebral column (Fig. 2). In type specimen of *Ceratosaurus "dentisulcatus"* (UMNH VP 5278: Utah Museum of Natural History specimen), the condition is similar to USNM 4735 and neural spines of anterior to middle dorsal vertebrae are taller than those of the tail. The mere tall height of neural spines in caudal vertebrae does not seem to have a particular correspondence with semiaquatic locomotion or lifestyle. For example, tall neural spines of the proximal caudal vertebrae occur in numerous fully terrestrial theropods (e.g. *Acrocanthosaurus*, *Concavenator*, *Deinocheirus*, *Majungasaurus*, *Yangchuanosaurus*). Moreover, according to Hone and Holtz (2019), neural spines of the caudal vertebrae in crocodylians are sub-circular in cross section and these tall spines also occur in the middle and distal caudals. However, tail of *Ceratosaurus* lacks tall neural spines in middle and caudal parts and spines retain typical theropod condition in having flat, blade like morphology. Therefore, there is no clear indication that *Ceratosaurus* tail is remarkably similar to crocodylians than other theropods and when they are compared in more detail, such suggest analogy of form is lacking.
2. The assumption of depth of chevrons related to enhanced swimming ability is considered as questionable here. All theropod chevrons are considerably deep, and such more deepened morphology also occur in, for example, *Herrerasaurus*, *Abelisaurus*, *Giganotosaurus*, *Gallimimus*, *Struthiomimus*, *Caudipteryx*, *Heyuannia* and *Conchoraptor*. None of these taxa were suggested to having had semiaquatic lifestyles. Of particular note is mosasaurids, the squamate reptiles that were peculiarly adapted to the full aquatic lifestyle, lack this feature. The main functions of chevrons in reptilian tail are to protect nerves or blood vessels and to serve attachment areas for caudofemoralis and ilioischiocaudalis muscles (Williston, 1925; Persons, Currie, 2011a, b), so it may be more likely that depth of chevrons are merely related to these functional aspects rather than lifestyle of animals. Lastly, the chevrons of *Ceratosaurus* differ little in morphology when compared to typical dinosaur condition, in having two rami forming the proximal end and laterally compressed distal portion where the distalmost part is mostly compressed (Madsen, Welles, 2000). The mid-caudal chevrons of *Ceratosaurus* closely resemble those of basal theropods, such as *Dilophosaurus wetherilli* (UCMP 37302: University of California Museum of Paleontology specimen) (Madsen, Welles, 2000) or *Cryolophosaurus ellioti* (Smith *et al.*, 2007). However, in

are indeed impossible to reject this. Here, the author reexamines this hypothesis by comparing modern animals and other non-avian dinosaurs with observations of Bakker and Bir (2004), to test whether these features can be best interpreted as adaptation for semiaquatic lifestyle, or they are equivocal or erroneous, or actually does not support the hypothesis.

## DISCUSSION

The important thing that should be noted is as noted by Hone and Holtz (2019), the term “semiaquatic” is poorly defined in the literature and may refer to almost every terrestrially-capable tetrapod that spends some time in water. For example, modern water deers (*Hydropotes inermis*) do spend a considerable time in water, but they do prefer more arid environments when they are not feeding. Bakker and Bir (2004) point to adaptations in *Ceratosaurus* that are reminiscent of modern crocodylians, coupled with an inferred flexibility of its tail. Therefore, “semiaquatic” life-



**Fig. 2. The holotype skeleton of *Ceratosaurus nasicornis* (USNM 4735: Smithsonian National Museum of Natural History specimen). Modified from Gilmore (1920)**

modern crocodylians, chevrons have slightly expanded distalmost parts (pers. obs.). Thus, there is no clear indication of deep chevron is linked directly to an adaption for swimming in *Ceratosaurus* nor it has the analogous form of crocodylians.

3. Theropod tails were highly flexible and muscular (Persons, Currie, 2011a, b) and the author agrees that they were probably allowed them to swim when the need arose (e.g. crossing river, chasing prey or escaping from predators). However, the same notion also means although increased tail flexibility could be advantageous for swimming, but it does not necessarily indicate semiaquatic lifestyle. Almost all theropod tails have increased amount of lateral flexibility and musculature, including tyrannosaurids, abelisaurids and oviraptorosaurs (Persons, Currie, 2011a, b, 2014) and none of these clades were suggested to have had semiaquatic affinities. Lateral swinging of the tail could be used for display, repulsion of predators, or agonistic behaviors between conspecific individuals of the same sex. For example, modern varanids use the tail to strike repeatedly in combination with biting for defense (Murphy, Mitchell, 1974). In summary, it is safe to say laterally flexible tail has parallel functions in terrestrial mode of life.

Moreover, in modern crocodylians, the first caudal is biconvex and others are procoelous (Williston, 1925) whereas in *Ceratosaurus*, caudal vertebra are amphicoelous (Mendez, 2014). One of the most striking feature in anterior caudals of *Ceratosaurus* is the presence of accessory hyposphene-hypantrum articulations (Madsen, Welles, 2000; Mendez, 2014). The hyposphene-hypantrum articulation is a lock-and-key configuration between successive vertebrae, and Apesteguia (2005) note the development of hyposphene-hypantrum articulations in sauropod evolution coincides with increased vertebral column rigidity and decreased flexibility of locomotion. In summary, there is no conclusive evidence for increased flexibility of tail in *Ceratosaurus* than other theropods and it actually has potential for decreased flexibility. It is worth to note that Delcourt (2018) interpreted this combined features of tail morphology (large caudofemoralis longus muscle, hyposphene-hypantrum articulations) of ceratosaurs as increases of the tail rigidity as well as enhanced overall speed and acceleration.

As noted by Arden *et al.* (2018) and Hone and Holtz (2017, 2019), modern crocodylians show numerous modifications in overall skeletal morphology that are adaptive to semiaquatic lifestyle, including elevated orbits, elongated body, reduced limbs and dorsally positioned nares so if the lifestyle of *Ceratosaurus* was analogous to these animals, it is expected that all or at least some similar modifications can be observed in this taxon as well. However, according to a survey of Persons and Currie (2016), lower leg proportions of *Ceratosaurus* fall into a range of typical terrestrial theropods. Moreover, the external nares are located at the tip of the snout as in other “normal” theropods, and are positioned much below the eyes (Fig. 3). Therefore, *Ceratosaurus* would have been improbable to have crocodile-like posture with only the nares and eyes exposed (Hone, Holtz, 2017, 2019; Fig. 4). Lastly, bauplan of *Ceratosaurus* differs little from typical theropod (Fig. 2) with no sig-

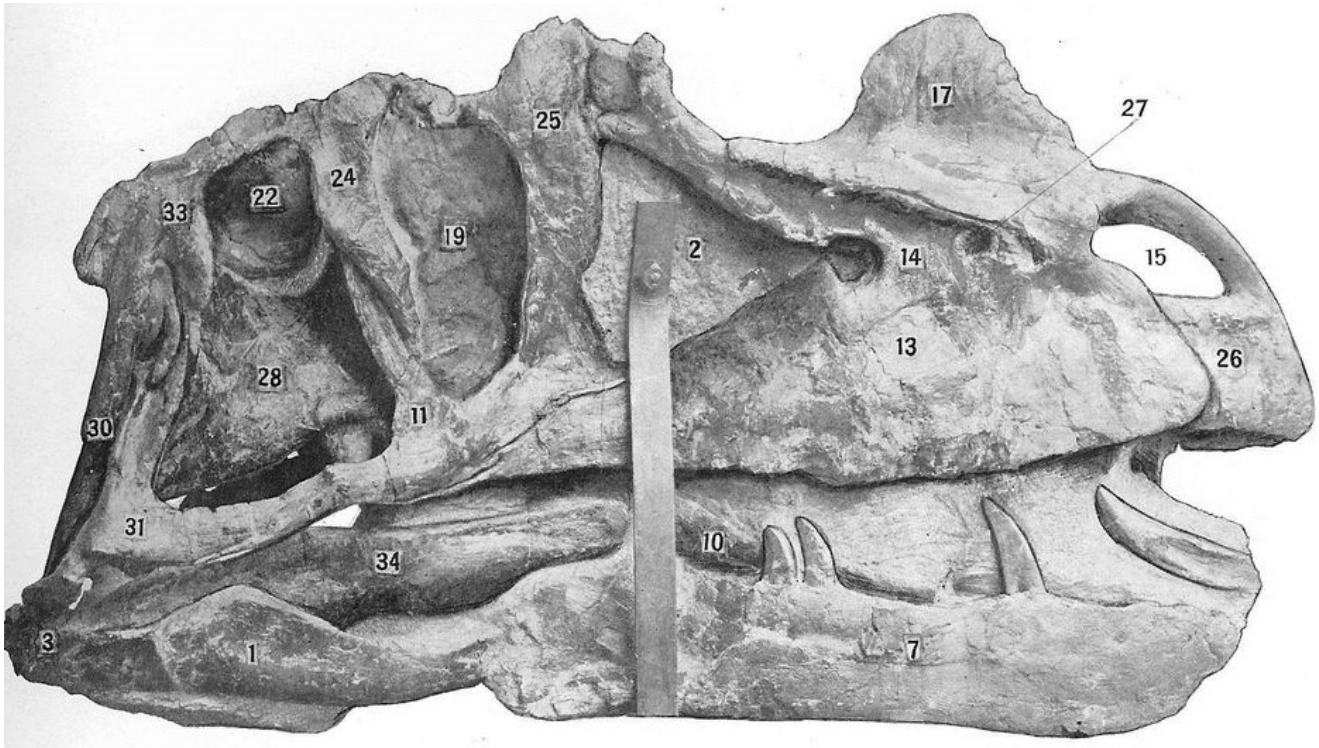


Fig. 3. The skull of *Ceratosaurus nasicornis* holotype (USNM 4735: Smithsonian National Museum of Natural History specimen). Notice the low external nares compared to orbit. Modified from Gilmore (1920)

nificant elongated torso. Thus, there are no divergent or unique combination of features in *Ceratosaurus* to support the mode of semiaquatic life like modern crocodilians.

It is possible, however, that *Ceratosaurus* had a varied diet when compared to other contemporaneous large theropods like *Allosaurus*. According to a survey by Bakker and Bir (2004), teeth of megalosaurids and *Ceratosaurus* were most common in sediments that correspond to watery environments like swamps or floodplains. Moreover, the premaxillary teeth and anterior dentary teeth of *Ceratosaurus* are conical and bear flutes in their lingual surface that are remarkably similar to those of baryonychine spinosaurids (Madsen, Welles, 2000; Fowler, 2007) and Dilophosauridae (Milner, Kirkland, 2007). Given that the combination of flutes and conical morphology of teeth usually occur in piscivorous tetrapods like crocodiles (Holtz, 1998; Hone, Holtz, 2017), this may imply a more proportion of fish in diet of *Ceratosaurus* than other contemporaneous theropods. Moreover, the nasals of *Ceratosaurus* are fused (Madsen, Welles, 2000) and fusion of nasals is potentially more resistant to torsional loads (Snively *et al.*, 2006). However, other cranial features (*e.g.* tall and narrow skull, blade-like lateral teeth, lack of ossified secondary plate) in *Ceratosaurus* correspond with other typical theropods so it may be more probable that *Ceratosaurus* was an opportunistic and generalist carnivore that could able to exploit the most common prey in both the terrestrial and aquatic habitats.



Fig. 4. *Crocodylus palustris* floating in water with exposed eyes and nostrils. Photo Credit: Radhika Kochhar. Adapted from the Wikipedia Commons

Fossils of *Ceratosaurus* are rare in the Morrison Formation: contemporaneous *Allosaurus* fossils outnumber those of *Ceratosaurus* at an average rate of 7.5 to 1 in sites where they co-occur (Foster, Chure, 2006). This rarity is surprising, as the Morrison Formation is the most rich source of dinosaur fossils in North America and *Ceratosaurus* have several features that might lead to a bias in favor of fossilization and more frequent recovery of fossils, such as relatively large size and the possibility of favoring watery habitats so it is reasonable to assume that *Ceratosaurus* was generally rare in the paleobiota of Morrison Formation.

If *Ceratosaurus* was able to exploit aquatic preys more than other theropods, this may suggest reduced competition with other theropods but opens the possibility of potential competition with other piscivorous reptiles like crocodylians. This combination of inferred unusual ecological position and fossil record, suggests the possible habitat preference for marginally productive environments in *Ceratosaurus*. If *Ceratosaurus* was specialized in such habitats, it may had a narrow ecological niche and such specialization could affect the individual populations (Hone *et al.*, 2010). Such hypothesis could explain the overall rarity of *Ceratosaurus* in the fossil record but occasional high numbers at marginal productive environments and small numbers in more arid inland habitats (Bakker, Bir, 2004). However, this is in the context of functional ability of teeth to pierce through soft flesh and grasping slippery objects, rather than oblique fish items and all predators would prefer watery habitats given their obvious need of water resource and increased chances of predation, given that prey items would be gathered to drink as well. Therefore, such hypothesis should be considered as tentative at this time.

## CONCLUSIONS

Currently suggested evidence for *Ceratosaurus* as crocodylian-like semiaquatic animal is either too loosely defined, or clearly differs from the condition in modern semiaquatic animals, especially crocodylians. Therefore, this hypothesis is tentatively rejected here. Nevertheless, *Ceratosaurus* shows several cranial modifications that may be related to increased proportion of fish as diet, so it is possible that this taxon was a specialized form for marginally productive habitats, similar to which suggested for spinosaurids as well (Charig, Milner, 1997; Amiot *et al.*, 2010; Hone *et al.*, 2010; Arden *et al.*, 2018). However, current data is insufficient to support this hypothesis conclusively so certainly, future discoveries as well as more detailed studies would be crucial to test this.

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