

# Possible Feeding Habits of *Cyclotosaurus cf.* *posthumus*

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## **Abstract**

The specimen *Cyclotosaurus cf. posthumus* collected by Jenkins et al. (1994) is described and possible feeding behavior is investigated. There are many similarities in cranial morphology and dentition to modern crocodylians, however, the organism probably was not well-suited for certain behaviors which modern crocodylians engage in for feeding on large prey.

## **Introduction**

Among Mesozoic temnospondyl amphibians, the capitosaurians are both well-known and poorly understood. Although specimens have been collected across all continents (Schoch 2000), many details of anatomy and paleoecology remain to be elucidated (Sulej and Majer 2005, Schoch and Milner 2000). In particular, the genus *Cyclotosaurus* typifies this statement, as specimens have been found from Thailand (Ingavat and Janvier 1981), Greenland (Jenkins

et al. 1994), and Europe including Germany and Poland (Sulej and Majer 2005), but the relationships between the various species have yet to be determined, and the postcranial skeleton is still largely unknown (Sulej and Majer 2005, Schoch and Milner 2000).

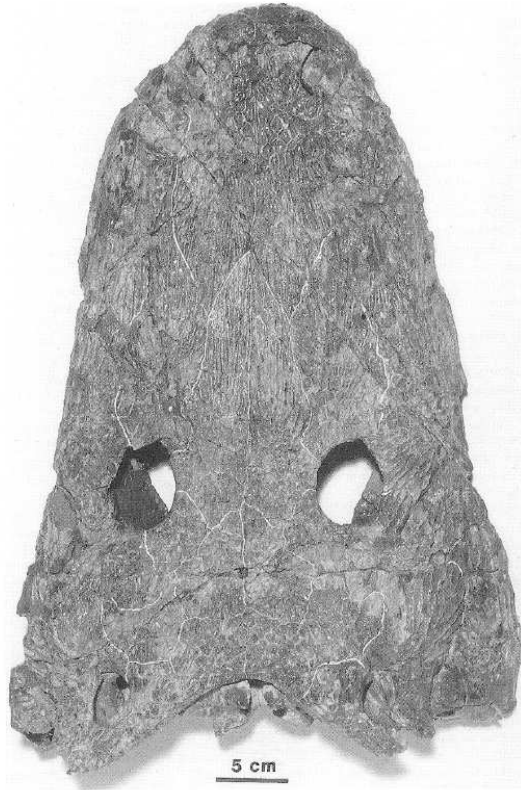
In the present paper, we describe a *Cyclotosaurus* skull specimen found in the Fleming Fjord Formation in East Greenland, collected by Jenkins et al. (1994), and we discuss several possible functional interpretations of certain cranial features in the specimen.

## Description

The specimen (MCZ 15/92/G) (see fig. 1, 2) was previously labeled *Cyclotosaurus posthumus* (Jenkins et al. 1994). We defer, as Jenkins et. al (1994) did a precise identification, as our concern in this paper is the feeding behavior of this organism, rather than phylogeny. The specimen consists of a partial skull and an associated mandible fragment, approximately 36 cm wide and 54 cm long. The specimen is slightly asymmetrical, due to post-mortem compression on the left side. The posterior region of the right squamosal and tabular bones and a small part of the left premaxilla bone are also missing.

### Skull roof (fig. 1a, 2a)

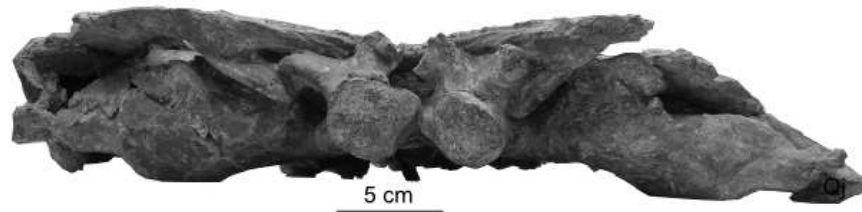
The skull roof bears extensive dermal sculpture, making some of the sutures hard to identify. However, most of the sutures in the posterior skull table are visible and have been highlighted on the specimen (fig. 1a). The specific pattern of sutures is likely to reflect the strain on the skull during biting (Thompson 1995), but we do not explore this here. The external nares open approximately anteroventrally and the margins are distinct (esp. on the right,



a



b



c

Figure 1: (a), (b) are from Jenkins et al. 1994, Figures 4 and 5, respectively. (a) Dorsal view. (b) Ventral view. (c) Occipital view.

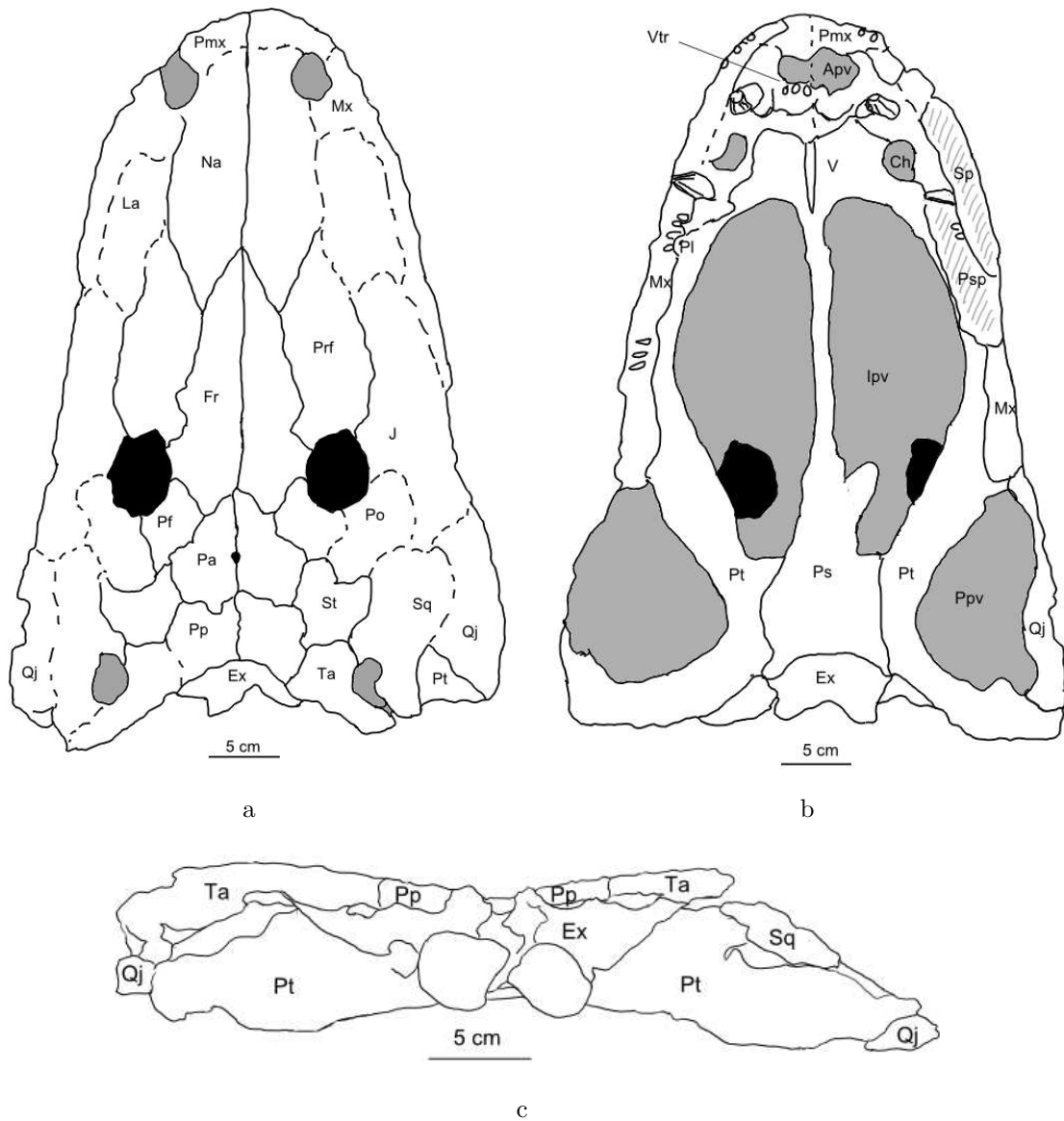


Figure 2: (a), (b) are modified from Jenkins et al. 1994, Figures 4 and 5. For abbreviations, see appendix. Regions filled with black are holes, regions filled with gray are depressions or fenestrae, and the hatched region in (b) is the associated mandibular fragment. (a) Dorsal view. (b) Ventral view. (c) Occipital view.

as damage to the left premaxilla has opened the left nares). The nasals, prefrontals, and other bones making up the rostrum are extremely elongate (fig. 2a), a condition with functional consequences to be discussed later. The tabular and squamosal bones extend past the postparietal bones, creating a tabular horn.

### **Palate (fig. 1b, 2b)**

The anterior palatal vacuity is wide and generally oval, though it is deformed in this specimen. This would hold the sympheseal fangs when the jaw is closed. On the anterior edge of the vacuity is the premaxilla, upon which a few small teeth are visible. This demarcates the position of the main outer tooth arcade. Posterior to the anterior palatal vacuity is a curved row of vomerine teeth (2b), which is flanked by two large tusks, which appear grooved, probably due to the labyrinthodont dentition. The choanae are round (see the left choana, in 1b as the right one is deformed). Posterior to the choanae are another set of large fangs, which head (on the right side) a row of smaller teeth. On the left, there are portions of the mandible attached to the skull, including the splenial and postsplenial bones. The large interpterygoid vacuity is split by a prominent, but narrow cultriform process of the parasphenoid. Near the left orbit is a thickened element rising from the frontal. The subtemporal fenestrae are deep and approximately kidney shaped (note that the quadratojugal wall is missing on the right side).

## **Occiput (fig. 1c, 2c)**

In occipital view, both the skull roof and the ventral margin are noticeably concave. The paired occipital condyles angle downwards slightly and angle inwards more greatly; the surfaces of the condyles are convex and form an approximate  $110^\circ$  angle when viewed from above (fig. 1a). The paired condyles imply that only vertical movement at the atlanto-occipital joint was allowed in *Cyclotosaurus cf. posthumus*.

## **Functional Interpretations**

Capitosaur, like stereospondyls in general were aquatic, carnivorous amphibians (Schoch and Milner 2000). Though the postcranial skeleton for *Cyclotosaurus* is poorly known, evidence from related taxa in the superfamily Capitosauroidae, such as *Mastodonsaurus* and *Paracyclotosaurus* suggest a mainly aquatic lifestyle (Schoch and Milner 2000). This evidence includes a dorsally flattened trunk and weak and poorly ossified limbs (Schoch and Milner 2000).

One of the earliest suggestions for the behavior of capitosaur was that they waited for prey to swim near, then quickly opened its jaws and swallowed the prey (Watson 1958). However, such a strategy requires a strategy of suction feeding which has been argued as implausible for several reasons. First, capitosaur have akinetic skulls, in contrast to the kinetic skulls of organisms with such behavior (Schoch and Milner 2000). Second, capitosaur lack a method of generating the pressures which are needed to pull in large prey, since the velocity of escape scales linearly with the size of the prey (Taylor 1987).

Damiani (2001) has proposed that capitosaurians were active surface or sub-surface predators and captured prey by rapid sideways sweeps of the head, probably opening and closing the jaws at the last moment. In particular, he points out that the flattened skull minimizes drag for lateral movement, whereas a forward lunge under water would have the effect of pushing the prey out of the way (Damiani 2001). Taylor (1987) has stated that a broad snout and skull are well-suited for such jaw motion, for similar reasons. In particular, Taylor (1987) remarked that the shape of the skull in aquatic predators is a balance between reduction of drag, which favors a narrower skull, and robustness, which favors a broader skull. In Recent crocodylians, taxa with narrower skulls tend to feed on small, fast fish, and taxa with broader skulls tend to be more generalist predators (Taylor 1987).

The skull of *Cyclotosaurus* is broad and dorsoventrally flattened, suggesting some adaptation for drag minimization, as well as some degree of robustness for handling moderately sized prey. The elongated rostrum is also a specialization for snapping, since it allows the animal to get closer to prey without the prey being alarmed by the main bulk of the animal (Taylor 1987). Without more of the postcranial skeleton, the specific suitability of *Cyclotosaurus* for the rapid sweeping motions that are required for this behavior cannot be evaluated, however the flattening of the skull means that the musculature would not necessarily need to be as extensive.

Both Taylor (1987) and Damiani (2001) stress the importance of strong adductor muscles for this behavior. The subtemporal fenestrae in *Cyclotosaurus cf. posthumus* are quite expanded and suggest that the adductor muscle mass was significant. Another important

motion for the sweep and snap behavior is skull-raising. In capitosaurids, the cleidomastoideus muscles are most important for this function, and the tabular horn provides an attachment surface (Howie 1970). Sulej and Majer (2005) have suggested that the lengthening of the tabular horn in cyclosaurids also yields greater strength by elongating the lever arm for this muscle. The concavity of the posterior border of the skull in *Cyclotosaurus cf. posthumus* suggests that it also had strong cleidomastoideus muscles. The angled structure of the atlanto-occipital joint would have made it less likely to come apart during the side-to-side motion, as well.

Taylor (1987) also states that the bending load is considerable for a predator snapping its jaws on prey. This may be the reason for the prominence of the supporting cultriform process and the pterygoids on the ventral surface of the skull. Busbey (1995) states that the broad head of crocodylians is well suited to absorb the forces involved in rolling motions, a behavior that has been observed in extant crocodiles to destabilize prey. However, two features in the skull specimen make this unlikely in *Cyclotosaurus*. First, the large interpterygoid vacuities and the thinness of the dermal bone make the skull much less robust. Second, the lack of a secondary palate also makes the skull less able to withstand the rolling motion. Thus, *Cyclotosaurus* probably limited the amount of rapid head motion after snapping its jaws shut on the prey.

The fact that the orbits, nares and otic fenestrae are dorsally positioned suggests that *Cyclotosaurus cf. posthumus* was more suited for activity at the surface than underwater. This is a feature common to crocodylians also (Schoch and Milner 2000, Taylor 1987), so the

hunting behaviors may be similar. Like crocodylians, *Cyclotosaurus* probably was able to effectively stalk normally terrestrial animals that entered the water.

The dentition of this specimen can be placed into two broad categories: the large fangs and the smaller tooth rows. The variation in tooth size is consistent with a snap-and-hold prey capture behavior. The fangs would function in crushing and puncturing the prey, and the tooth rows would assist in holding the struggling prey until it died (Taylor 1987). The closely spaced and equidistant teeth in the tooth rows is similar to that in Recent fish-hunting gavials (Schoch and Milner 2000), so fish were most likely an important part of the diet of *Cyclotosaurus*. The vomerine tooth row and the sympheseal fangs are at the anterior of the mouth, which is more evidence that *Cyclotosaurus* aimed with the anterior tip of the long rostrum. Taylor (1987) has argued that the end of the snout is often the most specialized because it moves most rapidly for a given angular velocity of the neck, and in an aquatic environment, the posterior parts of the snout face more drag, so they cannot be brought over the prey as easily.

These types of teeth, however, would prevent the animal from effectively biting off pieces of prey to swallow because of the lack of occlusion. In crocodylians, twist-feeding and shake-feeding is used to break down the prey into manageable pieces (Taylor 1987, Busbey 1995), but as we argued earlier, the more fragile skull of *Cyclotosaurus* makes these less likely. Thus *Cyclotosaurus* was probably limited to prey that could be swallowed without much processing. Schoch and Milner (2000) point out that stereospondyl amphibians had a strong retractor bulbi muscle attaching to the ventral surface of the skull, which would allow them

to pull their eyes into their skull to assist with swallowing. This behavior is consistent with that observed in modern frogs, which pull their eyes inwards to swallow prey more efficiently (Levine et al. 2004). Perhaps *Cyclotosaurus cf. posthumus* used this in conjunction with inertial or gravity feeding (in association with the well-developed skull-raising muscles).

## Conclusion

*Cyclotosaurus cf. posthumus* was probably like most capitosaurians in that it was an aquatic predator. The shape of the skull and the dentition suit it for certain crocodylian-type behaviors, such as a sideways sweeping and snapping motion for prey capture, but the skull of *Cyclotosaurus* was much less robust, which would keep it from attacking and tearing apart large prey using twist-feeding. The diet then probably consisted of fish of various sizes, as well as any other prey coming into the water that could be swallowed easily.

## Appendix

The abbreviations used in figure 2 are: Apv, anterior palatal vacuity; Ch, choana; Ex, exoccipital; Fr, frontal; Ipv, interpterygoid vacuity; J, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pa, parietal; Pf, postfrontal; Pl, palatine; Pmx, premaxilla; Po, postorbital; Pp, postparietal; Stf, subtemporal fenestrae; Prf, prefrontal; Ps, parasphenoid; Psp, postsplenial; Pt, pterygoid; Q, quadratum; Qj, quadratojugal; Sp, splenial; Sq, squamosal; St, supratemporal; Ta, tabular; V, vomer; Vtr, vomerine tooth row.

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