Feeding options in *Steneosaurus bollensis* (Mesoeucrocodylia, Thalattosuchia)

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Introduction

Steneosaurus bollensis is a longirostrine crocodilian of the Liassic (Toarcian, Early Jurassic) of the Swabian Jura, South Germany. For better understanding of possible feeding options in *S. bollensis*, a reconstruction of its jaw muscles is made and functionally interpreted.

Muscle reconstruction in *Steneosaurus bollensis* was mainly accomplished by comparison with extant crocodilian jaw muscles, based on data from the literature (Poglayen-Neuwall, 1953; Iordansky, 1964; Schumacher, 1973; Busbey, 1989; Shimada et al., 1993; Sato et al., 1994; Cleuren & De Vree, 2000; Endo et al., 2002), by comparing the position and shape of muscle scars on the particular bones (Bryant & Seymour, 1990), and the general configuration of the skull, respectively the inference of muscle anatomy as suggested by functional reasons (Rieppel, 2002).

Extant crocodilians possess several strongly developed adductor muscles for closing the mouth and only one jaw muscle for opening of the mouth (Iordansky, 1964; Schumacher, 1973; Busbey, 1989). Jaw opening is mainly achieved by a depression of the lower jaw by contraction of the M. depressor mandibulae (MDM) and simultaneously, the upper jaw is elevated by the contraction of several dorsal cervical muscles (Cleuren & De Veer, 2000). This system is here basically likewise assumed for *S. bollensis*.

Muscle reconstruction (Fig. 1)

Steneosaurus bollensis has a much flattener, dorso-ventrally compressed skull than extant crocodilians, with enlarged supratemporal and infratemporal fenestrae.

M. mandibulae externus superficialis (MAMES) in *S. bollensis* was reconstructed as a muscle mass filling the infratemporal fenestra. Because of the large infratemporal fenestra, the muscle was probably thicker and therefore stronger compared to extant crocodilians.

M. mandibulae externus medialis (MAMEM) was probably similar developed to extant crocodilians. MAMEM anteriorly was probably attached to a Cartilago transiliens (CT) over a tendinous sheet. The existence of a Cartilago transiliens (CT) is assumed in analogy with the conditions in extant crocodilians.

In *S. bollensis,* main part of the large supratemporal fenestra was probably filled by M. mandibulae externus profundus (MAMEP), but in the most anterior part of the supratemporal fenestra also M. pseudotemporalis (MPS) arose. The entire muscle mass of the MAMEP itself must have pulled almost vertically downwards, because the infratemporal fenestra and the mandible lie almost vertically ventral to the lateral bar of the supratemporal fenestra.

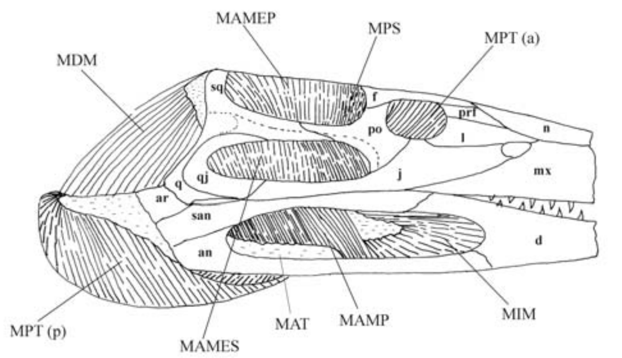

Fig. 1 — Jaw muscle reconstruction of *Steneosaurus bollensis* in lateral view. The anterior part of the skull (80% of the rostrum) is not considered here, because it was not necessary for the muscle reconstruction. Muscle abbreviations see text. **Bone abbreviations**: **an** – angular, **ar** – articular, **d** – dentary, **f** – frontal, **j** – jugal, **l** – lacrimal, **mx** – maxilla, **n** – nasal, **po** – postorbital, **prf** – prefrontal, **q** – quadrate, **qj** – quadratojugal, **sq** – squamosal.

S. bollensis possesses an extremely large external mandibular fenestra in the lower jaw compared to extant crocodilians, which can reach the size of the infratemporal fenestra. M. adductor mandibulae posterior (MAMP) had probably its origin on the ventral surface of the quadrate and the cranial adductor tendon (CAT) and inserted probably on a broad mandibular adductor tendon (MAT), which was attached to the jugal. A larger physical cross-section for the MAMP is supposed for *S. bollensis*, because of the enlarged mandibular fenestrae compared to extant crocodilians.

A large suborbital fenestra in *S. bollensis* indicates a well developed M. pterygoideus anterior (MPT (a)).

Unlike all other crocodilians, *S. bollensis* possesses an extremely flat pterygoid. The complete pterygoid lies almost horizontal in the skull. The wings of the pterygoids are broad but only slightly bent in ventral direction. The flat pterygoids in *S. bollensis* probably limited the diameter of M. pterygoideus posterior (MPT (p)), therefore the muscle was probably relatively thin compared to extant crocodilians.

It is supposed here that in *S. bollensis* the fibers of M. intramandibularis (MIM) were running from a Cartilago transiliens (CT) to the lateral surface of the angular like in extant crocodilians.

In lateral view, the retroarticular process in *S. bollensis* is relatively horizontal and only slightly extended in dorsal direction, in comparison to the retroarticular process of most other crocodilians, which is distinctly dorsally bent. Because of the horizontal alignment of the retroarticular process of *S. bollensis* the muscle fibers of M. depressor mandibulae (MDM) probably extended steeply from the posterior surface of the skull, in an angel of 50-60 degrees, in posteroventral direction, and inserted on the dorsomedial surface of the retroarticular process.

Discussion

In *Steneosaurus bollensis,* the assumed larger physiological cross-section of the MAMES, MAMEP, and probably the MPS indicates an increased force output of these muscles, compared to the conditions in extant longirostrine crocodilians. Furthermore, it is supposed that *Steneosaurus bollensis* possessed a weakly developed MPT (p), which was compensated by a strongly developed MAMEP, and possibly by an enlarged MPS. Similar to the conditions found in *Tomistoma schlegelii* and *Gavialis gangeticus* (Indian gharial) (Endo et al., 2002). The steep extend of the fibers of the MDM indicates a weaker load transmission for *S. bollensis* compared to the Indian gharial, but the elongation of the muscle indicates faster opening of the jaw, compared to the Indian gharial.

S. bollensis possesses a long and slender rostrum with numerous homodont, slender teeth with a pointed, slightly recurved apex. The rostrum is often compared with the similar elongated snout of *Gavialis gangeticus*, and has mostly been interpreted as a sign of piscivory in analogy with *G. gangeticus* (Hua & Buffetaut, 1997; Frey, 1988; Levy, 2003). The Indian gharial is an ambush hunter and catches its prey with a sudden lateral stroke of the jaws (Whitaker & Basu, 1982; Frey, 1988; Cleuren & De Vree, 2000; Pooley, 2002; Levy, 2003). The flat, nearly tubular snout decreases the drag in water during such lateral movements (Pooley, 2002). Because of the extremely flat skull and snout in *Steneosaurus bollensis*, a similar method for hunting is supposed for it.

According to the shape of the skull, tooth morphology, and jaw muscles reconstructed for *Steneosaurus bollensis*; it has options to catch small, agile prey, which did not struggle much. Quick bites at the tip of the snout as well as forceful bites close to jaw joint are possible. These conditions are typical for fish eaters, but the options for all types of small prey like, e.g. fish, crustaceans, belemnites, molluscs, cephalopods etc. were given. It is supposed that size is here a more restrictive factor than the kind of prey.

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