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Reconstruction of forelimb musculature of temnospondyl amphibian *Cyclotosaurus intermedius* Sulej & Majer, 2005 from the Late Triassic of Poland

Katarzyna Anna Lech

Abstract

Paper presents the result of study on musculature and movement of forelimb of *Cyclotosaurus intermedius* Sulej et Majer 2005, a capitosaurid amphibian from the Late Triassic of south-western Poland. The material examined in study was excavated between 2000 and 2008 year from a claystone quarry at Krasiejów. The reconstruction of forelimb musculature and movement during stepping, and swimming are presented. The reconstruction includes 17 muscles of the forelimb. Individual muscles were divided, according to their function, into 8 groups: flexors, extensors, elevators, depressors, abductors, adductors, supinators and pronators. The forelimb movement was split into 8 phases that illustrate contractions and decontractions sequence of different muscle groups during stepping. The two hypothesis on possible way of animal movement during swimming are presented considering the role of tail and limbs in this process.

Key words: functional anatomy, humerus, Krasiejów, musculature, shoulder girdle

Introduction

Cyclotosaurs (Cyclotosaurinae Fraas 1889) were subfamily of the Cyclotosauridae, which is one of five families included in the superfamily Capitosauroidea Säve-Södenberg 1935 (Schoch 2008). Adults were large predators with wide head and an overall length of around 3.5 metres. The significant reduction of lateral line sensory sulci, upraising eyes on the top of skull, assuring the wider visual area, rather thin pectoral girdle elements and partly ossified bodies of vertebrae suggest the semi-aquatic lifestyle of this animals (Dzik & Sulej 2007). They probably lived near the lake or river bank similar to recent crocodiles and alligators and were ecological equivalents of this reptiles in Triassic ecosystem.

Up to occuring of the Krasiejów material, the poscranial sceleton of cyclotosurs is practically unknown. The skull was described in majority of species. In *Cyclotosaurus robustus* (Meyer & Plieninger 1844) and *Cyclotosaurus hemprichi* Kuhn 1942 also the intercentum are known. The pleurocentrum and interclavicle were also described in *Cyclotosaurus posthumus* Fraas 1913 (Warren & Snell 1991, Schoch & Milner 2000).

Remains of *Cyclotosaurus intermedius* Sulej and Majer, 2005 discovered in Krasiejów contributed to extension of knowledge on this group of amphibians. They provide reference of the skull description, but also permits to reconstruct the shoulder girdle and the forelimb musculature and their mode of movement.

The shoulder girdle of *Cyclotosaurus intermedius* was first described by Sulej & Majer (2005). Later the reconstruction was verified and complement by Lech (2008). The study material consists of scapulocoracoids, dermal bones: cleithra, clavicles and interclavicle. The humers, were also studied.

The aim of this paper is to provide the reconstruction of forelimb musculature of *Cyclotosaurus intermedius*, describe the forelimb movement during stepping, and consider possible role of limbs during swimming.

Geological setting

The Krasiejów quarry is the vertebrate fossil site in southwestern Poland (Opole Silesia).

At the locality 14 metres of Late Triassic (Keuper; Carnian) strata are exposed. The tetrapod fossils are mostly disarticulated and occur mainly in two fossil-bearing horizons. In the lower lacustrine horizon, predominate bones of the temnospondyl amphibian *Metoposaurus diagnosticus krasiejowensis* (Sulej 2002), and the phytosaur *Paleorhinus* cf. *arenaceus* Fraas, 1896 (Dzik *et al*. 2000, Dzik 2001). In the upper deltaic horizon, the fossil assemblage is dominated by the aetosaur *Stagonolepis olenkae* (Sulej 2010) and a dinosauromorph *Silesaurus opolensis* (Dzik 2003). Between these horizons, a small accumulation of bones of the rauisuchian *Polonosuchus silesiacus* Sulej 2005 (Brussatte *et al.* 2009) have been discovered. Underneath the lower level, the assemblage of juvenile *Stagonolepis olenkae* bones have also been found. In this both bone beds fossils occurred only episodically and cyclotosaurid material have not been found (Książkiewicz & Lech 2006).

Material and methods

The examined *Cyclotosaurus* material include: interclavicles (ZPAL AbIII/166, ZPAL AbIII/367, ZPAL AbIII/887/1 , UOBS 02423A, UOBS 02425, UOBS 02432), clavicles (ZPAL/AbIII/397, ZPAL AbIII/472/27, ZPAL AbIII/620, ZPAL AbIII/881/3, ZPAL AbIII/1692, UOBS 02423B, UOBS 02424, UOBS 02429), cleithra (ZPAL AbIII/471/51, ZPAL AbIII/1079/2, ZPAL AbIII/1109/2, ZPAL AbIII/1172, ZPAL AbIII/2093, ZPAL AbIII/2094, UOBS 02426, UOBS 02427, UOBS 02428), scapulocoracoids (ZPAL AbIII/887/2, ZPAL AbIII/2256, UOBS 02430), humeri –(ZPAL AbIII/887/3, ZPAL AbIII/1676/2, ZPAL AbIII/2255, ZPAL AbIII/2257, UOBS 02116, UOBS 02431). ZPAL, = Institute of Paleobiology, Polish Academy of Sciences, Warsaw. UOBS = Department of Biosystematics, University of Opole.

Specimens, mostly disarticulated, were collected between the 2000 – 2008 from upper and lower bone horizon of Krasiejów claystone quarry (Dzik & Sulej 2007).

Detailed description of excavation methods used in Krasiejów was presented by Dzik (2003) and Lech & Książkiewicz (2010).

The bones occur at Krasiejów in clay or calcareous concretions. The method of preparation differs significantly between this two types of preservation. Fossils, covered only by the soft, not calcify clay stone, are prepared mechanically, by using chisels and scalpels to remove an excess of rock. Bones preserved in the calcareous concretion need more specific preparation methods. If the concretion layer on the surface of bone is thin, only the mechanic preparation is used. This method consists in splitting of small fragments of concretion by using chisels and scalpels Dremel Engraver Kit with carbide point replaced by needle. When the calcareous concretion is considerably thicker the mechanic preparation is preceded by the punctual etching with water solution of formic acid. This method is based on plotting with brush the acid on the surface of concretion and then removing the etched rock using chisel or scalpel. Procedure is repeated until obtaining the desirable thickness of calcareous concretion and afterwards fossil is being prepared mechanically. After and during the preparation process, the specimens were impregnated with dilute cyanoacrylic glue.

The musculature was reconstructed based mainly on Miner (1925) and in a lesser degree on Gilbert (1973), Romer (1922), Francis & Cole (1934). The muscles reconstruction was prepared based on method proposed by Ray (2006). It is supported on the recognition of muscle attachment founded on bones. Individual muscles were illustrated Fig. 1 as single or double arrows, that runs approximately between the origination and insertion of muscle, with the arrowhead directed towards the origin. A broken line was used to indicate the parts of muscles that have attachments on the invisible side of bones. The outline of bones presented on Fig. 1, was based on a reconstruction by Schoch (1999) and Watson (1958). Due to the fact that muscles attachment of shoulder joint are present on the vertebral column elements, on the figure was also placed the schematic drawing of this structure fragment. Humerus had been drawn in more vertically than in natural position to make muscles attachment better visible.

Results

On the base of the methods mentioned in previous chapter, the following muscles could be reconstructed. Muscles involved in the forelimb movement were divided according to their functions into 8 groups:

a. flexor muscles: *musculus biceps brachii*, *musculus brachialis inferior*,
b. extensor muscles: *musculus anconaeus (triceps) scapularis*, *musculus anconaeus (triceps) lateralis*, *musculus anconaeus (triceps) medialis*, *musculus anconaeus (triceps) coracoidalis*,
c. levator muscles: *musculus latissimus dorsi*, *musculus deltoideus scapularis*, *musculus deltoideus clavicularis*,
d. depressor muscles: *musculus pectoralis clavicularis*, *musculus pectoralis abdominalis, musculus pectoralis interclavicularis,*
e. abductor muscles: *musculus supracoracoideus*, *musculus deltoideus scapularis*, *musculus deltoideus clavicularis*,
f. adductor muscles: *musculus subscapularis*, *musculus latissimus dorsi*,
g. supinator muscles: *musculus deltoideus scapularis, musculus deltoideus clavicularis, musculus coracobrachialis brevis*, *musculus coracobrachialis longus*.
h. pronator muscles: *musculus pectoralis abdominalis, musculus pectoralis interclavicularis, musculus scapulohumeralis, musculus subscapularis*.

All muscles taking part in forelimb movement are presented on Fig. 1.

Discussion

Basing on comparison with recent taxa *Andrias davidianus* (Miner 1925, Francis & Cole 1934) and *Necturus* (Gilbert 1973), and musculature description of Permian amphibian *Eryops megacephalus* Cope,1877 (Miner 1925), the following role and function of individual muscles in forelimb movement during stepping was assumed.

The proposed model of the forelimb movement starts with the standing position, when the body weight is evenly distributed to both forelimbs. Angle between arm and forearm measures then about 90 degrees and the humerus is inclined backward, but not maximally adducted to body.

In the first phase, the body weight is moved onto the left forelimb, the arm of the right forelimb is elevated by contraction of *musculus latissimus dorsi*, *musculus deltoideus scapularis* and *musculus deltoideus clavicularis*. Simultaneously, the contraction of forearm flexors group - *musculus biceps brachii* and *musculus brachialis inferior* - take place.

In the second phase of forelimb movement the arm is abducted mainly by contraction of *musculus supracoracoideus*, with unremitting tension of *musculus deltoideus scapularis* and *musculus deltoideus clavicularis,* and with contemporary relaxation of *musculus latissimus dorsi.* In the final stage of abduction *musculus deltoideus scapularis* and *musculus deltoideus clavicularis* and auxiliary *musculus coracobrachialis brevis* and *musculus coracobrachialis longus* initiates the rotation forward

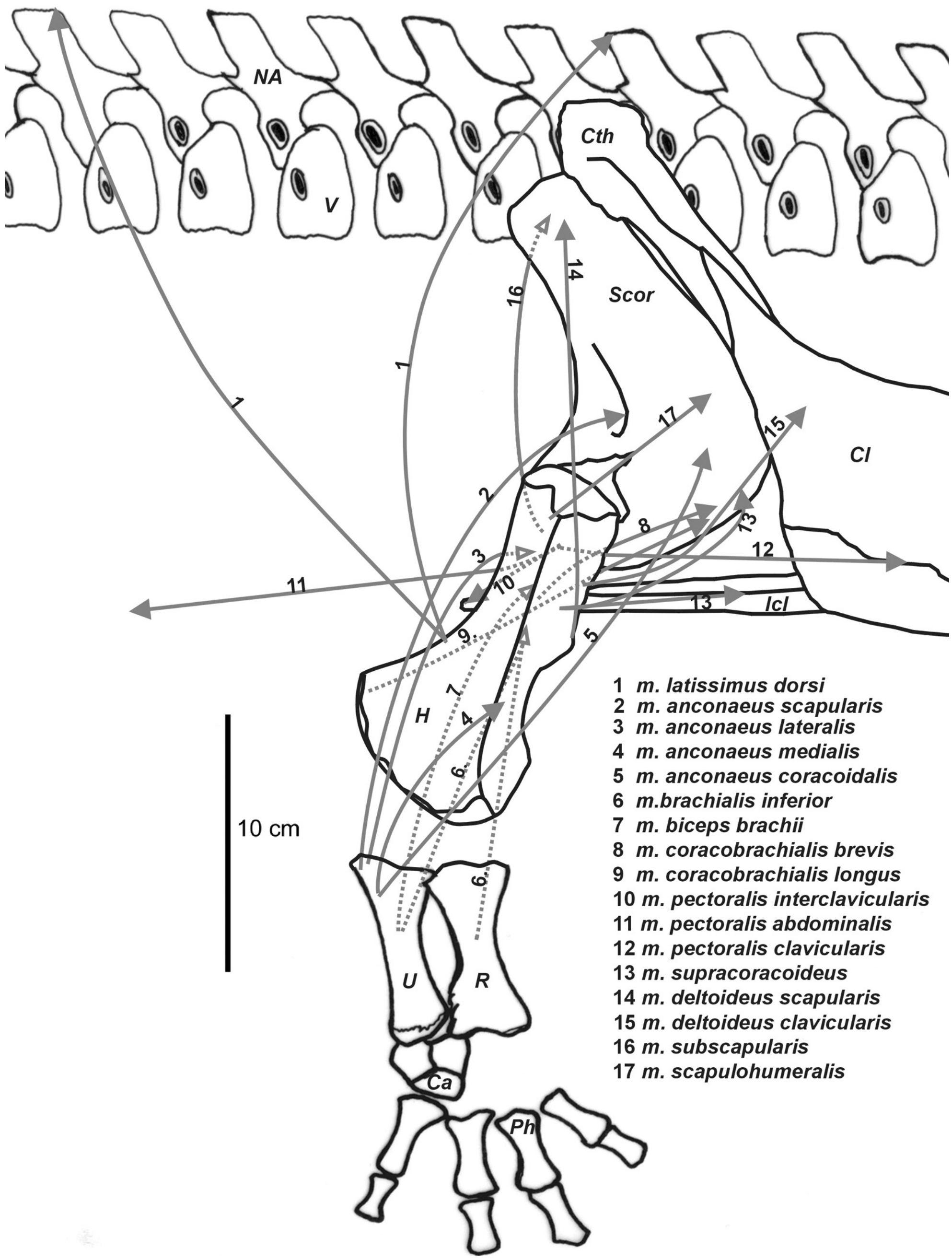

Figure 1. Reconstruction of forelimb musculature of *Cyclotosaurus intermedius* Sulej et Majer 2005 in lateral view. Abbreviations: Ca – carpus; Cl, clavicle; Cth, cleithrum; H – humerus, Icl, interclavicle; NA – neural arch; Ph – phalange; R- radius; Scor, scapulocoracoid; U – ulna; V- vertebrae.

of humeral head inside the shoulder joint acetabulum along the longitudinal axis of humerus, what causes the elevation of the forearm. Humerus reaches the maximum deflection forward at about 90 degree angle to the body longitudinal axis.

In the third phase, extension of the forearm takes place by contraction of extensors group: *musculus anconaeus (triceps) scapularis*, *musculus anconaeus (triceps) lateralis, musculus anconaeus (triceps) medialis* and *musculus anconaeus (triceps) coracoidalis.*

The fourth phase consist of humerus rotation backwards with lowering of forearm mainly by contraction of *musculus pectoralis abdominalis* and *musculus pectoralis interclavicularis* and auxiliary *musculus scapulohumeralis* and the recontraction of *musculus deltoideus scapularis, musculus deltoideus clavicularis*, *musculus coracobrachialis brevis* and *musculus coracobrachialis longus.*

In the fifth phase, humerus is lowered by contraction of *musculus pectoralis clavicularis* with contemporary contraction of the other forelimb muscles, which have muscle attachment on the on ventral side of body. Subsequently manus is being put on the ground and the body weight is being moved on the right forelimb. This position is being hold thanks to the pectoral muscles group (*musculus pectoralis abdominalis*, *musculus pectoralis interclavicularis* and *musculus pectoralis clavicularis*) and auxiliary working *musculus supracoracoideus*.

The sixth phase leads to a stabilisation of the radius and ulna positions towards the humerus by tension of forearm flexors and extensors.

In the next phase, a forward rotation is caused by the partial decontraction of *musculus pectoralis clavicularis* and *musculus supracoracoideus*. Simultaneous contraction of *musculus subscapularis* and permanently working *musculus pectoralis abdominalis* and *musculus pectoralis interclavicularis* effects in adduction of humerus to the animal body. This process is supported by contraction of *musculus latissimus dorsi.*

Afterwards the body weight is again being moved on the left forelimb. During this action the forearm is extended by the contraction of extensors group and progressive relaxation of *musculus pectoralis abdominalis, musculus pectoralis interclavicularis* and *musculus subscapularis*.

In the final phase of the forelimb movement, *musculus latissimus dorsi* adducts humerus to the animal body and its persisting activity causes insignificant humerus.

The contraction of flexors, taking place afterwards, occurs in adduction of forearm to arm. The *musculus deltoideus scapularis, musculus deltoideus clavicularis, musculus supracoracoideus* start working and the cycle retakes.

Possible movement of Cyclotosaurus intermedius during swimming

The role of forelimb in swimming is difficult to characterize without additional, deep analysis of pelvic girdle, hindlimb and vertebral column.

On the base of morphological features of shoulder girdle, especially posterolaterally and slightly ventrally directed coracoid glenoid on scapulocoracoid, and paddle-like shape of humerus two hypotheses of swimming models can be create:

Hypothesis 1

The major role in swimming is fulfilled by limbs.

Sulej (2007) claims that *Metoposaurus diagnosticus krasiejowensis* swim by symmetrical and synchronous movements of the limbs like marine turtles and sauropterygians. This metoposaurid amphibian had limbs with a large manus and pes, like in Dutuitosaurus *lyazidi* from the Argana Formation, that must have been used as flippers, similar like in those recent groups. The bone structure and morphology of the humerus also confirm this hypothesis (Steyer *et al*.2004, Barycka,2007). Metoposaurids had autopodium almost twice as large as *Mastodonsaurus giganteus* (Schoch 1999) or *Paracyclotosaurus davidi* (Watson 1958). The humerus of *Cyclotosaurus intermedius* and both mentioned capitosaurids is longer and its distal head is much narrower than in the metoposaurids. It may be related to the smaller manus than in metoposaurids and may suggest that the whole forelimb has not been organized as a flipper, but like a limb of land vertebrate. Therefore, it is rather improbable that this amphibian could swim in the similar mode like that proposed for *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002.

The mode of swimming characteristic for freshwater turtles seems also unlikely for *Cyclotosaurus intermedius*. In this case forelimbs should have been shorter than hindlimbs. In *Cyclotosaurus* and other capitosaurids, forelimbs had been longer than hindlimbs or both limbs pairs are quiet the same length. Moving in water by lateral strokes of all four limbs, working in diagonal pairs, similar like in stepping, seems to be improbable for as large predator like *Cyclotosaurus*.

A hypothesis where hindlimbs could play the most important role in swimming is highly improbable and it is not consider due to the body shape of Capitosauroidea (Welles & Cosgriff 1965; Schoch & Milner 2000).

Hypothesis 2

The major role during swimming is fulfilled by long, massive tail, which works as pulsation source. In this case the limbs stays adducted to the body and works only as stabilizers.

This way of movement is presented for example in crocodiles (Frey & Salisbury 2001). It also seems to be the most proper for *Cyclotosaurus*.

Summarising we can say that the recent knowledge about the construction of the postcranial skeleton of *Cyclotosaurus intermedius* does still not allow a precise determination of the way of movement of this amphibian in the water environment.

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Streszczenie

Rekonstrukcja umięśnienia kończyny przedniej *Cyclotosaurus intermedius* Sulej & Majer, 2005 (Amphibia: Temnospondyli) z późnego triasu Polski

Praca przedstawia wyniki badań nad muskulaturą i sposobem poruszania kończyny przedniej *Cyclotosaurus intermedius* SULEJ & MAJER, 2005, kapitozaura z późnego triasu południowo - zachodniej Polski.

Materiał wykorzystany w pracy został pozyskany w latach 2000 – 2008 podczas badań prowadzonych na terenie wyrobiska w Krasiejowie.

Autorka prezentuje model muskulatury płaza, opisuje sposób poruszania kończyny przedniej podczas kroczenia, rozważa także przypuszczalne sposoby pływania.

Model muskulatury uwzględnia 17 mięśni mających swoje miejsca przyczepu na kończynie przedniej (fig. 1). Poszczególne mięśnie zostały podzielone zgodnie z ich funkcją na 8 grup: zginacze, prostowniki, dźwigacze, obniżacze, odwodziciele, przywodziciele, odwracacze i nawracacze. Ruch kończyny przedniej został scharakteryzowany w 8 fazach, które obrazują sekwencje skurczów i rozkurczów różnych grup mięsni podczas kroczenia.

Autorka zaproponowała także 2 hipotezy dotyczące sposobu poruszania się w wodzie , rozważając rolę ogona oraz kończyn w tym procesie.