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A cautionary tail: *Cyrtura temnospondyla* Jaekel, 1904, an enigmatic vertebrate specimen from the Late Jurassic Solnhofen Limestone

La tortue qui se mord la queue : *Cyrtura temnospondyla* Jaekel, 1904, un énigmatique vertébré du calcaire de Solnhofen (Jurassique supérieur)

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ABSTRACT

The enigmatic vertebrate taxon *Cyrtura temnospondyla* is reassessed following the location and reuniting of both counterparts. The specimen, comprising a series of caudal vertebrae from the Tithonian Solnhofen Limestone, has variously been interpreted as derived either from a temnospondyl amphibian, or a turtle, or to be indeterminate. The redescription of this caudal series reveals that the vertebrae have a single centrum, in contrast to previous descriptions. This specimen is here interpreted to be the tail of a turtle more derived than *Proganochelys* and *Meiolania*, but is otherwise indeterminate and cannot be associated with any of the diagnosed taxa from the Solnhofen Limestone. *Cyrtura temnospondyla* lacks any diagnostic character and must therefore be considered a nomen dubium.

Keywords: Caudal vertebrae, Temnospondyl, Turtle, Late Jurassic, Solnhofen

RÉSUMÉ

L'énigmatique vertébré *Cyrtura temnospondyla* est réévalué suite à la redécouverte et la réunification de chacune de ses deux contre-empreintes. Ce specimen, qui consiste en une série de vertèbres caudales provenant du calcaire de Solnhofen (Tithonien), a été successivement interprété comme appartenant à un temnospondyle ou une tortue, ou bien comme étant indéterminable. La redescription de cette série caudale révèle que les vertèbres ont un centrum formé d'un seul element, au contraire de ce qui avait été décrit précédemment. Le specimen est ici interprété comme représentant la queue d'une tortue plus dérivée que *Proganochelys* et *Meiolania*, sans toutefois pouvoir l'identifier plus précisément. Il n'est possible d'associer ce reste à aucun taxon décrit dans le calcaire de Solnhofen. *Cyrtura temnospondyla* ne possède aucun caractère diagnostique et doit donc être considéré comme un nomen dubium.

Mots clés : Vertèbres caudales, Temnospondyle, Tortue, Jurassique supérieur, Solnhofen

1. Introduction

Cyrtura temnospondyla is known from a single and enigmatic fossil from the Tithonian Solnhofen Limestone, Germany. This specimen (MNB R 1890) consists of the distal portion of a tail with 14 articulated caudal vertebrae. Jaekel (1904) originally described this material as the tail of a temnospondyl amphibian, notably based on the apparent presence of large intercentra and smaller pleurocentra. At the time, temnospondyl amphibians were thought to have disappeared in the Triassic and Jaekel's (1904) claim should have attracted attention. Yet, probably because of its fragmentary nature, most subsequent authors overlooked this material. When mentioned, *Cyrtura temnospondyla* was either considered undiagnostic (Huene, 1956; Piveteau, 1955), or tentatively referred to turtles, without further discussion (Sukhanov, 1964; Romer, 1956, 1966). In contrast, Kuhn (1964) reaffirmed the original interpretation of Jaekel (1904).

In the past three decades, genuine temnospondyl amphibians have been described from Jurassic and even Early Cretaceous deposits in many parts of the world, but not in Europe (see Maisch and Matzke, 2005 for a detailed review of the fossil record of post-Triassic temnospondyls). In their description of the first unequivocal post-Triassic temnospondyl amphibian, Warren and Hutchinson (1983) briefly reconsidered *C. temnospondyla* based on a cast of the specimen and concluded that it was not a temnospondyl. After consulting E.S. Gaffney, they further concluded that *C. temnospondyla* had no chelonian affinities and considered it as an indeterminate reptile.

One of us (ARM) was able to study part of the specimen in Berlin in 1987, and subsequently mentioned it a couple of times during meetings in the 1990’s. At the 1993 Palaeontological Association Review Seminars, ARM gave a lecture entitled "A Bavarian tail" in which this fossil tail was tentatively referred to a sauropterygian, either a plesiosaur or a pliosaur. However, for several anatomical reasons (e.g., the length of the centra), this conclusion was not entirely satisfactory. In 1995, during the 2nd International Symposium on Lithographic Limestones, ARM gave a second lecture entitled "A cautionary tail" in which he concluded that *C. temnospondyla* was probably a turtle after all. Subsequently, Schoch and Milner (2000) and Maisch and Matzke (2005) cited this conclusion, but did not provide further information. The purpose of the present paper is to settle the issue of the identification of *Cyrtura temnospondyla* and to determine the taxonomical status of this species.

Institutional Abbreviations: FMNH: Field Museum of Natural History, Chicago, USA; MNB: Museum für Naturkunde, Berlin, Germany.

2. Material

The holotype and only specimen of *Cyrtura temnospondyla* (MNB R 1890) consists of a series of 14 articulated caudal vertebrae forming the distal tip of a tail. Associated with this vertebral series is a small disarticulated bone interpreted as a chevron (see below). The specimen actually consists of two slabs of lithographic limestone: the main slab with the bony material (MNB R 1980.1; Fig. 1) and the counter-slab (MNB R 1890.2; Fig. 2) preserving only the imprint of the vertebrae and isolated bone. Interestingly, ARM had access only to the counterpart (MNB R 1890.2) while visiting the MNB in the late 1980's. Because the same curator (the late Dr Herman Jaeger) hosted ARM's visit and sent the cast to Warren and Hutchinson (1983), it can be safely assumed that the latter authors also saw the counter-slab. According to Maisch and Matzke (2005), the other slab was originally in Münich, but is now unaccounted for. In fact, the main slab was also housed in the MNB, but in a different part of the collection, and was relocated only in 2010. Both slabs have now been reunited.

3. Description

The specimen is about 200 mm long in total (Fig. 1). The last four or five vertebrae decrease rapidly in size, which indicates that the tail remained relatively thick almost up to its end. Most vertebrae are damaged to some extent. Each vertebra consists of a single centrum with a fused neural arch. The centra are relatively short and cotton-reel shaped (i.e., cylindrical with slightly expanded anterior and posterior sections), even in posteriormost vertebrae. They appear to have been amphicoelous. A superficial blood vessel has left a groove on the lateral surface of each centrum. This groove extends from the posterodorsal corner to the middle of the ventral margin of each centrum in lateral view. In two of the vertebrae, a second groove branches off the first one in the middle of the centrum and extends anteriorly. The pre- and postzygapophyses are well-defined, even on posterior caudals, and set close to the centrum. The neural arch is low and the neural spine is relatively poorly developed. Transverse processes are present at least up to the tenth preserved caudal vertebra, but their lateral development is uncertain.

An isolated fragment of bone is preserved close to the anterior part of the tail. The imprint reveals a proximal head slightly expanded forming an articular surface, an elongate body slightly arched, and a distal part terminating bluntly (Fig. 2). This bone can therefore be confidently identified as a haemal arch, or chevron. The first four caudal vertebrae have no associated haemal arches, but they may have been disarticulated. A roundish bony element, intercentral in position, is associated with each subsequent vertebra. Each of these elements appears to be in articulation with the centrum directly anterior to it. Because the caudal series is preserved in lateral view, it is uncertain whether these elements are paired or not. However, they are probably best interpreted as haemal arches as well (see below).

4. Discussion

Jaekel (1904), Kuhn (1964), and Warren and Hutchinson (1983) all interpreted MNB R 1890 as having centra divided into intercentrum and pleurocentrum (Fig. 1a). For Jaekel (1904) and Kuhn (1964), the larger element in each vertebra was the intercentrum, whereas the smaller unit was the pleurocentrum. In contrast, Warren and Hutchinson (1983) interpreted the larger element as the pleurocentrum, which suggested reptilian rather than amphibian affinities. However, close examination of the specimen reveals that the centra are in fact single. What previous authors interpreted as a separation between putative inter- and pleurocentrum is in fact a groove left by a superficial blood vessel on the lateral surface of the single centrum. Consequently, this tail does not belong to any primitive tetrapod with a multipart centrum (i.e., temnospondyls, anthracosaurs).

MNB R 1890 is characterized by single, relatively short, cotton-reel shaped centra that do not reduce gradually in size (Fig. 1). Among potential mid-Mesozoic candidates, the distal extremity of the tails of lizards, crocodiles, rhamphorhynchoid pterosaurs, dinosaurs, early birds, and mammals all have long centra reducing gradually in size posteriorly. Similarly, ichthyosaurs can be ruled out as well because their centra are flat, hockey-puck shaped discs reducing gradually in size distally. This leaves only turtles and plesiosaurs, if we restrict ourselves to groups that are known during the Late Jurassic. Many plesiosaurs have caudal centra that vary from disc-like to cotton-reel shaped. Haemal arches and caudal ribs are usually present most of the length of the tail. However, several characteristics exhibited by MNB R 1890 are inconsistent with an attribution to plesiosaurs: the centra of MNB R 1890 are too long; the zygapophyses are set too close to the centrum; the neural arches are too weakly developed dorsally.

Unfortunately, caudal vertebrae are rarely described in details in the literature, either for modern or fossil turtles, which greatly hinders comparisons. The tail is usually much reduced in most modern turtles. The caudal vertebrae are generally reduced to a cylindrical centrum and a low neural arch. The fusion of these elements is relatively delayed and may never happen in aquatic forms (Romer, 1956). Haemal arches (chevrons) are usually absent in modern forms. In contrast, the tail remains long and muscular in modern snapping turtles (Chelydridae) and *Platysternon megacephalum*. In *Chelydra serpentina* (e.g., FMNH 22056), the caudal centra are longer than those of MNB R 1890, and the neural spine is lower. Zygapophyses are set close to the centrum and are well developed all the way to the tip of the tail. In contrast to most modern turtles, haemal arches are present and occur on all caudal vertebrae but the anteriormost ones. However, these haemal arches never reach the development observed in MNB R 1890. Caudal vertebrae also remain relatively robust and well-developed in modern sea turtles, especially in males (Wyneken, 2001).

The characteristics exhibited by MNB R 1890 (short, cotton-reel-shaped centra; low neural arch; zygapophyses and transverse process developed up to the tip of the tail) are finally only consistent with an identification as a turtle tail. The presence of well-developed haemal arches even on posteriormost caudal vertebrae and the amphicoelous articulations suggest a plesiomorphic morphology. Conversely, the low neural arch and reduced transverse process indicate that the turtle to which this tail belonged was more derived than *Proganochelys quenstedti* and *Meiolania platyceps* (Gaffney, 1985, 1990). More precise identification is hampered by lack of comparative material. If turtles are fairly abundant in many Kimmeridgian and Tithonian European deposits, notably in the Solothurn Limestone, caudal vertebrae, let alone articulated tails, are relatively uncommon. The tail is however partly known in some Eurysternidae. The tail is long and slender in *Idiochelys fitzingeri* (Meyer, 1839; Rütimeyer, 1873). *Eurysternum wagleri* was initially described as having a short and stout tail (Joyce, 2000; Zittel, 1877), but a recent reassessment revealed that the tail was also long and rather slender in this species (Anquetin and Joyce, in press). This is also confirmed by several beautiful, undescribed specimens in private collections (e.g., Karl and Tichy, 2006). Joyce (2000) described the tail of *Solnhofia parsonsi* has being intermediate in length between that of *Idiochelys fitzingeri* and that of *Eurysternum wagleri*. Based on published figures, the tail of *Solnhofia parsonsi* appears slenderer than that of the two aforementioned taxa. As far as we can tell, the caudal vertebrae of these three eurysternids are apparently amphicoelous, but detailed description of articular areas is missing. A long and relatively stout tail is also known in at least one specimen referred to the panpleurodire *Platychelys oberndorferi* (Karl and Tichy, 2006). However, the anatomy of the caudal vertebrae is not described in details in any of the aforementioned taxa, which prevents comparison with *Cyrtura temnospondyla*. Additionally, all of these taxa are small to moderately-sized turtles with the biggest *Eurysternum wagleri* probably reaching about 35–40 cm in carapace length (Anquetin and Joyce, in press), whereas most known specimens of *Idiochelys fitzingeri*, *Solnhofia parsonsi*, and *Platychelys oberndorferi* are under 20 cm in carapace length. In contrast, the incomplete tail MNB R 1890 is about 20 cm in length and must have belonged to a much larger turtle. At the time, Thalassemydidae were large coastal marine turtles with carapace reaching more than 80 cm for the largest individuals (JA, unpubl. data), but the anatomy of their tail is not known. Therefore, mostly because of the scarcity of comparative material, the characteristics of MNB R 1890 remain undiagnostic at the species level. The best option is therefore to identify MNB R 1890 as Testudinata indet. and to consider *Cyrtura temnospondyla* as a nomen dubium (see below).

MNB R 1890 is nevertheless characterized by remarkable haemal arches. Starting from the fifth preserved caudal vertebra, these structures are rounded in lateral view, instead of slender and elongate. To our knowledge, such haemal arches have never been described in turtles. The Late Jurassic crocodylian *Geosaurus* is known to have somewhat similarly inflated haemal arches (Fraas, 1902). The posterior third of the caudal series in *Geosaurus* is strongly deflected ventrally and bears a double-lobed tail. Anterior to the deflection, the haemal arches are elongate and slender. Posterior to the deflection, the haemal arches are bean-shaped in lateral view and connected to the centra by means of a short rod of bone. The resemblance stops here though, and the caudal vertebrae described herein are clearly distinct from those of *Geosaurus*. Still, the peculiar haemal arches of MNB R 1890 may allow a better identification of this specimen in the future, when more comparative material is known.

5. Systematic paleontology

TESTUDINATA Klein, 1760 (sensu Joyce et al., 2004)

Cyrtura temnospondyla Jaekel, 1904

Taxonomic assessment: Nomen dubium.

Type material: *Cyrtura temnospondyla* is based on a single specimen (MNB R 1890), which is the holotype by monotypy. The holotype specimen consists of two slabs: the main slab with the bony elements (MNB R 1890.1) and the counterpart (MNB R 1890.2), which only preserves a mould of the bony elements.

Type horizon and locality: Solnhofen Limestone, Late Jurassic (Tithonian), Germany. There is no reference to the exact locality either in the available literature, or in the MNB catalogue. Only in recent MNB labels is the reference to Solnhofen crossed out and replaced by 'Eichstätt', but we are unable to confirm this information.

Illustrations of type: Jaekel (1904, figure 6; Fig. 1a); Kuhn (1964, figure 1a); Figures 1 and 2.

Referred specimens: None.

Remarks: MNB R 1890 can be confidently identified as a turtle tail (see above). However, in the current state of knowledge, its anatomical characteristics do not allow to recognize a taxon at the species level. Therefore, *Cyrtura temnospondyla* is a valid name, but must be considered a nomen dubium.

Acknowledgements

This paper is dedicated to Dr France de Lapparent de Broin in recognition of her major contribution to the study of fossil turtles. Opinionated, obstinate, and meticulous, she succeeded in the 70s male-dominated academic ecosystem. For the new generation of fossil turtle specialists, she has been very generous with her vast knowledge. JA would like to thank Johannes Müller and Florian Witzmann for access to the MNB collection. The late Herman Jaeger (MNB) was most helpful to ARM at a more difficult time. Daniela Schwarz-Wings (MNB) kindly looked through the history of MNB R 1890. Jean-Claude Rage and Alexandra Houssaye (MNHN, Paris) provided helpful insights on vertebral anatomy. Márton Rabi and an anonymous reviewer provided valuable comments that improved the quality of the manuscript. JA was partly funded by a postdoctoral grant from the Simone and Cino del Duca Foundation (2008 Foundation Prize awarded to Philippe Janvier, MNHN, Paris). The "Section d'archéologie et paléontologie" is funded by the Federal Roads Office (FEDRO, 95%) and the Republic and Canton of Jura (RCJU, 5%).

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Figure captions

Fig. 1. *Cyrtura temnospondyla*: a, modified from Jaekel (1904, figure 6 — not to scale); b, photograph of MNB R 1890.1; c, interpretative drawing of MNB R 1890.1. Abbreviations: bvt,

blood vessel trough; cen, centrum; ch, chevron bone; hae, haemal arch; ns, neural spine; postz, postzygapophysis; prez, prezygapophysis.

Fig. 1. *Cyrtura temnospondyla* : a, modifiée d'après Jaekel (1904, figure 6 — pas à l'échelle) ; b, photographie de MNB R 1890.1 ; c, dessin interprétatif de MNB R 1890.1. Abbréviations : bvt, vaisseau sanguin ; cen, centrum ; ch, chevron ; hae, arc hémal ; ns, épine neurale ; postz, postzygapophyse ; prez, prézygapophyse.

Fig. 2. *Cyrtura temnospondyla*: photograph of MNB 1890.2, the natural mould of MNB R 1890.1. Specimen illuminated from bottom of picture to simulate a positive profile.

Fig. 2. *Cyrtura temnospondyla* : photographie de MNB R 1890.2, l'empreinte naturelle de MNB R 1890.1. Spécimen éclairé par le bas de l'image pour simuler un relief positif.

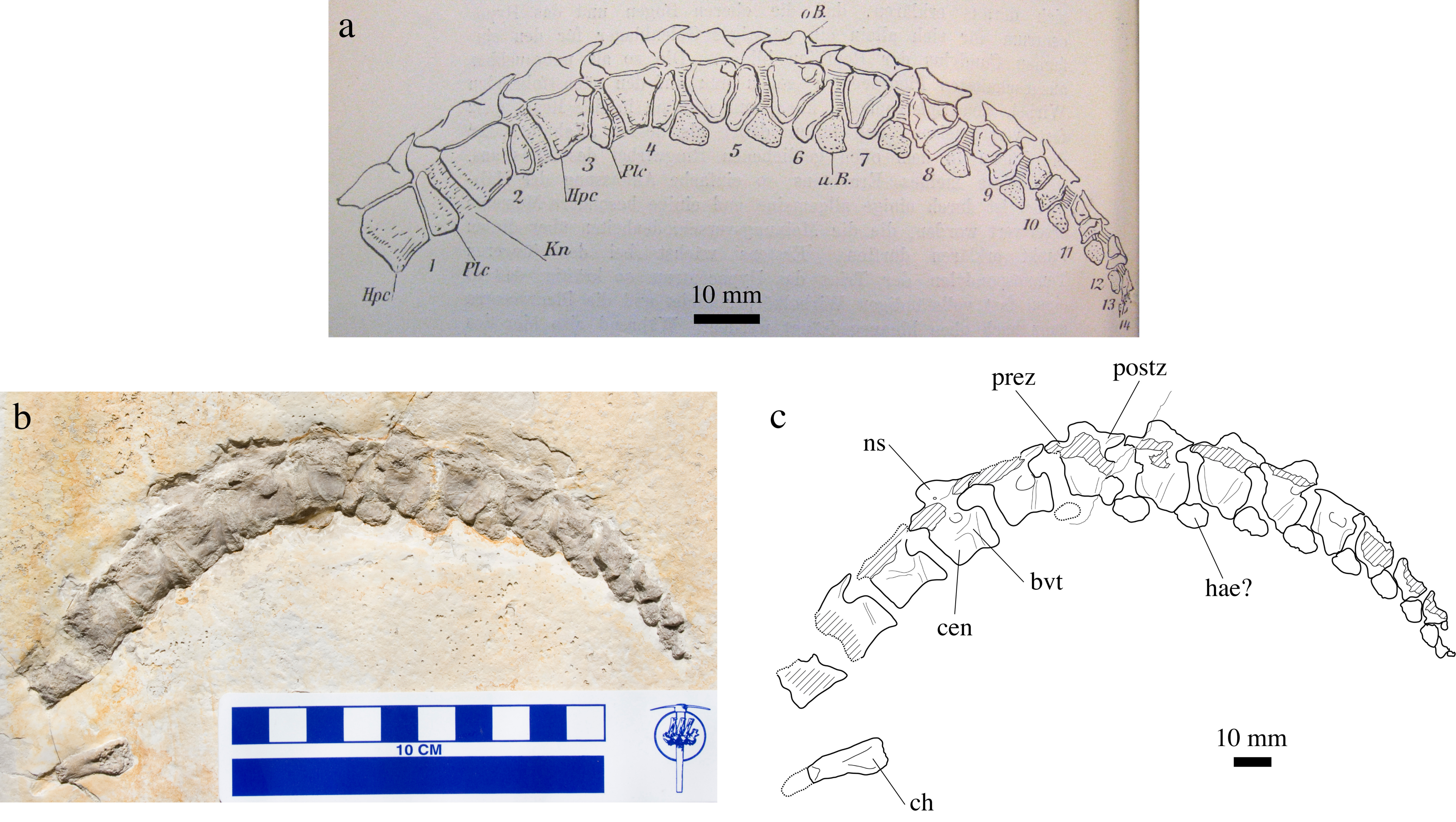
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Figure2