



Mandibular dentition in the Late Triassic temnospondyl amphibian *Metoposaurus*

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The Temnospondyli are a large and diverse group of stem-tetrapods (*sensu* Laurin and Reisz 1997) known from the Early Carboniferous to the Early Cretaceous; their remains have been found on all continents, from Greenland to Antarctica. The Metoposauridae are a short-ranging temnospondyl group recorded only from the Late Triassic; they are characterized by an anterior position of the orbits, a broad parasphenoid and a large quadrate foramen. However, unclear is the taxonomic value of the external location of tusks on the dentary. Our analysis of tooth rows in *Metoposaurus diagnosticus krasiejowensis* from the Triassic (Late Carnian) of Krasiejów (Silesia, SW Poland) shows that the external location of tusks on the dentary is not a synapomorphy for Metoposauridae but a character of great intra-specific variability. Variability of the arrangement of the internal tooth row on the upper jaw has also been observed.

Introduction

The external location of tusks on the dentary as a character typical of metoposaurids was first reported by Warren and Davey (1992). Hunt (1993) also accepted this conclusion and, lastly, Schoch and Milner (2000) included this character in their list of metoposaurid synapomorphies. In none of these papers, however, were any illustrations provided to substantiate this statement. Moreover, the earlier data do not support this conclusion. These data (Case 1932; Dutuit 1976) clearly show that the tusk pair always occupies its normal position on the symphyseal plate rather than within the marginal tooth row.

The main purpose of the present study is to test the position of tusk in the dentary in the light of recent discoveries in Poland of abundant metoposaurid remains, inclusive of numerous skulls and mandibles with well-preserved dentition (Dzik et al. 2000; Sulej 2002).

Institutional abbreviations.—UOBS, Department of Biosystematics, University of Opole, Opole, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and geological setting

The metoposaurid materials covered by this study are assigned to the subspecies *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002, and come from the Upper Triassic of Krasiejów (Opole, southwest Poland). The fossil-bearing horizon includes two lev-

els yielding metoposaurid remains and is currently correlated with Late Carnian Lehrberg Beds in the western part of the Germanic Basin (Dzik 2001; Sulej 2002). Apart from metoposaurids, the local vertebrate assemblage also includes the amphibian *Cyclotosaurus intermedius* Sulej and Majer, 2005, phytosaurs (*Paleorhinus*; see Dzik 2001), the aetosaur *Stagonolepis* (Dzik et al. 2000), the dinosauromorph *Silesaurus opolensis* Dzik, 2003 and the rauisuchian *Teratosaurus silesiacus* Sulej, 2005. Among the invertebrates, most numerous are bivalves (Dzik et al. 2000) and spinicaudatan crustaceans (Olempska 2004).

Our study is based on four complete skulls (UOBS 02068–02070, ZPAL AbIII 685/1) and eight mandibles (UOBS 01288, UOBS 02059–02061, UOBS 02067, ZPAL AbIII899, ZPAL AbIII970/1 and ZPAL AbIII1671).

Description

The general pattern of palatal and mandibular dentition in metoposaurids is very conservative and is well known from descriptions and compilations by Chase (1963) and Warren and Davey (1992). The palatal dentition (Fig. 1A), shared with many other Triassic temnospondyls, includes the marginal teeth row situated on the premaxilla and maxilla, the palatal on the palatine and ectopterygoid, and a pair of tusks each on vomer and palatine. All these teeth are acrodont. Additional rows of small acrodont teeth are also found on the palatine and the vomer. The parchoanal tooth row is located along the medial edge of the choanae, on the palatine and the vomer. The postfenestral tooth row is situated along the posterior edge of the premaxillary aperture. In the specimens studied, these rows are not joined; a break is visible halfway through the medial edge of the openings for the tusks. In the lower jaw (Fig. 1B), the most distinct is the long row of acrolepudont marginal teeth along the entire dentary. Alveoli for tusks are located near the mandibular symphysis. Parallel to the lingual face of the symphyseal region of the mandible is an acrodont parasymphyseal tooth row.

However, in the Krasiejów material studied here, deviations in the configuration of tooth rows have been observed. In mandibles, there are two patterns in the structure of the symphyseal portion; in five specimens (UOBS 01288, UOBS 02060–02061, UOBS 02067, ZPAL AbIII899) the tusk pair occupies a normal position on the symphyseal plate with smaller dentary teeth positioned labially (Fig. 2A). In others (UOBS 02059, ZPAL AbIII970/1 and ZPAL AbIII1671) an expansion of tusk bases to the labial dentary

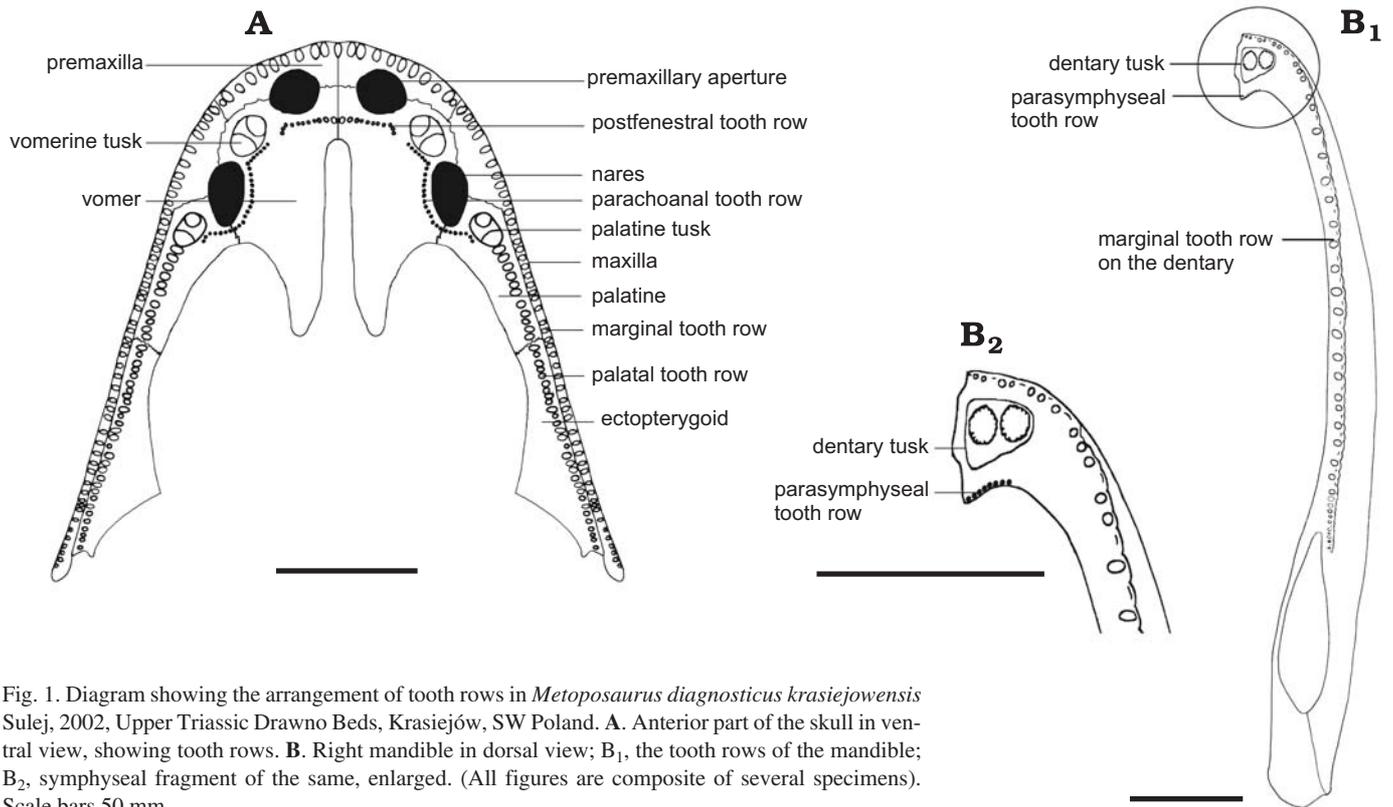


Fig. 1. Diagram showing the arrangement of tooth rows in *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002, Upper Triassic Drawno Beds, Krasiejów, SW Poland. **A.** Anterior part of the skull in ventral view, showing tooth rows. **B.** Right mandible in dorsal view; B₁, the tooth rows of the mandible; B₂, symphyseal fragment of the same, enlarged. (All figures are composite of several specimens). Scale bars 50 mm.

margin is seen (Fig. 2B). Moreover, the parasymphyseal tooth row is absent in specimen ZPAL AbIII 970/1.

Compared to the variability of symphyseal dentition, variation in the palatal tooth system as found hitherto in the Polish subspecies *Metoposaurus diagnosticus krasiejowensis* is much rarer. In smaller specimens (UOBS 06068, 06070) the palatal and ectopterygoid components of the row are not aligned but form an obtuse angle, with their adjacent teeth showing size decrease (Fig. 2C). In the largest skull studied (UOBS 02069), the tooth row on the palatine merges gradually into the ectopterygoid row (Fig. 2D). In addition, there is variation in the number of palatal tusks. Normally in one alveolus is tusk and replacement pit. Exceptionally, in specimen ZPAL AbIII 685/1, there are three teeth in the vomerine tusk pits.

Discussion

Inclusion of the tusk in the marginal dentary row, described by Warren and Davey (1992) as a unique character of mandibular dentition in *Metoposaurus*, seems to be a misinterpretation of the actual condition. The tusk always rests on the symphyseal plate and never converts into part of marginal tooth row. The photographs presented here (Fig. 2A, B) confirm this conclusion. According to Dutuit (1976), the reduction or loss of a few neighbouring marginal teeth can be a consequence of the expansion of the tusk bases with growth. This hypothesis is in opposition to new observations on the Krasiejów material. In specimens analysed here, the labial localisation of the dentary tusk is seen in smaller mandibles. This indicates that this character can

be a juvenile feature. Confirmation of this hypothesis requires further research on more specimens.

However, as shown by new *Metoposaurus* material, this character is only a variation rather than a stable diagnostic feature. Its previous interpretations as a synapomorphy may have suffered from insufficient characterisation of metoposaurids mandibles, having been based primarily on the description of *Buettneria bakeri* (Case 1931; Jupp and Warren 1986). Additional data were supplied by Branson and Mehl (1929) and Dutuit (1976). Their descriptions were based solely on isolated finds, and thus cannot be representative of all the *Metoposauridae*; it is especially difficult to state whether a particular feature is constant or variable.

The presence of other variability is very rare. Parasymphyseal teeth are a common feature in Triassic temnospondyls, also in metoposaurids (Case 1922; Warren and Davey 1992). The absence of symphyseal teeth in ZPAL AbIII 970/1 may be a preservational artefact, similar to what Clack (1988) suggested for *Ichthyostega*. These are very small acrodont teeth, which can easily be destroyed during taphonomic processes. Some deviation from the typical pattern of the main palatal row found in two smaller individuals (UOBS 06068, 06070) may also suggest that it is a juvenile character.

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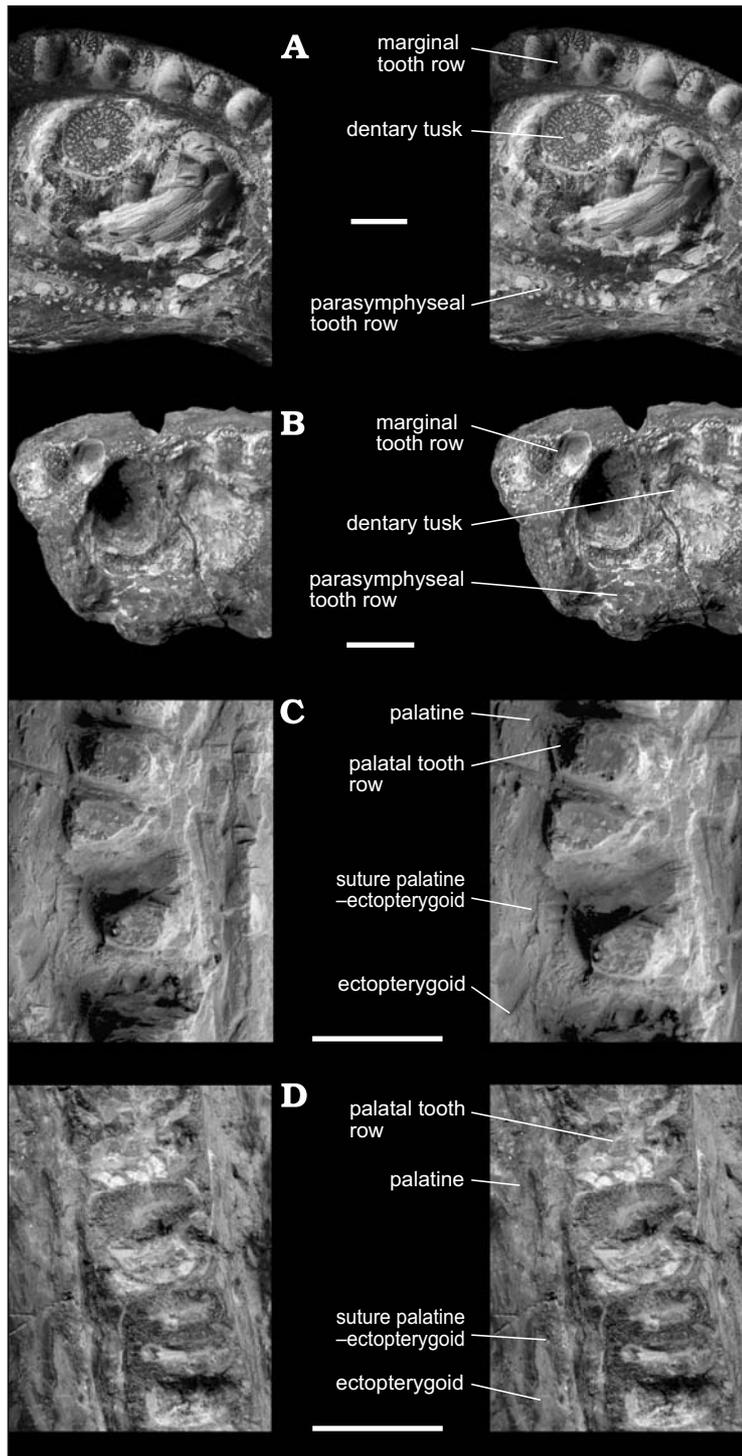


Fig. 2. Stereo-photographs of fragments of tooth rows in complete mandibles and upper jaws in *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002, Upper Triassic Drawno Beds, Krasiejów, SW Poland. **A.** Dorsal view of the symphyseal portion of a right mandible (UOBS 02061), showing marginal dentition and dentary tusk bases not expanded onto tooth-bearing dentary margin. **B.** Dorsal view of the symphyseal portion of a right mandible (UOBS 02059), showing dentary tusk bases expanded onto tooth-bearing margin, with loss of some marginal teeth. **C.** Ventral view of part of the palatal tooth rows in an upper jaw (UOBS 02068), near the suture between the palatine and ectopterygoid. **D.** Ventral view of part of the palatal tooth rows in an upper jaw (UOBS 02069) close to the suture of the palatine and ectopterygoid. Scale bars 5 mm.

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