

The latest metoposaurid amphibians from Europe

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With 4 figures

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Abstract: The occurrence and taxonomy of metoposaurids in the Central European Keuper Basin is reviewed. New finds from stratigraphically higher horizons (Uppermost Carnian – Middle Norian) are reported, giving an extended temporal range for the family in Europe. *Metoposaurus diagnosticus diagnosticus* is present in the Schilfsandstein (Middle Carnian: Julian) and the Lehrbergschichten (Upper Carnian: Tuvalian). The Lehrbergschichten material is characterized by more pronounced reticulate sculpturing, and teeth with laterally compressed, carinate crowns. The chronosubspecies *M. diagnosticus krasiejowensis* first appears in the Kieselsandstein (Carnian/Norian boundary) in Württemberg. The latest record is a well-preserved specimen of *M. diagnosticus krasiejowensis* in the collections of the Natural History Museum, London. This was previously incorrectly assumed to be derived from the Schilfsandstein of Feuerbacher Heide, but originates from the Middle Stubensandstein of the Trossingen area, probably from Aixheim. It demonstrates the presence of metoposaurids well into the Norian of Europe, coeval with the deposition of the first dinosaur-bearing strata.

Zusammenfassung: Die Taxonomie und stratigraphische Reichweite der Metoposauridae im Mittelkeuper des Germanischen Beckens wird neu beleuchtet. Neuere Funde aus stratigraphisch höheren Formationen belegen die Präsenz von Metoposauriden in Europa bis ins Mittlere Nor. Die Chronosubspezies *Metoposaurus diagnosticus diagnosticus* reicht vom Schilfsandstein (Mittleres Karn: Jul) bis in die Lehrbergschichten (Oberes Karn: Tuval). In den Lehrbergschichten finden sich Formen mit deutlich retikulater Dermalskulptur und gekielten Fangzähnen. Diese Unterart wird abgelöst von *M. d. krasiejowensis* im Kieselsandstein, die nun dank eines stratigraphisch neu eingestuften Fundes im Londoner Naturkundemuseum auch im Mittleren Stubensandstein nachgewiesen werden kann. Dieses Stück wurde bisher irrtümlich dem Schilfsandstein der Feuerbacher Heide zugeschrieben, doch läßt sich das anhand von Knochenhaltung und Sedimentmatrix ausschließen. Vielmehr stammt der Fund aus dem Mittleren Stubensandstein und zeigt große Ähnlichkeit mit den Wirbeltierresten aus Aixheim. Dies ist der erste Beleg für das Vorhandensein von Metoposauriden in den höheren, dinosaurierführenden

Schichten des Mittelkeupers und zugleich der jungste Nachweis der Familie in Europa.

Introduction

The Metoposauridae of the Carnian (Upper Triassic) of Germany were among the first temnospondyl amphibians to be collected and described. The family has now been recognised from the Carnian and Norian of Europe, North America, India, North Africa and probably Madagascar. The intrinsic taxonomy of the family suffered from excessive species creation for much of its early history, but over the last decade, a more rigorous approach to diagnosis of species has resulted in the reduction of the family to a small number of clearly defined species, with many taxa recognised as *nomina dubia* (HUNT 1993). However, HUNT's reassessment created two new monotypic genera on relatively minor criteria. As published, the Metoposauridae at present comprises four genera based on large Carnian specimens (*Metoposaurus*, *Buettneria*, *Arganasaurus*, *Dutuitosaurus*) and one smaller relict genus in the Carnian-Norian of North America (*Apachesaurus*). Consequently, it has been suggested that large metoposaurids such as *Metoposaurus* and *Buettneria* were restricted to the Carnian and stratigraphically diagnostic of this stage (LUCAS & HUNT 1993: 327; HUNT 1993: 91; LUCAS 1999: 510). However, a suite of new specimens and one reassessed older specimen demonstrate the presence of large metoposaurids in the Upper Carnian - Middle Norian of Germany, and also show that the later material represents a different taxon from the earlier Middle Carnian material. This has recently been demonstrated by SULEJ (2002) using comparisons of German material with new Polish specimens from Krasiejów in Silesia, and creating two subspecies of *Metoposaurus diagnosticus* to encompass the two sequential taxa. However, the new German specimens used by SULEJ were not described or figured, one illustrated specimen was misidentified and another was incorrectly placed stratigraphically.

In the following work, three Upper Carnian-Norian skulls are discussed. Two are undescribed or briefly described specimens from Baden-Württemberg mentioned by SULEJ (2002). The third, and most significant specimen is a skull in the collections of the Natural History Museum London, which was acquired as part of the HÄBERLEIN collection in 1862. It was subsequently listed by LYDEKKER (1889) as from the Stuttgart area, and asserted as being from the Carnian Schilfsandstein at Feuerbacher Heide by FRAAS (1889). It was subsequently described with FRAAS' locality assignment by WATSON (1919) and noted as distinct by HUNT (1993). In 1998, the authors examined this specimen at the Natural History Museum and concluded that, not only was it distinct from the typical Schilfsandstein *M. diagnosticus*

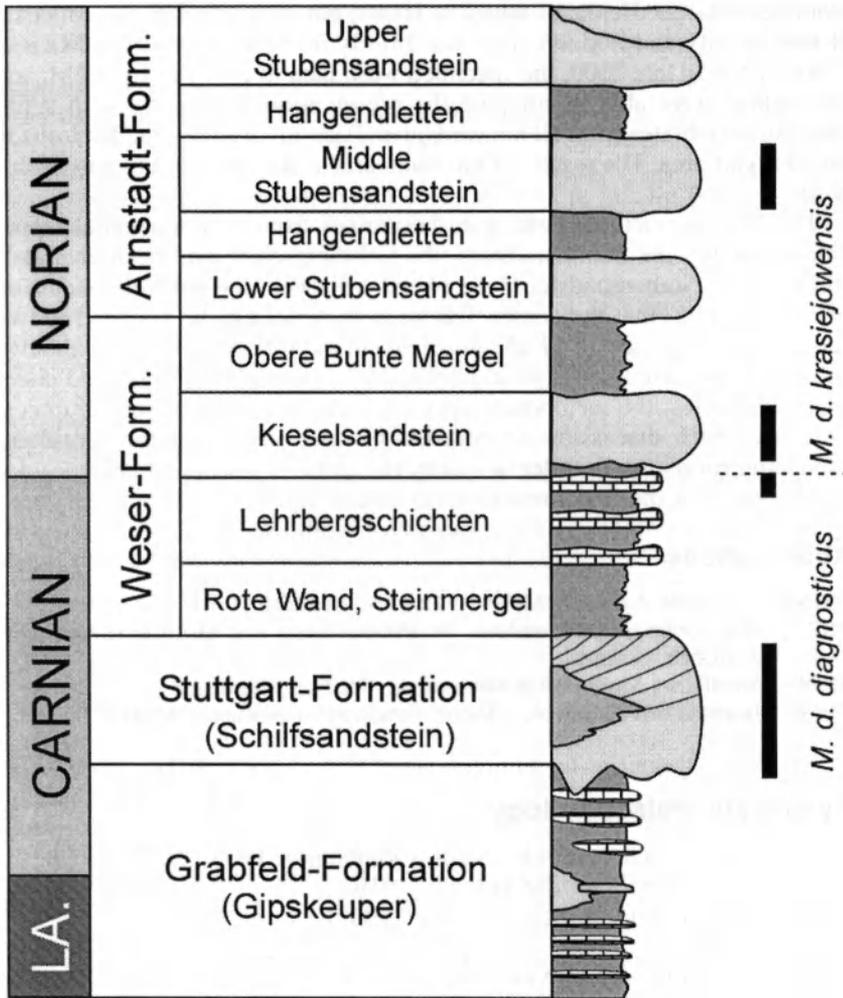


Fig. 1. Stratigraphical range of *Metoposaurus* in the Keuper of Germany. Chronostratigraphy based on BEUTLER et al. (1999) and the results of the present study.

from Feuerbacher Heide, as noted by HUNT, but it clearly was not collected at that locality and horizon. This was briefly noted by SCHOCH & MILNER (2000: 124). In late 2000, the specimen was taken to Stuttgart by ARM, and the authors were able to compare the preservation and matrix with a full range of vertebrates from all known Upper Triassic localities and horizons in the Stuttgart area. The results of this comparison are presented as part of this work.

The German metoposaurid material derives from four sequential Upper Triassic beds - the Schilfsandstein, the Lehrbergschichten, the Kieselsandstein and the Stubensandstein (Fig. 1) and we accept the general conclusion of SULEJ (2002) that the central European material can be assigned to two sequential subspecies of *M. diagnosticus*. In the following account, the two subspecies are discussed in stratigraphical/evolutionary sequence, and under each subspecies, the metoposaur specimens are reviewed in stratigraphical sequence. Each discussion is preceded by an overview of the specimen-producing formation in order to clarify the stratigraphical and palaeoecological context of the four metoposaurid assemblages.

Abbreviations

- BMNH The Natural History Museum, London, England.
 BSP Bayerische Staatssammlung für Palaontologie und historische Geologie, München, Germany.
 SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany.
 ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Systematic Palaeontology

- Superfamily Trematosauroidae SAVE-SODERBERGH 1935
 Family Metoposauridae WATSON 1919
 Genus *Metoposaurus* LYDEKKER 1890

Metopias MEYER 1842 non GORY 1823

Diagnosis: Lacrimal enters orbit margin (shared with *Buettneria perfecta*). Interclavicle with very small central pitted area. Lateral line sulci shallow.

Metoposaurus diagnosticus (MEYER) LYDEKKER 1890

Diagnosis: As for genus, this being the only species. The long linear union of clavicles anterior to interclavicle identified as an autapomorphy for *Metoposaurus diagnosticus* by HUNT (1993) was shown by SULEJ (2002) to be subject to considerable variation within metoposaur populations and therefore of uncertain significance.

Holotype, locality and horizon: See *M. diagnosticus diagnosticus* below.

Metoposaurus diagnosticus diagnosticus (MEYER 1842) SULEJ
2002 Fig. 2

- Metopias diagnosticus* MEYER 1842, p. 302.
Metopias diagnosticus MEYER; MEYER & PLIENINGER 1844, p. 18, pl. 10, fig. 1.
Metopias diagnosticus MEYER; MEYER 1847-55, p. 146, pl. 60.
Metopias diagnosticus MEYER; FRAAS 1889, p. 137, pl. 11.
Metoposaurus diagnosticus (MEYER); LYDEKKER 1890, p. 152, fig. 35.
Metopias diagnosticus MEYER; FRAAS 1896, p. 8, pls. 1-2.
Metopias diagnosticus MEYER; ZITTEL 1911, p. 172, fig. 304.
Metopias stuttgartiensis FRAAS 1913, p. 285; pl. 17.
Metoposaurus diagnosticus (MEYER); SCHMIDT 1928, p. 380, fig. 1069.
Metoposaurus diagnosticus (MEYER); ROMER 1947, p. 251, fig. 41.
Metoposaurus diagnosticus (MEYER); COLBERT & IMBRIE 1956, p. 411, pl. 25.
Metoposaurus diagnosticus (MEYER); HUENE 1956, p. 94.
Metoposaurus diagnosticus (MEYER); SHISHKIN 1964, p. 117.
Metoposauridae spec. nov. SEEGIS 1997, p. 154, pl. 27.
Metoposaurus diagnosticus (MEYER); SCHOCH & MILNER 2000, p. 124, figs. 86, 87.
Metoposaurus diagnosticus (MEYER); SENGUPTA 2002, p.41, fig. 13A-C
Metoposaurus diagnosticus diagnosticus (MEYER); SULEJ 2002, p 538, figs 2-3.

Diagnosis (after SULEJ 2002): Expansion angle of sutures separating parietals from supratemporals is 12.81° , so parietals appear almost parallel-sided. Parietal more elongate anterior of foramen with parietal length following the regression formula $y = 0.31x + 4.59$ (y = prepineal length of parietal; x = skull width). Tabulars anterior to quadrate condyles. In Lehrbergschichten material, dentary teeth laterally compressed and keeled.

Holotype: SMNS 10825, partial skull roof and palate figured by MEYER & PLIENINGER (1844, pl. 10, fig. 1).

Type locality: Feuerbacher Heide north of Stuttgart, Baden-Württemberg, southwestern Germany.

Type horizon: Schilfsandstein (km2), Julian, Middle Carnian.

Stratigraphical range: Schilfsandstein (km2), Julian, Middle Carnian to Lehrbergschichten (km3), Upper Carnian.

Geographical range: Southwestern Germany (east-central Baden-Württemberg).

Referred material:

From the Schilfsandstein at Feuerbacher Heide: complete skull roof, exposed ventrally (SMNS 1011) and the counterpart steinkern of the posterior half (SMNS 1010), complete skull prepared from both sides (SMNS 4943), two intercentra (SMNS 59768).

From the Schilfsandstein at Hanweiler: SMNS 5143, a right skull half (roof and palate) with articulated two-thirds of the trunk.

From the Lehrbergschichten at Sonnenberg, near Stuttgart: Lingual portion of a mandible (SMNS 210), partial symphysis (SMNS 309), intercentrum (SMNS 10505), an interclavicle (SMNS 11423), three ribs (SMNS 12713), right cla-



Fig. 2. *Metoposaurus diagnosticus diagnosticus* from the Lehrbergschichten from near Helfenberg in northern Baden-Württemberg, SMNS 56633. Dorsal view $\times 0.65$.

vicle (SMNS 12714), left clavicle (SMNS 17943, holotype of *M. stuttgartiensis*). From the Lehrbergschichten of other localities north of Stuttgart, SEEGIS (1997) listed six additional specimens comprising keeled fangs (SMNS 80754, 80759, 80762), an angular (SMNS 80755), an anterior mandible portion with laterally compressed teeth (SMNS 80758), and the complete skull (Fig. 2) described below (SMNS 56633) from near Helfenberg, Baden-Württemberg.

The Schilfsandstein material

The Schilfsandstein (Stuttgart Formation: km2, Julian, Middle Carnian) is a unit formed by well-cemented, medium-grained sandstones derived from the Scandinavian highlands and transported throughout the extensive Middle Keuper Basin in large-scale braided river systems (WURSTER 1964; BEUTLER & HAUSSER 1982). It falls into two different facies, a pond facies representing floodplains and a fluvial facies produced by river channels of several hundred metres to few km in diameter (BACHMANN & BEUTLER 1996; BEUTLER et al. 1999). The fluvial facies occasionally yields fossils, especially plant material and vertebrate bones. These are concentrated in small accumulations or rarely in larger assemblages. One particularly rich Fossilagerstätte produced the first known material of *Metoposaurus diagnosticus*, at the Feuerbacher Heide locality close to Stuttgart (MEYER 1842; MEYER & PLIENINGER 1844; FRAAS 1889). This material includes the holotype of the type species of the genus. In the Schilfsandstein, *Metoposaurus* co-occurs with the capitosauroids *Cyclotosaurus* and *Mastodonsaurus*, and the large trematosaurid *Hyperokynodon* (MEYER 1844; FRAAS 1889, 1913; HELLRUNG 1987; SCHOCH 1999). After *Cyclotosaurus robustus*, which dominates the assemblage at the Feuerbacher Heide, *Metoposaurus diagnosticus* constitutes the second most frequent stereospondyl in these beds, present as mostly medium (30 cm skull) to large (45-50 cm skull) specimens. The Feuerbacher Heide has yielded complete skulls and isolated postcranial elements, but the bulk of the disarticulated material is formed by flat dermal bones, suggesting some selective transport. Bones are dark-brown to black, and skulls are crushed flat. Plant material, especially calamites, is abundant and contributes even to the matrix filling the steinkerns. Amniotes are much rarer than amphibians and are known from only two enigmatic finds: the probable crocodylomorph *Dyoplax* (LUCAS et al. 1998) and a phytosaur (HUNGERBUHLER 2001).

The Schilfsandstein material comprises the classical European *Metoposaurus* specimens from Feuerbacher Heide and Hanweiler. The type specimen of *M. diagnosticus diagnosticus* is a partial skull SMNS 10825 figured by MEYER & PLIENINGER (1844 Pl. 10 fig.1) and HUNT (1993 Fig. 5C). SULEJ (2002 fig. 2) incorrectly figured a skull as this holotype but his figure depicts the snout of the more complete Schilfsandstein specimen SMNS 4943, previously illustrated by FRAAS (1889 plates XII-XIII) and HUNT

(1993 fig. 5A-B). FRAAS (ibid., Pl. XII) depicted this specimen with a small lacrimal not extending to the orbit and this has subsequently been taken to be a diagnostic character of *Metoposaurus diagnosticus* in contrast to many other metoposaur taxa (e.g. ROMER 1947, HUNT 1993, MILNER 1994). SULEJ (2002) reinterpreted this specimen as having a lacrimal which puts a narrow process back to contact the anterolateral edge of the orbit. We have reexamined SMNS 4943 and concur with SULEJ's interpretation. Of the other major specimens from Feuerbacher Heide, the lacrimal shape is not visible in the holotype SMNS 10825, but the inner face of the left lacrimal is visible on the right side of the internal surface of the skull of SMNS 1011. In this specimen, the suture between the lacrimal and the prefrontal can be seen to extend back to the orbit margin, so two specimens from Feuerbacher Heide show this condition. SULEJ (2002) cited other specimens with this condition but they are from later horizons and discussed separately.

Specimen BMNH 37938 is a small skull acquired by the Natural History Museum in 1862. LYDEKKER (1889) attributed its origins simply to the Stuttgart area but FRAAS (1889 p.137 footnote) stated that it came from Feuerbacher Heide and was followed in this judgement by WATSON (1919), HUNT (1993) and SULEJ (2002). We argue that the matrix and the bone preservation are entirely distinct from that of material from Feuerbacher Heide and the provenance of this specimen is discussed below.

The Lehrbergschichten material

The Schilfsandstein Formation is succeeded by the Weser Formation (km3, Tuvalian, Upper Carnian) that includes the Lehrbergschichten, a thin section of reddish-brown, purple, and greenish-gray siltstones, claystones, and dolomites. They formed in playa lakes and represent seasonally fluctuating environmental conditions (SEEGIS 1997). Throughout southern Germany they are subdivided by thin dolomitic layers (Lehrberg-Bänke) into three units, the intermediate beds being known as the Rote Wand. The whole Lehrbergschichten unit is topped by an erosive sandstone body, regionally known as either Kieselsandstein (Baden-Württemberg) or Blasensandstein (Bavaria). The Carnian-Norian boundary is presumed to fall at the base of the Kieselsandstein (BACHMANN et al. 1999). SULEJ (2002) treated the Rote Wand and Lehrbergschichten as sequential beds but in fact the Rote Wand and Lehrberg-Banke are alternating sediments within the Lehrbergschichten. While vertebrate fossils are generally rare, the fauna of the Lehrbergschichten is dominated by metoposaurids, which occur in a broad range of sizes. Other finds include dipnoans, coelacanth, plagiosaurids, phytosaurs, and moderately advanced cynodonts (SEEGIS 1997). The fragmentary nature of most finds makes precise systematic assignment impossible.

FRAAS (1913) first described diagnostic metoposaurid material from this unit and referred this to a new species, *Metoposaurus stuttgartiensis*. This material consists of clavicle fragments, vertebral centra, and ribs from the Sonnenberg mountain range. The holotype, a left clavicle (not interclavicle, as stated) of a relatively large specimen was argued by HUNT (1993) not to be critically diagnostic below family level. SCHOCH & MILNER (2000) followed this view. However, the interclavicle in the original material (SMNS 11423) does show the very reduced area of central pitting surrounded by very elongate striations, which does appear to characterise *Metoposaurus* sensu stricto (COLBERT & IMBRIE 1956: 428; SULEJ 2002: 541).

In 1995, geologist Dr. DIETER SEEGIS of Schorndorf discovered a small metoposaurid skull (SMNS 56633) in a section of green claystones from the Rote Wand immediately above the third Lehrbergbank (Fig. 1) in the Amalienhof vineyard near Sohlbach-Beilstein north-east of Helfenberg, northern Baden-Württemberg. The find constitutes the first diagnostic specimen from that horizon. SEEGIS (1997) briefly reported this and other new finds of metoposaurids in the Lehrbergschichten in an extensive monograph of that stratigraphical unit. SMNS 56633 is a relatively complete small skull (175 mm) preserved in dorsal view (Fig. 2). It is obviously a juvenile specimen, which can be concluded from the very delicate bones, the weak sculpturing, and small size. The sutures are mostly straight and well-defined, and the lacrimal makes a substantial contribution to the orbital rim, its suture with the jugal runs sagittally on both sides. As observed by SULEJ (2002), the parietal-supratemporal sutures are almost parallel and the pre-pineal region of the parietals is relatively long. In these respects it corresponds to the condition in *M. diagnosticus diagnosticus* from Feuerbacher Heide and we endorse SULEJ's placing of this material in that subspecies. A jaw fragment with some marginal teeth (SMNS 80758) and several isolated palatal fangs (SMNS 80754, 80759, 80762) of larger specimens (probably reaching 35 cm skull length) reveals new data on the dentition of the Lehrbergschichten metoposaurids. Firstly, the marginal teeth and palatal fangs are all keeled; and secondly, the marginal teeth are slightly expanded above the base and appear very slightly spatulate rather than conical. Well-preserved teeth are not known for the Feuerbacher Heide material so the immediate taxonomic significance, if any, of these dental character-states is impossible to assess.

A simple extrapolation from SULEJ's (2002) assignment of SMNS 56633 to *M. diagnosticus diagnosticus* would be that the Lehrbergschichten/Rote Wand material could be assumed to all belong to this subspecies, although most of it is indeterminate below generic level. Curiously, in his final systematic summary, SULEJ (2002: 545) assigned the interclavicle from Sonnenberg to *Metoposaurus diagnosticus krasiejowensis* without any morphological justification. He appears to have (i) assumed that the Lehr-

bergsschichten succeeded the Rote Wand, and (ii) that the presumed correlation of the Drawno Beds with the Lehrbergsschichten meant that the less determinate metoposaur material could be referred to *Metoposaurus diagnosticus krasiejowensis*. In fact, SMNS 56633 from the Rote Wand is from a higher horizon (above the 3rd Lehrbergbank) than the Sonnenberg material (from below the first Lehrbergbank). Thus *M. diagnosticus diagnosticus* occurs up to the highest parts of the Lehrbergsschichten and all earlier material is likely to belong to this subspecies. This does present problems for the supposed correlation of the Drawno Beds with the Lehrbergsschichten, as discussed further below.

Metoposaurus diagnosticus krasiejowensis (MEYER) SULEJ
2002 Figs. 3-4

Metopias diagnosticus MEYER; MIALL 1875, p. 157.

Metoposaurus diagnosticus (MEYER); LYDEKKER 1890, p. 153.

Metoposaurus diagnosticus (MEYER); WATSON 1919, p. 32, figs. 18-20.

Buettneria perfecta (CASE); HUNT 1993, p. 78, fig. 8C-D (non CASE).

Buettneria perfecta (CASE); SCHOCH & MILNER 2000, p. 124 (non CASE).

Metoposaurus diagnosticus krasiejowensis (MEYER); SULEJ 2002 p. 535, figs 4, 5, 6A, 7, 8.

Diagnosis (after SULEJ 2002): Expansion angle of sutures separating parietals from supratemporals is 21.81° so parietals visibly narrow posteriorly. Parietal less elongate anterior of foramen with parietal length following the regression formula $y = 0.29x - 5.74$ (y = prepineal length of parietal; x = skull width). Tabulars level with quadrate condyles. In adult stages, sculpturing is more pronounced and lateral line sulci are deeper than in *M. diagnosticus diagnosticus*.

Holotype: ZPAL Ab III 358, a complete skull figured by SULEJ (2002 fig. 4).

Type locality: Krasiejów, Opole, Poland.

Type horizon: Drawno Beds, ? Upper Carnian, Upper Triassic.

Stratigraphical range: In Central Europe: Drawno Beds, ? Upper Carnian, Kieselsandstein (km3, Laciian, Lowermost Norian), and from the Middle Stubensandstein (km4, Alaunian, Middle Norian).

Geographical range: Baden-Württemberg through southeastern Poland.

Kieselsandstein specimen: SMNS 80573, an impression of skull roof (Fig.3) from near Fichtenberg, Baden-Württemberg.

Blasensandstein specimen: A possible referred specimen was a complete skull (BSP 1931 X 3, lost presumed destroyed in 1944) from Ebrach, Upper Franconia, Bavaria.

Stubensandstein specimen: BMNH 37938, a well-preserved skull lacking premaxillae and parts of the skull table (Fig. 4); locality not documented but probably Aixheim-Neuhaus, Baden-Württemberg.

Size range of skulls: Kieselsandstein: 28 cm ; Blasensandstein: 44 cm; Stubensandstein: 32 cm.

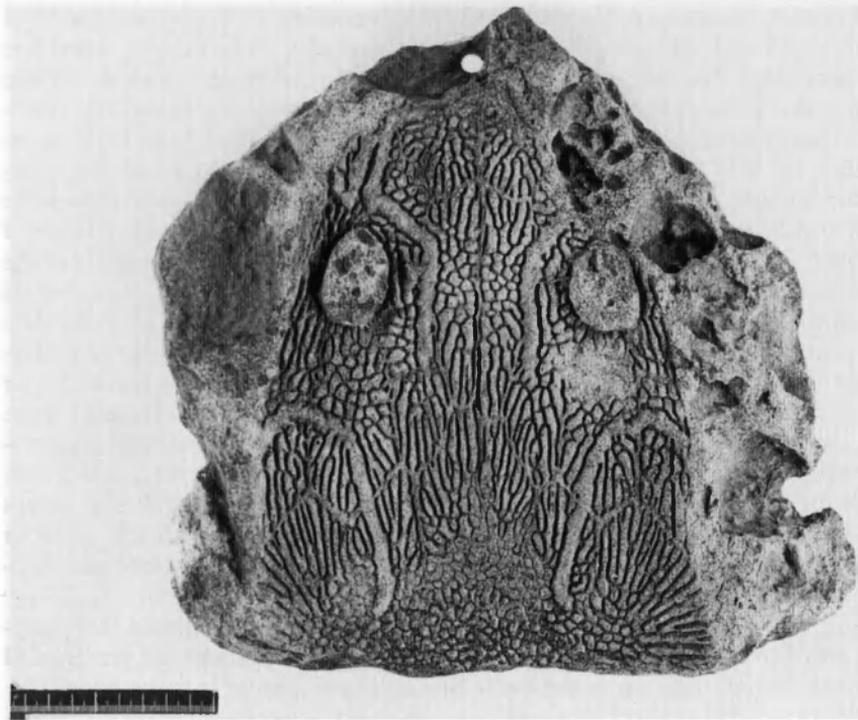


Fig. 3. *Metoposaurus diagnosticus krasiejowensis* from the Kiesel­sandstein of Fichtenberg in northern Baden-Württemberg. SMNS 80573. Dorsal view $\times 0.3$.

The Kiesel­sandstein specimen

The Kiesel­sandstein (Upper Weser Formation: km3, Laci­an, basal Norian – MENNING 1995) is a medium-grained, silicified green to brown sandstone which was washed from the Bohemian and Vindelician Highlands into the Keuper Basin. It is clearly of fluvial origin and marks a pronounced change in the sedimentary regime, being the first evidence of sediment transport from southern and eastern directions in Central Europe (WURSTER 1964). In Württemberg, the Kiesel­sandstein is generally very poor in vertebrate fossils. It contains the oldest dinosaur tracks (*Grallator* sp. and smaller theropod tracks) in southwestern Germany, but otherwise has yielded only one metoposaurid skull imprint from near Fichtenberg. This is described below for the first time, although it was mentioned briefly by SULEJ (2002).

A weathered imprint of a skull roof (SMNS 80573) in a coarse sandstone was found in 1960 by WILHELM FRITZ in the Kiesel­sandstein northwest of

Fichtenberg, northern Württemberg. The specimen preserves nearly 80% of the skull roof, including the pronounced sculpturing, sutures, and lateral line sulci (Fig. 3). The main body of the skull roof is represented but the peripheral elements – premaxillae, maxillae, quadratojugals and tabulars – are not preserved. This is the first and only metoposaurid from that formation in Württemberg, and it has close resemblance to both the Lehrsbergsschichten and Stubensandstein finds. The specimen is sufficiently large that the sutures are clearly visible as slender ridges and they match those of other *Metoposaurus* in almost all respects. The right lacrimal (left on the imprint) can be seen to border the anterolateral rim of the orbit for about a third of the lateral region of its circumference. Of particular systematic significance is that the two parietal-supratemporal sutures converge posteriorly, and that the pre-pineal length of the parietal is relatively much shorter than in Feuerbacher Heide specimens of similar large size. Both of these character-states firmly associate this specimen with *Metoposaurus diagnosticus krasiejowensis*, as argued by SULEJ. The lateral-line sulci are deeply impressed, particularly in the snout region. The dermal sculpture shows reticulate pitting in the centre of all ossifications and over all the posterior skull table, with characteristic trematosauroid arch of striate-elongate sculpture across the middle of the skull table.

This Kieselsandstein specimen is the oldest German specimen that corresponds to SULEJ's *M. d. krasiejowensis*, and it demonstrates the presence of large metoposaurs up to the basal Norian of the European sequence.

The Blasensandstein specimen

The Blasensandstein of northern Bavaria (Upper Franconia) forms a roughly coeval equivalent of the Kieselsandstein, and is characterized by similar petrographic composition and origin. The Ebrach locality in Upper Franconia has produced an interesting vertebrate fauna encompassing phytosaurs, cyclotosaurids, plagiosaurids, a metoposaurid, and dipnoans (KUHNS 1932). KUHNS erected a separate species (*Metoposaurus heimi*) for the metoposaurid (KUHNS 1932: 119). The holotype specimen was lost, presumed destroyed during the 1939-1945 war and the surviving photographs do not permit it to be diagnosed critically at species level, so it is not included in the synonymy here. However, in the context of the other specimens reported here, it is likely that it was a specimen of *M. diagnosticus krasiejowensis*.

The Stubensandstein specimen

The Stubensandstein Formation (Arnstadt Formation: Alaunian, km4, Lower-Middle Norian) encompasses three (or regionally four) sandstone bodies separated by claystone intercalations. According to BEUTLER et al. (1999), the sandstones formed in extensive river systems, which transported debris



Fig. 4. *Metoposaurus diagnosticus krasiejowensis* from the Middle Stubensandstein of Baden-Württemberg. BMNH 37938. Dorsal view $\times 0.4$.

from the Vindelician Highlands in the south and the Bohemian Highlands in the northeast of the basin. The Stubensandstein is a poorly cemented medium- to coarse-grained sandstone that readily weathers and which is clearly distinguishable from the Kieselsandstein/ Blasensandstein in most cases.

The vertebrate fauna of the Middle Stubensandstein is substantially different from that of older formations. As in other horizons, stereospondyl

amphibians are frequent elements, especially *Cyclotosaurus* but also *Gerrothorax* (FRAAS 1913). Amniotes are more diverse: the primitive turtle *Proganochelys*, the phytosaurs *Mystriosuchus* and *Nicrosaurus*, the aetosaurs *Aetosaurus* and *Paratypothorax*, the crocodylomorph *Saltoposuchus*, and the dinosaurs *Halticosaurus*, *Procompsognathus*, and *Sellosaurus* (SCHOCH & WILD 1999). These taxa are not distributed uniformly in a single facies but are known from different assemblages in slightly or essentially different sedimentary facies (e.g. Aixheim, Pfaffenhofen, Magstadt and Heschlach).

Until recently, metoposaurid remains were not known from the Stubensandstein Formation, which covers the largest part of the Lower Norian interval. While examining stereospondyl material in the Natural History Museum, London, the authors recognized a well-preserved metoposaurid skull from Southern Germany in which the matrix and bone preservation was quite unlike that of vertebrates from the Schilfsandstein or Lehrbergschichten. The coarse, calcareous sandstone has a greenish colour and is poorly cemented, which is a typical feature of the Stubensandstein, and by which it is also distinguished from the Kieselsandstein in many regions (GEYER & GWINNER 1991). As we argue below, preservation and facies strongly suggest the stratigraphical position of the find to be Middle Stubensandstein, most similar to specimens from Aixheim.

BMNH 37938 comprises an incomplete skull, about 32 cm long, now largely prepared (Fig. 4). It is characterized by whitish to whitish-yellow bone embedded in a coarse green sandstone. Both the label and BMNH registration catalogue specify that it is from Württemberg and stems from the HABERLEIN collection. It came to the Natural History Museum in 1862 as part of the batch of specimens accompanying the first specimen of *Archaeopteryx lithographica*. It was first mentioned by MIALL (1875: 157) and listed by LYDEKKER (1890:153) as a specimen of *M. diagnosticus* from 'the Middle Keuper near Stuttgart, Württemberg'. Neither LYDEKKER, nor the BMNH catalogue gave any more precise locality information. FRAAS (1889:137 footnote) confidently asserted that it was from Feuerbacher Heide. As the preservation (white three-dimensional bone) is extremely different from the black crushed bone at Feuerbacher Heide, this seems a remarkable attribution and it is questionable if FRAAS ever saw the specimen. After it had been prepared further, WATSON (1919: 32-35) briefly described it, repeating FRAAS' opinion that the specimen was from Feuerbacher Heide and hence from the Schilfsandstein. As a result, the skull was assumed by later workers to be just another specimen from the type assemblage of *Metoposaurus diagnosticus* and not meriting further study. However, HUNT (1993: 78-79) concluded that it was distinct from *M. diagnosticus* (partly on the basis of the spurious differences in the lacrimal configuration) and reassigned it to *Buettneria perfecta* but did not question Wat-

son's locality and horizon attribution. In 1998, we concluded that the source of this specimen required reassessment and noted this (SCHOCH & MILNER 2000: 124).

There is some confusion in the literature about the correct catalogue designation for this specimen. HUNT (1993) referred to it as NHM (BMNH) R 37938. SULEJ (2002) variously referred to it as NHM 37938, SNMS 37 and SMNS 37 (!). The correct designation is BMNH 37938. The change in name from British Museum (Natural History) to Natural History Museum, London, has not affected the institutional acronym. The specimen was added to the collections in 1862 when a single general catalogue number was given. The R-prefix catalogue for the fossil reptile, amphibian and bird collection was initiated later.

Attribution to Feuerbacher Heide can be ruled out with certainty because of both bone preservation (black and crushed) and facies (yellow-brown sandstone) at that locality. The same can be said about Kieselsandstein and Blasensandstein, which also differ considerably in sedimentary facies and type of bone preservation. The Blasensandstein, which has yielded whitish bones at Ebrach, is in Upper Franconia (KUHN 1932), can be ruled out also since the original label attached to the palate of the specimen specifies 'Württemberg' and not 'Franken', and there is no reason not to consider this authentic. In 2000, we made direct comparisons in Stuttgart between this specimen and material from most of the significant localities and horizons in the Upper Triassic of Baden-Württemberg. The preservation (three dimensional creamy-white bone) and facies (green coarse sandstone) closely resemble those of the locality at Aixheim near Villingen-Schwenningen, situated in the Middle Stubensandstein and dated as Lower – Middle Norian. This site has produced two specimens of *Proganochelys quenstedti* and several skulls of *Mystriosuchus planirostris*, and was known early in the nineteenth century. The excellent state of the specimen suggests that it was discovered in an open quarry rather than in a field rock (unlike the heavily weathered SMNS 80573). *Metoposaurus diagnosticus krasiejowensis* was an element of what may be called the 'Aixheim Facies' in association with *Mystriosuchus* and *Proganochelys*.

This is the best preserved specimen among the post-Schilfsandstein (post-Julian) finds of *Metoposaurus*. The sculpturing, suture lines, and lateral line sulci are excellently preserved. The largest part of the skull roof and a good portion of the palate are present. As is typical of Stubensandstein and unlike Schilfsandstein finds, the specimen is almost uncrushed and preserved three-dimensionally. WATSON'S (1919) description of this specimen has meant that it has frequently been used as the representative skull for the cranial anatomy of *Metoposaurus diagnosticus* in preference to the type material from Feuerbacher Heide.

In the snout, only the premaxillae are absent (WATSON 1919), and most of the posterior rim of both skull table and cheek are lacking, as well. In the palate, the basicranial region is incomplete, and the anteriormost palatal region is broken off. The sutures are more curved than in other specimens, but very clear and never truly serrated. The ornament pattern matches that of the Kieselsandstein find precisely, with elongated ridges confined to very few regions (anterior parietals, supratemporals, and squamosals). The ridges themselves are almost never continuous and straight as in juveniles or in adults of *Metoposaurus diagnosticus*, but run in zig-zag fashion. Only the left parietal supratemporal suture is visible but this shows a marked convergence to the midline posteriorly (Fig. 4). The angle of forward widening is not safely measurable, but resembles that of the Drawno Bed material. The pre-pineal length of the parietal is 63 mm in a 32 cm skull and this relatively short distance corresponds to the condition in *M. diagnosticus krasiejowensis*, in fact it appears to be relatively even shorter than the preparietal length in the Drawno Bed material. Thus this specimen can not only be attributed to the Stubensandstein on preservation and matrix grounds but also corresponds to the later subspecies of *M. diagnosticus*.

Systematic discussion

Chrono-subspecies of *M. diagnosticus*

SULEJ (2002) demonstrated that the Schilfsandstein and Drawno Beds *Metoposaurus* material could be consistently separated on characteristics of the parietal and that this separation merited subspecific distinction. Our further examination of the Lehrbergschichten, Kieselsandstein and Stubensandstein material fully supports this interpretation. The material from the different horizons is sufficiently similar that it cannot be safely distinguished in the absence of the middle region of the skull table and there is no evidence for more than one form in any formation. The simplest interpretation is that the central European *Metoposaurus* material represents a single population undergoing one minor morphological saltation around the Tuvalian-Lacian boundary in the Upper Carnian (km3).

Metoposaurus and *Buettneria*

The rational assignment of metoposaurid species to defined genera continues to be highly problematic. The recognition by SULEJ that FRAAS' (1889) interpretation of the lacrimal of *Metoposaurus* was mistaken and that it borders the orbit, revives the problem of that status of *Buettneria*. The taxonomy of both HUNT (1993) and SENGUPTA (2002) are predicated on the assumption that FRAAS' interpretation of the lacrimal of the type material was correct. The position and shape of the lacrimal is a key feature in

grouping metoposaurid species and the new situation that arises is that there are three groups:

- a) *Metoposaurus diagnosticus*, *Buettneria perfecta* and *Buettneria malerensis* with compact lacrimal entering the orbit margin but not the naris margin.
- b) *Arganasaurus lyazidi* with an elongate lacrimal entering the naris margin but not the orbit margin.
- c) *Metoposaurus bakeri*, *Dutuitosaurus ouazzoui* and *Apachesaurus gregorii* with a compact lacrimal separated from orbit and naris.

If lacrimal position were the only criterion, it would be logical to again reduce *Buettneria* in synonymy with *Metoposaurus* as did ROY CHOWDHURY (1965). It would also be logical to assign '*M.*' *bakeri* to another genus. However, like SULEJ (2002: 539) we feel it prudent to restrict this paper to the taxonomy of the European material and to suggest that a more rigorous cladistic analysis of the Metoposauridae needs to be undertaken in the light of this and other new observations by SULEJ (2002) and SENGUPTA (2002).

Biochronological significance

M. diagnosticus chrono-subspecies

Within the western Germanic basin, it appears that *M. diagnosticus diagnosticus* characterises the Julian-Tuvalian assemblages (Schilfsandstein and Lehrbergschichten) of the Middle and Upper Carnian, whereas *M. diagnosticus krasiejowensis* characterises the Lácian-Alaunian assemblages (Kieselsandstein and Stubensandstein) of the Lower to Middle Norian. SULEJ suggested that the presence of *M. diagnosticus krasiejowensis* supported the argument that they were equivalent to the Lehrbergschichten, and so Upper Carnian. The distribution of characters among the successive skulls found in this study suggests the Lehrbergschichten material is *M. diagnosticus diagnosticus* and that *M. diagnosticus krasiejowensis* characterises only Norian beds in the western Germanic Basin. Thus the Drawno Beds would equate to basal Norian Kieselsandstein or younger beds on the basis of the metoposaur material alone. This is, of course, only one of many lines of evidence that will ultimately lead to correlation of the Drawno Beds, but it differs from SULEJ's (2002) interpretation and so needs to be emphasised.

The genus *Metoposaurus*

Extension of the range of European *Metoposaurus* up to the Middle Norian, substantially negates its value as a biostratigraphical indicator at a generic level. The genus can be anticipated to occur in any European continental beds of Middle Carnian to Middle Norian age. In several studies, LUCAS (1998, 1999 and earlier cited work) has used *Metoposaurus* as one of several

index fossils to characterise an Otischalkian Land Vertebrate Faunachron (e. g. LUCAS 1998: 364) approximating to the Lower-Middle Carnian (LUCAS 1998: 366 and fig.14). The new records demonstrate its presence over his Otischalkian, Adamanian and Revueltan Land Vertebrate Faunachrons and are a reminder of the fundamentally ephemeral nature of biostratigraphy based on sudden appearances and disappearances at a generic level. Biostratigraphy based on sequential morphologies in a potential single population in a single sedimentary basin utilises more precisely defined constraints on appearances and disappearances which are more likely to endure. The point at which one *M. diagnosticus* subspecies replaces the other may only be of local value within Europe but it is more likely to be of enduring utility.

Palaeoecology

In three of the four *Metoposaurus*-bearing assemblages in the western Central European Basin, the genus occurs with different permutations of other taxa (the Kieselsandstein specimen has no immediately associated vertebrates). In the fluvatile facies at Feuerbacher Heide (Julian / early Carnian), *M. diagnosticus diagnosticus* is a rare member of an assemblage dominated by the large capitosaur *Cyclotosaurus*. In the Tuvalian (late Carnian), *M. diagnosticus diagnosticus* is associated with phytosaurs and plagiosaurs in addition to capitosaurs; in playa lakes such as documented by the Lehrbergschichten it reaches higher frequencies. In the Middle Norian (Alaunian), *Metoposaurus* was apparently much rarer and confined to a *Mystriosuchus* (phytosaur)-*Proganochelys* (turtle) assemblage. Contemporaneous plagiosaurs, capitosaurs, crocodylomorphs, and dinosaurs are preserved in different sedimentary facies. Apart from the metoposaur-phytosaur association, found elsewhere in the world, there seems to be no clear pattern of habitat or associated fauna.

One interesting correlation that may be noted is between the subspecies of *Metoposaurus diagnosticus* and the source of the sedimentation in which it occurs. *M. diagnosticus diagnosticus* is found in the Schilfsandstein and Lehrbergschichten, the sediments comprising both these beds being derived from the Scandinavian Highlands to the north. *M. diagnosticus krasiejowensis* occurs in the later Kieselsandstein and Stubensandstein, both of which derive from the Bohemian and Vindelician Highlands. The change in source for the water and transported sediments may well have had extended ecological effects on the basin and some of the observed faunal changes may be indirectly associated with this.

Conclusions

The new records reported here, particularly BMNH 37938, add substantial information to the stratigraphical range of metoposaurids in Europe. While the family had been assumed to have disappeared from the continent by the end of the Carnian (Tuvalian), the Stubensandstein find demonstrates their presence well into the Middle Norian (Alaunian). This means that metoposaurids existed in Europe at least 5 myr longer than previously presumed.

The systematics of the German metoposaurids involves two taxa, separable only as subspecies, as argued by SULEJ. In the Schilfsandstein (Julian) and Lehrbergschichten (Tuvalian) *Metoposaurus diagnosticus diagnosticus* is present in different facies and assemblages. Lacial-Alaunian metoposaurids differ in the shape of the parietal from *M. diagnosticus diagnosticus*, which merits subspecific separation, as *M. diagnosticus krasiejowensis*. European metoposaurids appear to all have the lacrimal bordering the orbit margin and are identical to *Buettneria perfecta* in this respect. The problem of defining genera of metoposaurid requires further consideration.

Metoposaurus occurs with three rather different sequential faunal assemblages in Central Europe. In Julian time it was a rare companion of the large capitosaur *Cyclotosaurus*. In the Tuvalian and by the Carnian-Norian boundary, *Metoposaurus* is associated with phytosaurs and plagiosaurids in addition to capitosaurids; in playa lakes such as documented by the Lehrbergschichten it reaches higher frequencies. In the Middle Norian (Alaunian), *Metoposaurus* may have been much rarer and confined to assemblages with phytosaurs and turtles. Contemporaneous plagiosaurids, capitosaurids, crocodylomorphs, and dinosaurs are preserved in different sedimentary facies.

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