Phytosaur remains from the Norian Arnstadt Formation (Leine Valley, Germany), with reference to European phytosaur habitats

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A b s t r a c t

Most inferences on phytosaur ecology are based on comparisons with extant crocodilians, in particular with reference to similarities in their skull morphology. In addition, the sedimentary environment of their place of embedding provides information on their life habitat and the potential lifestyle of these animals. Here we report on newly discovered phytosaur remains from the Norian Arnstadt Formation, which support the interpretation that the European phytosaur genera *Mystriosuchus* and *Nicrosaurus* had different ecological preferences. While *Mystriosuchus*, similar to *Paleorhinus*, was semi-aquatic and piscivorous, *Nicrosaurus* had a terrestrial lifestyle and probably preyed on tetrapods. Comparing the habitats of the different European phytosaur genera reported in literature, it is also concluded, that *Mystriosuchus* and *Paleorhinus* tolerated, contrary to *Nicrosaurus*, a wide range of salinity.

K e y w o r d s : Phytosaurs, habitats, lifestyle, Triassic, Norian, Arnstadt Formation.

Z u s a m m e n f a s s u n g

Rückschlüsse zur Ökologie von Phytosauriern basieren meistens auf dem Vergleich mit lebenden Krokodilen, vor allem wegen der ähnlichen Schädelmorphologie. Neben diesen Merkmalen kann auch das Ablagerungsmilieu des Einbettungsortes Informationen zu Lebensraum und Lebensstil dieser Tiere liefern. In der vorliegenden Arbeit werden Neufunde von Phytosaurier-Resten aus der norischen Arnstadt Formation beschrieben. Diese unterstützen die Interpretation, dass die europäischen Phytosaurier-Gattungen *Mystriosuchus* und *Nicrosaurus* zwei unterschiedliche ökologische Nischen besetzten. Während *Mystriosuchus*, ähnlich wie *Paleorhinus*, einen semiaquatischen Lebensstil hatte und sich hauptsächlich von Fischen ernährte, hatte *Nicrosaurus* einen terrestrischen Lebensstil und machte wahrscheinlich Jagd auf Tetrapoden. Ein Vergleich der Habitate verschiedener Phytosaurier-Gattungen auf Grundlage von Literaturdaten legt die Schlussfolgerung nahe, dass *Mystriosuchus* und *Paleorhinus* im Gegensatz zu *Nicrosaurus* breite Salinitätsbereiche tolerierten.

C o n t e n t s

1. Introduction

Phytosaurs are a Late Triassic clade of extinct archosaurs showing a striking convergence to modern crocodiles. Within the Germanic Basin, they have been reported from Late Carnian to Early Rhaetian sediments (von Huene 1923; Hungerbühler 2002). The best-known phytosaurs are certainly the Norian phytosaurs from the fluvial Stubensandstein (Löwenstein Formation) of the Stuttgart area in Southwest-Germany. In turn, the hitherto scarce occurrence of phytosaur finds in North-German deposits of the same age, such as the predominantly lacustrine Arnstadt Formation (Beutler 2005), remained puzzling. In 2002 then, during the construction of the motorway A38 south of Göttingen, new phytosaur remains were discovered in this formation. These remains and their sedimentary context are described in this paper.

With respect to the habitat of phytosaurs, the common view that these archosaurs inhabited freshwater environments has been challenged by records in marine sediments in Italy (Renesto & Paganoni 1998) and Austria (von Huene 1939; Buffetaut 1993). Consequently, the new phytosaur finds reported here, as well as a review of published occurrences, may help to specify the lifestyle of the different phytosaur genera.

Abbreviations

BMNH Natural History Museum, London, UK
BSPG Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany
GZG Geowissenschaftliches Zentrum Göttingen, Germany
NMW Naturhistorisches Museum, Wien, Austria
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
ZPAL Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland

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2. Location, stratigraphic and sedimentological context

The newly discovered phytosaur remains were found in the Arnstadt Formation, which is Norian in age (Beutler 2005). These sediments were exposed in 2002 during the construction of the motorway A38 approximately 10 km SSW of Göttingen, northern Germany (Fig. 1). The fossils were found at the SE side of the motorway cutting (topo-

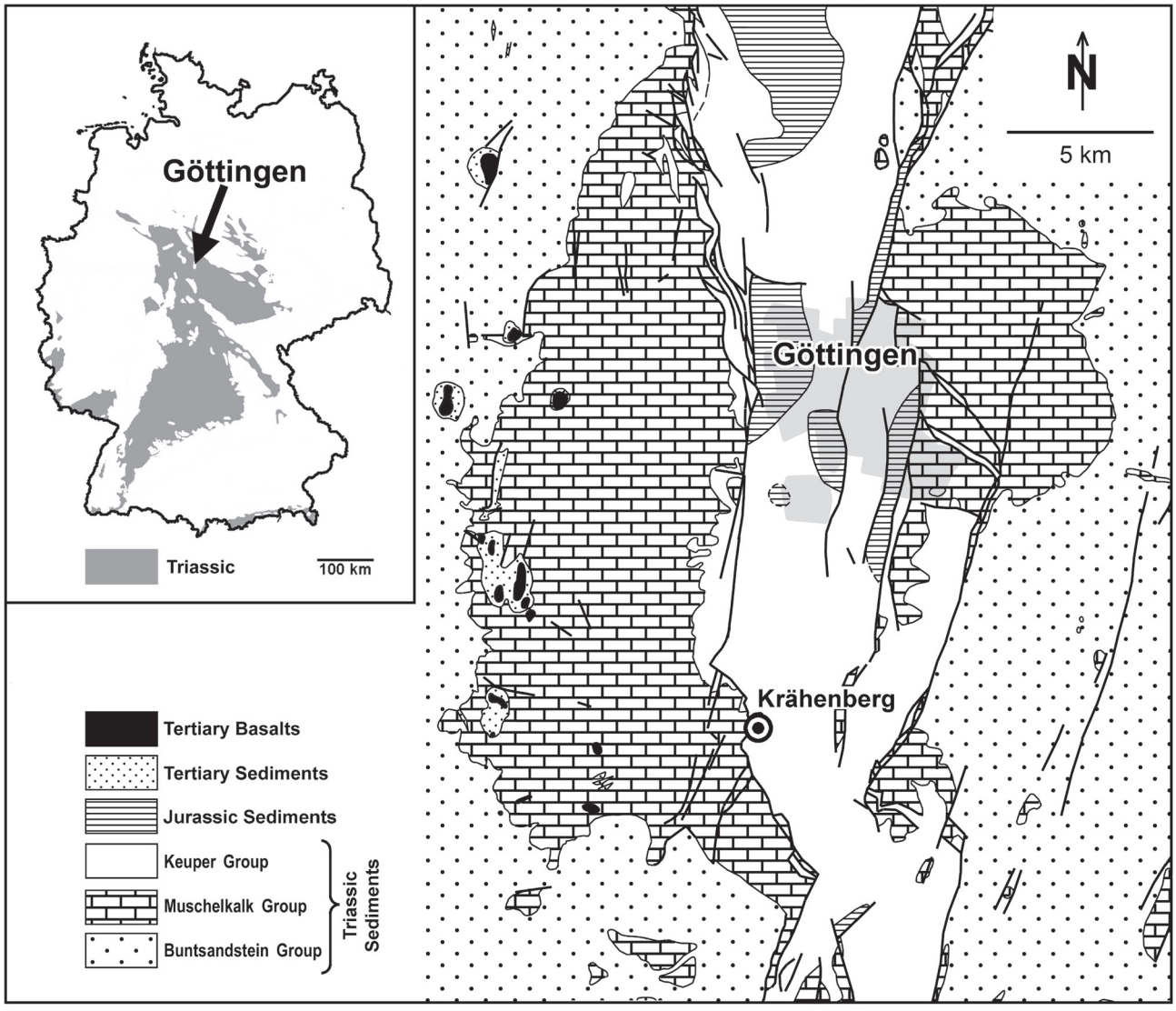

Fig. 1. Geological map of the vicinity of Göttingen, Lower Saxony, and location of phytosaur locality Krähenberg at the motorway A 38. Quaternary cover sediments are not shown. After Stille & Lotze (1933), Ritzkowski (1990), and Grüger et al. (1994).

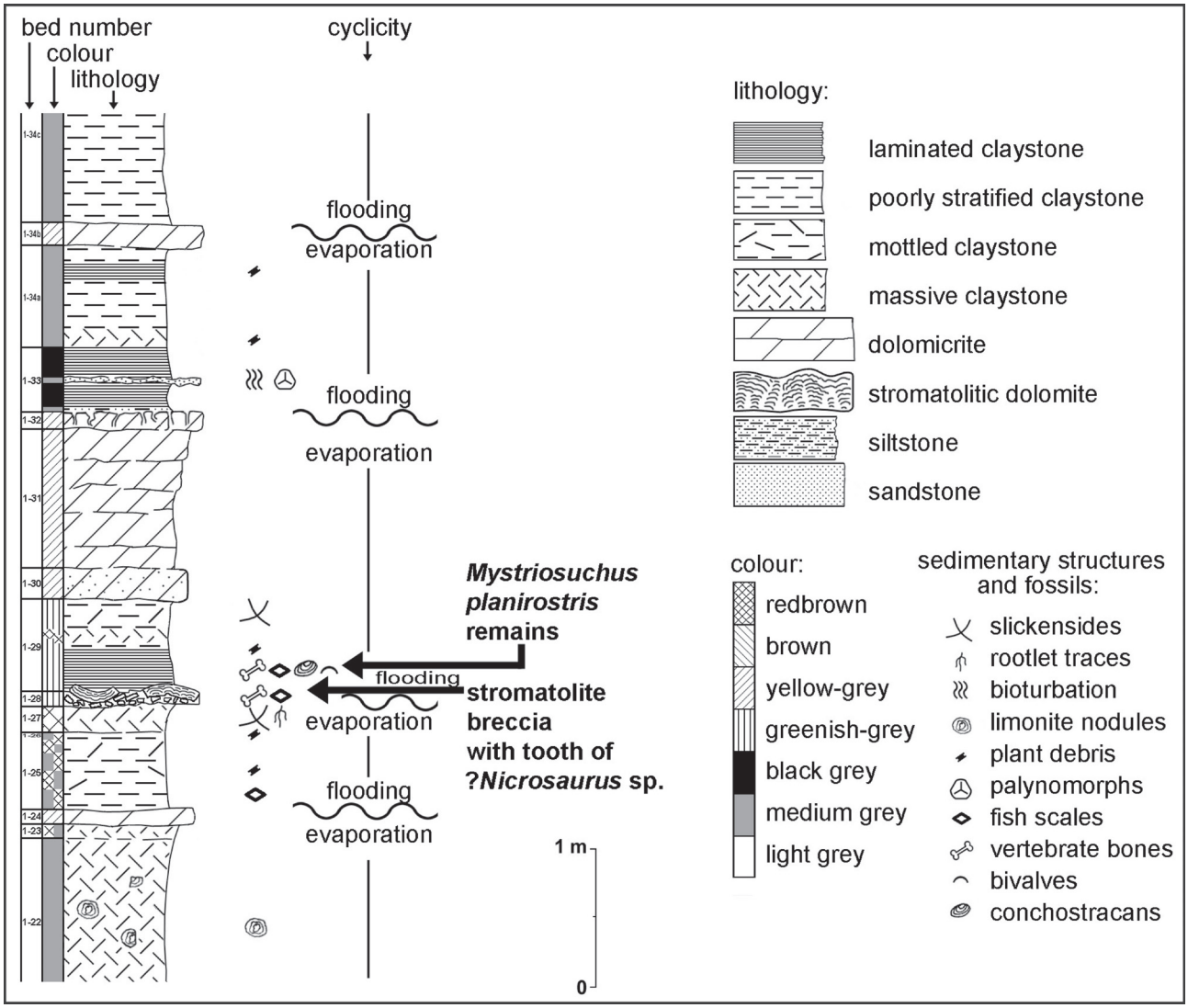

Fig. 2. Detailed section of phytosaur-bearing lacustrine cycle of the "Middle Grey Series", Krähenberg south of Göttingen. Precise horizon of ?*Nicrosaurus* and *Mystriosuchus* remains are indicated by arrows.

graphic map 1 : 25 000, sheet 4525 Friedland; east 35 61 325, north 57 00 625).

The Arnstadt Formation, formerly known as "Steinmergelkeuper", is a predominantly lacustrine sedimentary succession of central parts of the Germanic Basin (Beutler et al. 1999). Freshwater influx into this closed basin was maintained by braided to meandering fluvial systems draining the Bohemian Massif and Vindelizian High in the South. The corresponding deposits of these marginal parts of the basin are coarse siliciclastics and floodplain deposits of the Löwenstein Formation (formely known as Stubensandstein and Burgsandstein; Beutler et al. 1999).

In the investigated area, the Arnstadt Formation is approximately 100 m thick (Vath 2005; Arp et al. 2005), subdivided into three members (Naumann 1911; Dockter et al. 1970; Beutler et al. 1999): (1) Lower Red Series ("Untere Bunte Folge"): sediments of a playa lake system, (2) Middle Grey Series ("Mittlere Graue Folge"): cyclic sediments of a perennial freshwater to saline lake system, and (3) Upper Red Series ("Obere Bunte Folge"): sediments of a playa lake system, after discontinuity overlain by floodplain deposits with fluvial intercalations (crevasse splay). There is no indication of marine influence in the Arnstadt Formation.

Vertebrate remains were recovered from one lacustrine, flooding-evaporation cycle in the upper part of the "Middle Grey Series", exposed at the Krähenberg (Fig. 2). Within this cycle, vertebrate remains occur in two

horizons: (1) within the matrix of a stromatolite breccia at the cycle basis, and (2) within laminated dark claystones 10 cm above the stromatolite breccia.

At the same locality, further vertebrate remains occur in a bone-bed near the basis of the Middle Grey Series (Arp et al. 2005). This bone-bed contains, apart from fish scales, a totally different vertebrate assemblage, with scutes of amphibians, teeth of *Ceratodus* and dorsal spines of sharks. In addition, a conglomerate composed of reworked paleosol nodules at the discontinuity within the Upper Red Series commonly shows rounded, indeterminable bone fragments.

3. Systematic palaeontology

Phytosauria Jaeger, 1828
Phytosauridae Jaeger, 1828
Pseudopalatinae Long & Murry, 1995

Genus *Mystriosuchus* E. Fraas, 1896

Type species: *Mystriosuchus planirostris* (von Meyer, 1863).

Diagnosis. – Very slender and long rostrum, may have a premaxillary crest. The anterior rim of the naris is

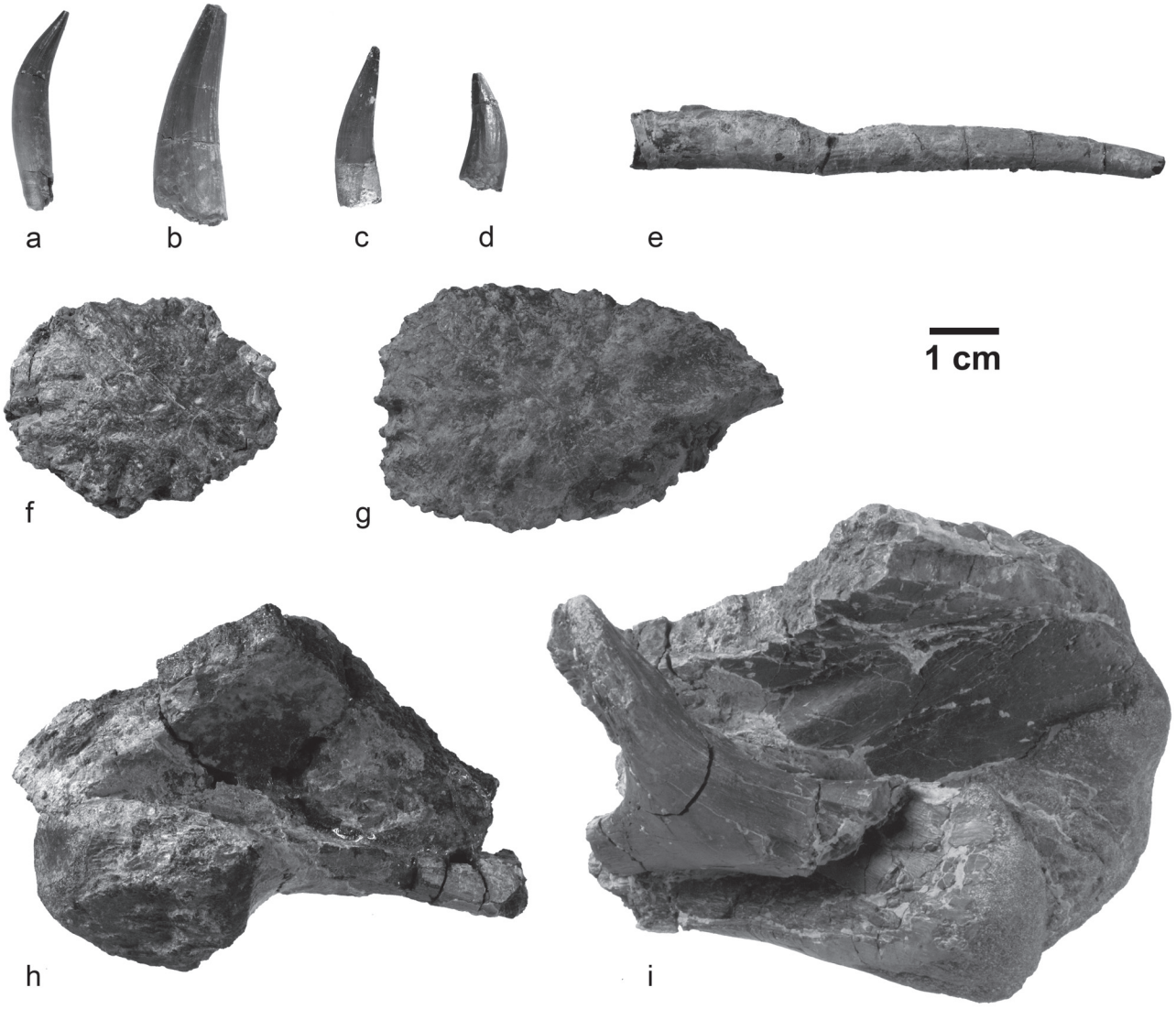

Fig. 3. *Mystriosuchus planirostris* (Meyer, 1863); Arnstadt Formation, Krähenberg section south of Göttingen. – **a**. Tooth; GZG.V.20301. **b**. Tooth; GZG.V.20302. **c**. Tooth; GZG.V.20303. **d**. Tooth; GZG.V.20304. **e**. Gastral rib; GZG.V.20305. **f**. Osteoderm; GZG.V.20306. **g**. Osteoderm; GZG.V.20307. **h**. Squamosum; GZG.V.20309. **i**. Side view of quadratum and quadratojugale; GZG.V.20308.

at the same level as the anterior rim of the antorbital fenestra. The naris is at the level of or below the skull roof. The skull roof is highly sculptured. The postorbital part of the skull is narrow, high and anteroposteriorly abbreviated. The quadrate foramen is very large. The postorbitosquamosal bar is broad and hangs very slightly over the supratemporal fenestra, which is fully opened in dorsal view. The extremity of the posterior process of the squamosal is not broadly rounded. The teeth have a circular cross-section and are long and slender (HUNGERBÜHLER 2002).

D i s t r i b u t i o n . – Upper Triassic of central Europe; south-western Germany: Middle Keuper, middle Stubensandstein (HUNGERBÜHLER 2002); northern Germany: Arnstadt Formation; Austria: Dachsteinkalk (BUFFETAUT 1993); northern Italy: Dolomia Principale, Calcare di Zorzino Formation (RENESTO & PAGANONI 1998; RENESTO & LOMBARDO 1999)

Mystriosuchus planirostris (VON MEYER, 1863)
Fig. 3a–i

* 1863 *Belodon planirostris*. – VON MEYER, p. 241, pl. 41, figs. 1–13.
1896 *Mystriosuchus planirostris*. – E. FRAAS, p. 16, fig. 9, pl. 5.
1906 *Mystriosuchus planirostris*. – MCGREGOR, p. 36, figs. 3, 4.

S t r a t u m : Middle part of Arnstadt Formation, Krähenberg section, 10 cm above basis of bed 1-29 (Fig. 2).

D e s c r i p t i o n . – All *Mystriosuchus* remains described here were found close together, with, except for fish scales, no further remains of other vertebrates associated at this place or lateral in the same layer and bed. Therefore, the *Mystriosuchus* remains are considered as belonging to one individual.

The four teeth of the animal are long and slender with a circular cross-section; the surface is ornamented with small ridges; they have two unserrated carinae. The tooth GZG.V.20301 (Fig. 3a) has a nearly complete root with a length of 1.1 cm and a complete length of about 2.9 cm. At its widest point it has a thickness of 0.4 cm. The largest recovered tooth, GZG.V.20302, has a length of 3.1 cm (Fig. 3b). Two further teeth, GZG.V.20303 (Fig. 3c) and GZG.V.20304 (Fig. 3d), closely resemble GZG.V.20301, but are smaller (L: 2.3 cm and L: 1.7 cm). GZG.V.20305 is the anterior portion of a gastral rib (Fig. 3e), L: 7.7 cm, W: 0.8 cm, H: 0.7 cm. The scutes (Fig. 3f–g) are parts of the ventral scutes of the animal (GZG.V.20306: L: 4 cm, W: 3 cm, H: 1 cm; GZG.V.20307: L: 6 cm, W: 3.5 cm, H: 0.5 cm). GZG.V.20309 (Fig. 3h) is the right squamosal. GZG.V.20308 is part of the right quadrate and the quadratojugal of the animal (Fig. 3i); L: 8 cm, W: 6 cm, H: 7 cm.

D i s c u s s i o n . – The material is crushed, still permitting identification. In contrast to the material of the SMNS, the present finds form part of a very large animal, certainly an adult. The joint of the quadratojugal and the squamosal is well preserved and diagnostic. The form of the squamosal is only known from *Mystriosuchus planirostris*, this includes *Mystriosuchus westphali* as a sexual dimorphism (KIMMIG, unpublished data). Also the only specimens in the SMNS collection showing a similar squamosal are the *Mystriosuchus planirostris* specimens.

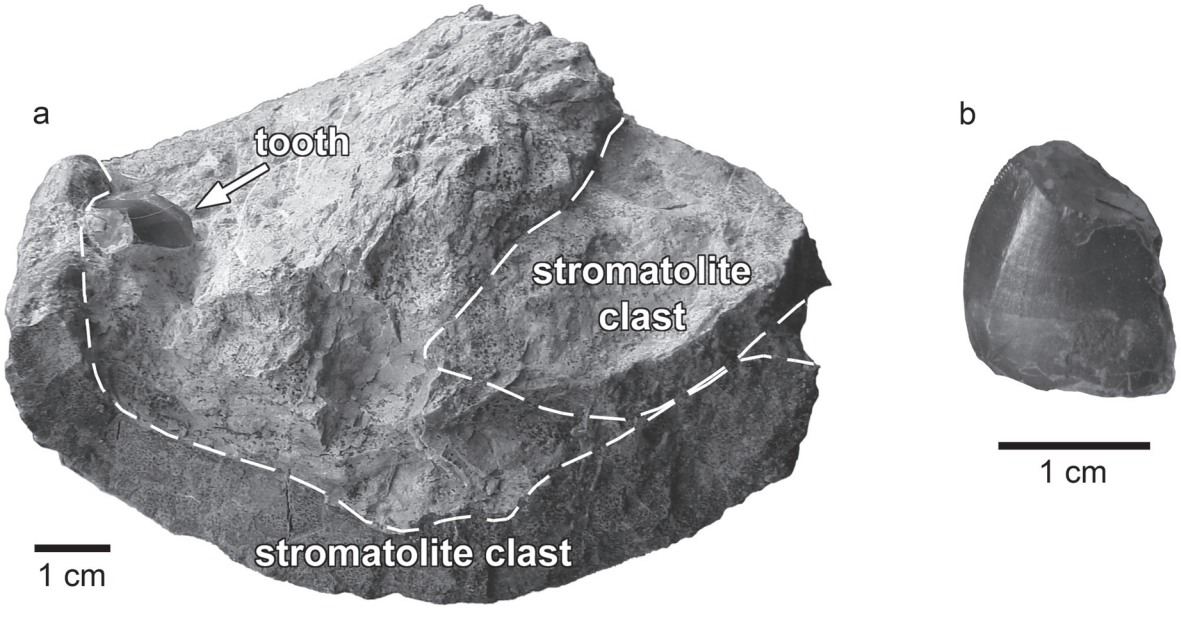

Fig. 4. Tooth of ?*Nicrosaurus* sp.; Arnstadt Formation, Krähenberg section south of Göttingen; GZG.V.20300. – **a**. Hand specimen of stromatolite breccia with tooth in situ. **b**. Enlarged view of the same tooth.

Mystriosuchus westphali has a slightly different opisthotic process (Hungerbühler 2002).

Genus *Nicrosaurus* Fraas, 1866

cf. *Nicrosaurus* sp.
Fig. 4a–b

Specimen: One tooth (GZG.V.20300).
Stratum: Middle part of Arnstadt Formation, Krähenberg section, bed 1-28 (stromatolite breccia, Figs. 2, 4a).

Description. – The tooth has a maximum length of 1.5 cm, is 1.3 cm wide and about 0.5 cm thick (Fig. 4b). The tip of the tooth is missing. The tooth has a triangular appearance and anterior and posterior serrations which both extend to the root. There are three to four denticles per mm. The tooth is laterally compressed.

Discussion. – Flat, serrated teeth similar to the present specimen in shape and size are not known from the phytosaur genus *Mystriosuchus* (see e. g., Hungerbühler 2002), but have been described from *Nicrosaurus* (e. g., Hungerbühler 2000).

Apart of *Nicrosaurus*, *Angistorhinopsis*, which is described from nearby locations, shows a tripartite dentition with flat serrated teeth (von Huene 1923), but its taxonomic status is unclear (Hungerbüehler 2000). Due to the taxonomic uncertainty of *Angistorhinopsis*, even the Berlin Museum of Natural History material from Salzgitter (Hungerbühler 2000) is taxonomically unidentifiable (Rauhut pers. comm.), the tooth is attributed to cf. *Nicrosaurus* (Hungerbühler 2000). *Angistorhinopsis* might be considered as a distinct higher developed phytosaur taxon (Maisch pers. comm.). Teeth from other archosaurs described in literature or examined by the first author in museum collections in Stuttgart (SMNS), Munich (BSPG), and Warsaw (ZPAL) from these and similar deposits differ from the one described. No other taxon has teeth with a similar thickness or size.

4. Interpretation

The phytosaur remains described in this study were found within a single flooding-evaporation cycle of a hydrologically closed palaeolake system, but come from two distinct levels within this cycle:

(1) *Nicrosaurus*, further bone fragments as well as numerous fish scales were recovered from the martix of a stromatolite breccia (bed 1-28) at the cycle basis.

(2) *Mystriosuchus* skull fragments, gastral rib, teeth and scutes were found 5–10 cm above the basis of the cycle, embedded within laminated claystones (bed 1-29) that contain unionid bivalves and conchostracans.

The stromatolite breccia formed, after a period of evaporation with shoreline stromatolite growth, by subaerial exposure, desiccation, and subsequent flooding (Arp et al. 2005). While stromatolite laminae exhibit a dendroid micropeloidal framework with agglutinated conchostracan fragments and fish scales, the matrix between the stromatolite clasts shows fish scales as well as mm- to cm-sized bone fragments. Therefore, the *Nicrosaurus* tooth embedded between the stromatolite clasts may be derived from a species that populated marginal-lacustrine swamps affected by temporary desiccation and salinity fluctuations. This specimen as well as associated fish may have died during a prolonged desiccation period at the end of a climatically driven lacustrine flooding-evaporation cycle, and were washed into the lake together with large clasts of marginal-lacustrine stromatolites by a subsequent catastrophic flooding. An alternative explanation could be that the tooth is derived from a scavenger that fed on dead fish. This would explain the isolated occurrence of this tooth.

Strong seasonality during the Norian in the Germanic Basin (Reinhardt & Ricken 2000) suggests an annual origin of the 0.5 to 2 mm thick claystone laminae of bed 1-29 of the Krähenberg section. Therefore, the skull fragments and other remains of *Mystriosuchus* were embedded in laminated claystones during a freshwater period, at least decades after the initial catastrophic flooding event of this lacustrine cycle. Because of that, the *Mystriosuchus* remains probably are derived from a successively disintegrating cadaver, which drifted and finally sunk to its final burial during the early freshwater period of this lacustrine-evaporitic cycle. This specimen therefore is considered to be introduced via fluvial inflow, and originated from a fluvial freshwater habitat.

Based on the new material alone, this interpretation remains speculative, but a survey of other European phytosaur occurrences provides additional arguments for different lifestyle and habitats of *Mystriosuchus* and *Nicrosaurus*.

5. Occurrences and habitats of European phytosaurs

5.1. Carnian

The oldest currently known phytosaur remains were recovered from the Late Carnian Drawno beds at Krasiejów in SW of Poland, an equivalent to the Weser Formation of the central Germanic Basin. Supposed earlier records are either lost (e. g. a supposed phytosaur from the Buntsandstein Group; Jaekel 1910) or likely do not belong to phytosaurs, such as *"Zanclodon" arenaceus* Fraas 1896 from the Stuttgart Formation (i. e., Schilfsandstein) (Hungerbühler 2001).

During the Late Carnian, the area of Krasiejów was situated in the eastern part of the Germanic Basin, at this

time in the subtropical belt. The climate was arid to semi-arid and included seasonal rainfalls. The bone-bearing Krasiejów sediments are grey to dark-red lacustrine claystones, intercalated between red palaeosol claystones of fluvial floodplains (Zatón et al. 2005).

The phytosaurs recovered from the lacustrine claystones have been referred to *Paleorhinus* cf. *arenaceus* Fraas, 1896 (Dzik & Sulej 2007). However, following Hungerbühler (2001) the preservation of the mandibular fragment *"Zanclodon" arenaceus* Fraas, 1896 (SMNS 80737) of the Schilfsandstein of southwest Germany is not sufficient to identify the genus unequivocally, so that an assignment to *Paleorhinus angustifrons* Kuhn, 1936, is preferred in here. The Krasiejów phytosaurs are associated with ganoid and dipnoid fish, and the amphibian *Metoposaurus diagnosticus krasiejowensis* (Dzik & Sulej 2007).

The invertebrate fauna of the bone-bearing sediments comprises unionid bivalves, ostracodes, a cycloid crustacean species and the conchostracan *Laxitextella*. Among the ostracods, *Darwinula* occurs in large numbers and points to ecologically instable conditions. Nonetheless, a charophyte assemblage composed of four species suggest prolonged freshwater conditions (Zatón et al. 2005). The palaeolake therefore has been hydrologically open, with freshwater influx from meandering fluvial systems from S to SE (Dzik & Sulej 2007).

The terrestrial fauna is more divers than the lacustrine and is dominated by archosaurs. These include sphenodonts, pterosaurs, the aetosaur *Stagnolepis* sp., the rauisuchian *Teratosaurus silesiacus* and ornithodirians. The ornithodirians are represented by *Silesaurus opolensis*. There are only a few insects known from the outcrop, which are part of the Coleoptera. The terrestrial flora is dominated by conifers, which seem to be similar to that of the Schilfsandstein in Baden-Württemberg.

Slightly younger than Krasiejów lake sediments (Zatón 2005) are phytosaurs of the Carnian Blasensandstein of Ebrach in Franconia (Hunt & Lucas 1991). Initially described as *Ebrachosuchus neukami* and *Francosuchus angustifrons* by Kuhn (1936), the specimens are now considered as representatives of the genus *Paleorhinus*. Contrary to other Carnian phytosaur-bearing localities, the strongly lithified sandstones of Ebrach represent a fine-grained braided river system (Frings 1982). Apart of phytosaurs remains, the lungfish *Ceratodus*, bivalves and amphibians have been discovered in these deposits.

A further Carnian phytosaur occurrence has bee reported by von Huene (1939) from the Opponitzer Schichten (an equivalent of the Raibl Beds) of the Northern Alps, Austria. The Opponitzer Schichten are Late Carnian in age and predominantly marine. The specimen, a skull fragment of *Paleorhinus* sp. (NMW 1905/13), has been derived from dark grey to black shale (Hunt & Lucas 1991). Beside the phytosaur, unionid bivalves and marine gastropods have been found. The vertebrate fauna seems to be limited to ganoid fish (von Huene 1939). The co-occurrence of unionid bivalves and marine gastropods in the sediments, point to a brackish environment at the depositional time.

5.2. Norian

The Stubensandstein (Löwenstein Formation) of Stuttgart and Trossingen-Aixheim in Southwest-Germany (Fraas 1896; Berckheimer 1938) are certainly the most famous phytosaur locations in Europe. The phytosaur-containing sandstones are of the same age than the Arnstadt Formation, where the remains described in this paper originate. Indeed, both formations share the same phytosaur genera, *Nicrosaurus* and *Mystriosuchus*. Even that there are four species mentioned by Hungerbühler & Hunt (2000) and Hungerbühler (2002), a potential sexual dimorphism is given (Kimmig 2009): *Mystriosuchus planirostris*, *Mystriosuchus westphali*, *Nicrosaurus kapffi*, and *Nicrosaurus meyeri*.

However, in Southwest-Germany, *Nicrosaurus* and *Mystriosuchus* apparently both occur in the first and second Stubensandstein (Hungerbühler & Hunt 2000). Both lithostratigraphic levels comprise arkosic sandstones, separated by redbrown mudstones of floodplains. Vertebrate remains are largely restricted to [the unit "sc3" of] the second Stubensandstein, which represents sheet flood sandstones at the transition distal alluvial plain to playa lake (Hungerbühler 2002). Phytosaur remains are mostly restricted to disarticulated specimens, largely isolated skulls, mandibles, vertebrae and scutes. Specimens of both phytosaur genera therefore were subject to fluvial transport, and were buried during flooding events. Their life habitat therefore was rather a freshwater river or an area adjacent to that, but not a lake. This interpretation is consistent with the fossils associated: ganoid fish (e. g., *Semionotus*), the dinosaur *Sellosaurus*, bivalves and plant remains.

Contrary to the phytosaur occurrences in the siliciclastic, non-marine Norian deposits of the Germanic Basin, phytosaurs reported from Tethyan realm were discovered in marine limestones and shales. The *Mystriosuchus* specimens that have been found in the uppermost part of Calcare di Zorzino (Norian, Bergamo Prealps, Italy) are so well preserved, that they have only been transported for a short time (Renesto & Paganoni 1998; Gozzi & Renesto 2003). The same might be true for *Mystriosuchus* remains of the slightly younger Argillite di Rivia di Solto (Bergamo) (Renesto 1998). The phytosaurs seem to have lived on islands that contained freshwater reservoirs or in a shallow marine habitat, close to the emerged lands (Renesto & Paganoni 1998). Other animals are represented by the

placodont *Psephoderma*, the thalattosaur *Endennasaurus*, some diapsids and insects.

One further occurrence has been reported from the Norian Dachsteinkalk-Formation of the Totes Gebirge, Austria (Buffetaut 1993), which is a shallow marine-lagoonal limestone. Again, the phytosaur remains belong to the genus *Mystriosuchus*, and have initially been considered as been introduced post mortem (Renesto & Paganoni 1998). The state of preservation and the distance to land, however, support a burial of the specimens at the place of death (Buffetaut 1993).

5.3. Late Norian to Early Rhaetian

Excluding plateosaur fragments that have been misidentified as phytosaurs (e. g., from the Exter Formation of Kreuzberg in Göttingen; von Huene 1908: 100, fig. 90), unequivocal phytosaur findings have been published for the upper part of the Arnstadt Formation of Halberstadt and Salzgitter (von Huene 1923). From the first locality, well known for its plateosaurs (Jaekel 1914; Sander 1992), isolated teeth and fragmentary remains of *Mystriosuchus* and a further, *Nicrosaurus*-like phytosaur described as "*Angistorhinopsis ruetimeyeri* von Huene" were recovered (von Huene 1923). However, a precise systematic assignment of the latter specimen to a specific genus currently cannot be made. The deposits in which the phytosaur remains have been discovered are grey calcareous sandstones, and are younger than the massive, grey-redbrown mottled claystones that contained the *Plateosaurus* skeletons. However, further *Mystriosuchus* remains were mentioned by Kuhn (1939) from a sandstone below the Plateosaur bed.

A detailed sedimentological study of the Halberstadt deposits is not available, but based on the description of Kuhn (1939) the sandstones can be interpreted as fluvio-deltaic channel fillings, intercalated between fine-grained floodplain deposits that may have acted as *Plateosaurus* traps (Sander 1992). For the fragmentary phytosaur remains, a post mortem transport from fluvial tributaries is implied.

The second locality, Steinlah near Salzgitter, yielded a number of *Nicrosaurus*-like remains ("*Angistorhinopsis Ruetimeyeri* von Huene") embedded in a grey, pyrite-rich dolomite with "oolitic fabric" (von Huene 1923: 116). Based on this description, the sediment is a reworked dolocrete palaeosol, similar to that known from the base of the upper part of the Arnstadt Formation (e. g., clay-pit Hottenrode, Arp 2004: 169 ff.). Strikingly, *Mystriosuchus* remains appear to be absent from this terrestrial sediment.

Phytosaur remains similar or identical to those from Salzgitter have been reported from the Late Norian to Early Rhaetian of Niederschöntal, Swiss Jura Mountains, and were described as *Angistorhinopsis ruetimeyeri* (von Huene 1911). Skull fragments, vertebrae, scutes and laterally compressed serrated teeth are present. The latter can be taken as indicative of a *Nicrosaurus* relative, since *Rutiodon*, which has long slender teeth with a circular cross-section, like *Mystriosuchus*, is confined to *Rutiodon carolinensis* Emmons, 1856 and only occurs in North America (Long & Murry 1995). The possibility of a relationship to *Leptosuchus* is also improbable, because this genus is restricted to the Late Carnian of North America (Long & Murry 1995). The detailed stratigraphic position of the phytosaur-containing bed at Niederschöntal is not precisely given, but likely belongs to the Trossingen Formation (Knollenmergel), an equivalent to the upper part of the Arnstadt Formation. The association with shark remains *(Hybodus)* (Huene 1911), fish scales and reworked dolocrete nodules points to a mixed aquatic and terrestrial source of components.

From the Cenger Formation at Çal Dağ in the Lycian Taurus/Turkey, Buffetaut et al. (1988) described phytosaur remains. These consist of some teeth and a caudal vertebra and they certainly belong to phytosaurs. Similar to the Niederschöntal remains they were initially referred to *Rutiodon ruetimeyeri*, but may rather present remains of *Nicrosaurus*. Embedding sediments are red polygenetic sandstones with dipnoan toothplates (Buffetaut et al. 1988) as well as possible marine fish (Monod et al. 1983). Based on that, the phytosaur remains were embedded at a temporary freshwater to saline lake.

The phytosaur remains from the "Lower Rhaetian" of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France) are the only known remains from France. The bone-bed, from which the phytosaur remains were described, is an intraformational conglomerate (coarse sands and small pebbles) at the base of a sandstone (base of "Upper Keuper"), which overlays green claystones of the "Middle Keuper" (Godefroit & Battail 1997). Granulometric analysis of the sandstones suggest a nearshore marine to marine-deltaic environment (Al Khatib 1976 in Godefroit & Battail 1997), but clear evidence for any marine influence has not been provided. Lithology and lithostratigraphic position rather suggest a fluvial or fluvio-deltaic channel deposit, with vertebrate remains redeposited from fluvial and terrestrial areas. Likewise, the chronostratigraphic age of the bone-bed is considered to be similar to the phytosaur-bearing sandstones at Halberstadt, i. e., Late Norian to Early Rhaetian (Godefroit & Cuny 1997). Numerous teeth have been recovered, among them representatives of phytosaurs. The latter have been referred to *Rutiodon ruetimeyeri* (von Huene) by Buffetaut & Wouters (1986), while Godefroit & Cuny (1997) question a precise determination and consider the remains as undetermined heterodont phytosaurs. However, some of the teeth are identical to teeth describe by von Huene (1923) as "*Angistorhi-*

nopsis Ruetimeyeri" from Halberstadt and Salzgitter (cf. GODEFROIT & CUNY 1997: 7), and to the ?*Nicrosaurus* tooth described in this paper. In addition, remains of pterosaurs, dinosaurs and amphibians are known from this location. The most extraordinary finds from Saint-Nicolas-de-Port are certainly the Late Triassic mammals (GODEFROIT & BATTAIL 1997).

6. Summary and conclusions

Nicrosaurus as well as *Mystriosuchus* have been recovered from fluvial channel deposits (Halberstadt, Saint-Nicolas-de-Port) and distal-alluvial sheet flood sandstones (e. g., Trossingen-Aixheim). However, *Nicrosaurus* has been found also in reworked palaeosols (Salzgitter) and marginal-lacustrine sandstones or breccias resting on subaerial exposure planes (Çal Dağ; Krähenberg: this paper). This points to a terrestrial source of the *Nicrosaurus* material, and hence a more terrestrial and swamp-inhabiting lifestyle. This view is in agreement with the massive snouted cranial morphology similar to modern crocodiles (HUNT 1989), suggesting predation of tetrapods rather than fish.

In turn, open-lacustrine sediments (Krasiejów, Krähenberg: this paper), fluvial (Ebrach), and even shallow-marine carbonate platform deposits (Bergamo, Totes Gebirge) yielded *Paleorhinus* and *Mystriosuchus* remains, respectively. This observation supports the view that these slender snouted genera, which resemble extant gavials (HUNT 1989; HUNGERBÜHLER 2002), had a semiaquatic lifestyle, hence predating fish. Similar to modern gavials, *Paleorhinus* and *Mystriosuchus* apparently tolerated salinities from fluvial freshwater to brackish lacustrine and temporary marine conditions, possibly an adaptation to the common inland lakes of fluctuating salinities on Pangaea during the Late Triassic. Indeed, this capacity may explain their wide distribution in North America, India, Africa and Europe (LUCAS & HUBER 2003). On the other hand, as a result of his lifestyle confined to land and freshwater swamps, *Nicrosaurus* remained restricted to the Germanic Basin.

7. References

ARP, G., HOFFMANN, V.-E., SEPPELT, S. & RIEGEL, W. (2004): Trias und Jura von Göttingen und Umgebung. – In: REITNER, J., REICH, M. & SCHMIDT, G. (eds.): Geobiologie 2 [74. Jahrestagung der Paläontologischen Gesellschaft, Göttingen, 02. bis 08. Oktober 2004. Exkursionen und Workshops]: 147–192; Göttingen (Universitätsdrucke).

ARP, G., BIELERT, F., HOFFMANN, V.-E. & LÖFFLER, T. (2005): Palaeoenviromental significance of lacustrine stromatolites of the Arnstadt Formation ("Steinmergelkeuper", Upper Triassic, N-Germany). – Facies, **51**: 433–455.

BERCKHEMER, F. (1938): Wirbeltierfunde aus dem Stubensandstein des Strombergs. – Aus der Heimat, **51**: 188–198.

BEUTLER, G. (2005) (ed.): Stratigraphie von Deutschland IV – Keuper. – Courier Forschungsinstitut Senckenberg, **253**: 1–296.

BEUTLER, G., HAUSCHKE, N. & NITSCH, E. (1999): Faziesentwicklung des Keupers im Germanischen Becken. – In: HAUSCHKE, H. & WILDE, V. (eds.): Trias. Eine ganz andere Welt: 129–174; Munich (Pfeil).

BUFFETAUT, E. (1993): Phytosaurs in time and space. – Paleontologia Lombarda, **2**: 39–44.

BUFFETAUT, E. & WOUTERS, G. (1986): Amphibian and reptile remains from the Upper Triassic of Saint-Nicolas-de-Port (eastern France) and their biostratigraphic significance. – Modern Geology, **10**: 133–145.

BUFFETAUT, E., MARTIN, M. & MONOD, O. (1988): Phytosaur remains from the Cenger Formation of the Lycian Taurus (Western Turkey) – Stratigraphical implications. – Geobios, **21**: 237–243.

DOCKTER, J., LANGBEIN, R., SEIDEL, G. & UNGER, K. P. (1970): Die Ausbildung des Unteren und Mittleren Keupers in Thüringen. – Jahrbuch für Geologie, **3**: 145–194.

DZIK, J. & SULEJ, T. (2007): A review of the early Late Triassic Krasiejów biota from Silesia, Poland. – Palaeontologia Polonica, **64**: 3–27.

FRAAS, E. (1896): Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. 18 pp.; Stuttgart (Schweizerbart).

FRINGS, U. (1982): Sedimentologische Untersuchungen im oberen Blasensandstein in Nürnberg. – Geologische Blätter für Nordost-Bayern und angrenzende Gebiete, **32**: 13–34.

GODEFROIT, P. & CUNY, G. (1997): Archosauriform teeth from the Upper Triassic of Saint-Nicolas-de-Port (northeastern France). – Palaeovertebrata, **26**: 1–34.

GODEFROIT, P. & BATTAIL, B. (1997): Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). – Geodiversitas, **19**: 567–631.

GOZZI, E. & RENESTO, S. (2003): A complete specimen of Mystriosuchus (Reptilia, Phytosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **109**: 475–498.

GRÜGER, E., JORDAN, H., MEISCHNER, D. & SCHLIE, P. (1994): Mittelpleistozäne Warmzeiten in Göttingen, Bohrungen Ottostraße und Akazienweg. – Geologisches Jahrbuch, Reihe A, **134**: 167–210.

HUENE, F. VON (1907–1908): Die Dinosaurier der Europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. – Geologische und paläontologische Abhandlungen, Supplement **1**: 1–419.

HUENE, F. VON (1911): Beiträge zur Kenntnis und Beurteilung der Parasuchier. – Geologische und Paläontologische Abhandlungen, Neue Folge, **10**: 67–121.

HUENE, F. VON (1923): Neue Beiträge zur Kenntnis der Parasuchier. – Jahrbuch der Preussischen Geologischen Landesanstalt, **42**: 59–160.

HUENE, F. VON (1939): Ein primitiver Phytosaurier in der jüngeren nordost-alpinen Trias. – Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B, Geologie und Paläontologie, **1939**: 139–144.

HUNGERBÜHLER, A. (2000): Heterodonty in the European phytosaur *Nicrosaurus kapffi* and its implications for the taxonomic utility and functional morphology of phytosaur dentitions. – Journal of Vertebrate Paleontology, **20**: 31–48.

HUNGERBÜHLER, A. (2001): The status and phylogenetic relationships of "*Zanclodon*" *arenaceus*: the earliest known phytosaur? – Paläontologische Zeitschrift, **75**: 97–112.

Hungerbühler, A. (2002): The Late Triassic phytosaur *Mystriosuchus westphali*, with a revision of the genus. – Palaeontology, **45**: 377–418.

Hungerbühler, A. & Hunt, A. P. (2000): Two new phytosaur species (Archosauria, Crurotarsi) from the Upper Triassic of Southwest Germany. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2000**: 467–484.

Hunt, A. P. (1989): Cranial morphology and ecology among phytosaurs. – In: Lucas, S. G. & Hunt, A. P. (eds.): Dawn of the age of dinosaurs in the American Southwest: 349–354; Albuquerque, New Mexico (Museum of Natural History).

Hunt, A. P. & Lucas, S. G. (1991): The *Paleorhinus* biochron and the correlation of the nonmarine Upper Triassic of Pangaea. – Palaeontology, **34**: 487–501.

Jaekel, O. (1910): Über einen Belodonten aus dem Buntsandstein von Bernburg. – Sitzungsberichte der Gesellschaft naturforschender Freunde, **5**: 197–229.

Jaekel, O. (1914): Über die Wirbeltierfunde in der oberen Trias von Halberstadt. – Paläontologische Zeitschrift, **1**: 155–215.

Kimmig, J. (2009): Functional morphology and systematic palaeontology of the Phytosauria (Archosauria; Crurotarsi). 118 pp., Master Thesis, Division of Biology, Imperial College London, London.

Kuhn, O. (1936): Weitere Parasuchier und Labyrinthodonten aus dem Blasensandstein des mittleren Keuper von Ebrach. – Palaeontographica, Abteilung A, **83**: 61–98.

Kuhn, O. (1939): Beiträge zur Keuperfauna von Halberstadt. – Paläontologische Zeitschrift, **21**: 258–286.

Long, R. A. & Murry, P. H. (1995): Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. – New Mexico Museum of Natural History and Science Bulletin, **4**: 1–254.

Lucas, S. G. & Huber, P. (2003): Vertebrate biostratigraphy and biochronology of the nonmarine Late Triassic. – In: Le Tourneau, P.M. & Olsen, P.E. (eds.): The great rift valleys of Pangea in eastern North America: 143–191; New York (Columbia University Press).

McGregor, J. H. (1906): The Phytosauria, with special reference to *Mystriosuchus* and *Rhytidodon*. – Memoirs of the American Museum of Natural History, **9**: 29–101.

Meyer, H. (1863): Der Schädel des Belodon aus dem Stubensandstein des oberen Keupers. – Palaeontographica, **10**: 227–246.

Monod, O., Meshur, M., Martin, M. & Lys, M. (1983): Découverte de dipneustes Triasiques (Ceratodontiformes, Dipnoi) dans la Formation de Cenger ("Arkoses Rouges") du Taurus Lycien (Turquie Occidentale). – Geobios, **16**: 161–168.

Naumann, E. (1911): Beitrag zur Gliederung des mittleren Keupers im nördlichen Thüringen. – Jahrbuch der Preußischen Geologischen Landesanstalt, **28**: 549–586.

Reinhardt, L. & Ricken, W. (2000): The stratigraphic and geochemical record of Playa Cycles: monitoring a Pangaean monsoon-like system (Triassic, Middle Keuper, S. Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology, **161**: 205–227.

Renesto, S. (1998): Remains of a juvenile phytosaur from the Late Triassic of Northern Italy. – Rivista Italiana di Paleontologia e Stratigrafia, **114**: 155–160.

Renesto, S. & Lombardo, C. (1999): Structure of the tail of a phytosaur (Reptilia, Archosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **105**: 135–144.

Renesto, S. & Paganoni, A. (1998): A phytosaur skull from the Norian (Late Triassic) of Lombardy (northern Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **104**: 115–121.

Ritzkowski, S. (1990): Die Schichtenfolge des Lias (Unterer Jura) im Raum Göttingen. 74 pp., 31 Anlagen; unveröff. Abschlußbericht, Niedersächsisches Ministerium für Wissenschaft und Kunst.

Sander, P. M. (1992): The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. – Palaeogeography, Palaeoclimatology, Palaeoecology, **93**: 255–299.

Stille, H. & Lotze, F. (1933): Erläuterungen zur Geologischen Übersichtskarte der Umgebung von Göttingen (Hochschul-Exkursionskarte Nr. 3). 67 pp.; Berlin (Preußische Geologische Landesanstalt).

Vath, U. (2005): Der Keuper im südlichen Niedersachsen bei Göttingen. – In: Beutler, G. (ed.): Stratigraphie von Deutschland IV – Keuper. – Courier Forschungsinstitut Senckenberg, **253**: 163–178.

Zantón, M., Piechota, A. & Sienkiewic, E. (2005): Late Triassic charophytes around the bone-bearing bed at Krasiejów (SW Poland) – palaeoecological and environmental remarks. – Acta Geologica Polonica, **55**: 283–293.

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