Clausthaler Geowissenschaften	5	59-77	13 Abb 1 Tab	Clausthal-Zellerfeld 2006

The Late Jurassic crocodiles of the Langenberg near Oker, Lower Saxony (Germany), and description of related materials (with remarks on the history of quarrying the "Langenberg Limestone" and "Obernkirchen Sandstone")

Hans-Volker Karl, Elke Gröning, Carsten Brauckmann, Daniela Schwarz & Nils Knötschke

Abstract: The present article mainly deals with the description of remains of different species of crocodiles from the Late Jurassic (Kimmeridgian) of Oker (close to the northern slope of the Harz Mountains in Lower Saxony/Germany). These include the following species: *Theriosuchus pusillus* Owen, 1878, *Goniopholis simus* Owen, 1878, *Machimosaurus hugii* (H. v. Meyer, 1837), *Steneosaurus* aff. *brevirostris* Owen, 1842, gen. et sp. indet. 1, and gen. et sp. indet. 2. Additionally, closely related crocodilian species from the late Jurassic as well as from the early Cretaceous (Berriasian, Bückeberg Member, "German Wealden") in other regions of Lower Saxony are discussed. Phylogenetically, the crocodile fauna from Oker consists of different basal neosuchians crocodylomorphs.

Key words: Crocodile, Neosuchia, *Goniopholis, Machimosaurus, Steneosaurus, Theriosuchus*, Langenberg Formation (Kimmeridgian, Late Jurassic), Bückeberg Member ("Obernkirchen Sandstone", "German Wealden", Berriasian, Lower Cretaceous), Obernkirchen, Lower Saxony (Germany).

Kurzfassung: Schwerpunkt des vorliegenden Artikels ist die Beschreibung der Reste unterschiedlicher Krokodil-Arten aus dem Ober-Jura (Kimmeridgium) von Oker (nahe dem Harz-Nordrand in Niedersachsen/Nord-Deutschland). Es sind dies folgende Arten: *Theriosuchus pusillus* Owen, 1878, *Goniopholis simus* Owen, 1878, *Machimosaurus hugii* (H. v. Meyer, 1837), *Steneosaurus* aff. *brevirostris* Owen, 1842, gen. et sp. indet. 1, and gen. et sp. indet. 2. Zusätzlich werden verwandte Arten aus dem höheren Jura und der tiefen Unter-Kreide (Berriasium, Bückeburg Member, „Deutscher Wealden") in anderen Regionen Niedersachsens diskutiert. Die Krokodil-Fauna von Oker besteht unter phylogenetischen Gesichtspunkten aus verschiedenen basalen Neosuchiern.

Schlüsselwörter: Krokodile, *Goniopholis, Machimosaurus, Steneosaurus, Theriosuchus*, Langenberg-Formation (Kimmeridgium, Ober-Jura), Bückeberg Member („Obernkirchen- Sandstein", „Deutscher Wealden", Berriasium, Unter-Kreide), Obernkirchen, Niedersachsen (Deutschland).

1 Introduction

Remains of fossil crocodiles from Northern Germany are known since the middle of the 19th century. H. v. Meyer described 1837/38 among others a tooth from the Kimmeridgian of Hannover as *Machimosaurus hugii*. Geoffroy´s genus *Steneosaurus* (1825) is known from the Jurassic of Lower Saxony with the synonyms *Glaphyrorhynchus aalensis* H. v. Meyer, 1842 (lower "Brown Jura" = Lower Middle Jurassic of Aalen) and *Sericodon jugleri* H. v. Meyer, 1845 ("Portlandian" of the Lindener Berg near Linden, now a quarter of Hannover). The first compilation on the Late Jurassic crocodiles of the surroundings of Hannover was published by Selenka (1867).

Koken (1887) grouped his new species *pugnax* and *minor* within the genus *Goniopholis* Owen, 1841; today they are regarded as synonyms of *G. simus* Owen, 1878. One skull from old collections of *Goniopholis simus* Owen, 1878 ("Bonn specimen") from the Lower Cretaceous (Berriasian) Bückeburg Member has recently been revised by Salisbury et al. (1999).

The skull of *Goniopholis* included in the present article was discovered by a private collector in Obernkirchen on plates of "Obernkirchen Sandstone" which were cut in the nearby-situated large quarries on the Bückeberg. The fossil was extended over two plates cut from the same piece of rock. One of them contains the lower part of the nearly 45 cm long skull from which the fossilized palatinal roof is removable, the other plate shows the cranium.

The first teeth of atoposaurid dwarf crocodiles from the late Jurassic of Lower Saxony were described by Thies et al., 1997. More recently, Thies & Broschinski (2001) described small teeth from the Kimmeridgian sequence of Oker as „Metasuchia fam., gen. et sp. indet." and interpreted them as belonging to a small durophagous crocodile. In the present article, also bone material of the atoposaurid *Theriosuchus pusillus* Owen, 1878 from Oker is addressed for the first time.

The present article mainly deals with the description of remains of different species of crocodiles from the late Jurassic (Kimmeridgian) of Oker (close to the northern slope of the Harz Mountains in Lower Saxony). Additionally, comments are included on related specimens from the Late Jurassic as well as from the Early Cretaceous (Berriasian, Bückeberg member) in other regions of Lower Saxony.

2 Geological and stratigraphical settings (Fig. 1)

2.1 "Langenberg Limestone"

The large quarry of the "Rohstoffbetriebe Oker GmbH & Co" is situated at the western slope of the Langenberg, between Oker and Schlewecke. It exposes a nearly 200m thick and largely calcareous to marly Late Jurassic sequence which reaches from the "Lower Coral Oolite" ("Unterer Korallen-Oolith"; higher Oxfordian; approximately *Perisphinctes pumilis* Zone) up to the "Upper Kimmeridge" (as traditionally used in Lower Saxony; = Lower Kimmeridgian of the British stratigraphy; approximately *Aulacostephanus autissiodorus* Zone). The exact correlation with the subboreal standard zonation based on ammonoids (Gramann et al. 1997) is far from clear because ammonoids are extremely rare in the Langenberg quarry. According to Look (1985: 393), the sediments of the Lower and Middle Coral Oolite are marine; upsection, starting with the Upper Coral Oolite, environments became more and more brackish. During the "Kimmeridge" the Langenberg area was part of a shallow-water basin; the depositional environment in this time-span is interpreted as a lagoon or bay. The detailed stratigraphy is based on microfossils (Pape 1970; Zihrul 1990).

The section is part of the southern flank of the Subhercynian Syncline. Due to the strong uplift of the Harz Mountains in post-Santonian times, the sequence is overturned and dips to the south with an angle of about 70°. Therefore the impressive and large bedding planes which are widely visible from the south are bottom planes of the strata. The hard components of the sequence are resistant to erosion and form a narrow and barely wooded ridge parallel to the main fault of the northern slope of the Harz Mountains ("Harz-Nordrand-Störung"). The whole Langenberg area and its surroundings are a major part of the "Geological German Square Mile" and internationally well-known for the strong and well exposed tectonics including remarkable stratigraphic gaps and discordances in a lot of outcrops.

The complete sequence has been described in detail by Pape (1970), Zihrul (1990) and Fischer (1991); compilations in a larger regional and stratigraphic frame are included in Look (1985: 388-393) and Gramann et al. (1997).

Most of the older materials of the Langenberg crocodiles have been collected without indication of an exact stratigraphic position but they can largely be allocated to the "Kimmeridge" of the traditional stratigraphy in Lower Saxony.

Common fossils of the "Kimmeridge" at the Langenberg are bivalves, gastropods, brachiopods and ichnofossils; in higher parts of the section, even nautiloids occur. As pointed out by Sturm & Brauckmann (1999: 53), remains of the colouring are not rare in certain bivalves and gastropods. Some layers, in particular in the so-called "Second Quarry" at the eastern slope of the Langenberg (where the same sequence is exposed), yield very small fragments of an amber-like resin.

The Langenberg quarry became still more famous after the discovery of dinosaur skulls and other remains in 1998. But unlike often published, these finds were not the first ones; a previously collected vertebra identified as a dinosaur bone for example is deposited in the collections of the Institute for Geology and Palaeontology of the Clausthal University of Technology. Other vertebrate fossils (mainly fishes, but also crocodiles, turtles etc.) are present; recently, Fastnacht (2005) presented a detailed description of a dsungaripterid pterosaur and Sander et al. (2006) described the skull of the dinosaur *Europasaurus holgeri*.

In the meantime a team of palaeontologists joint-

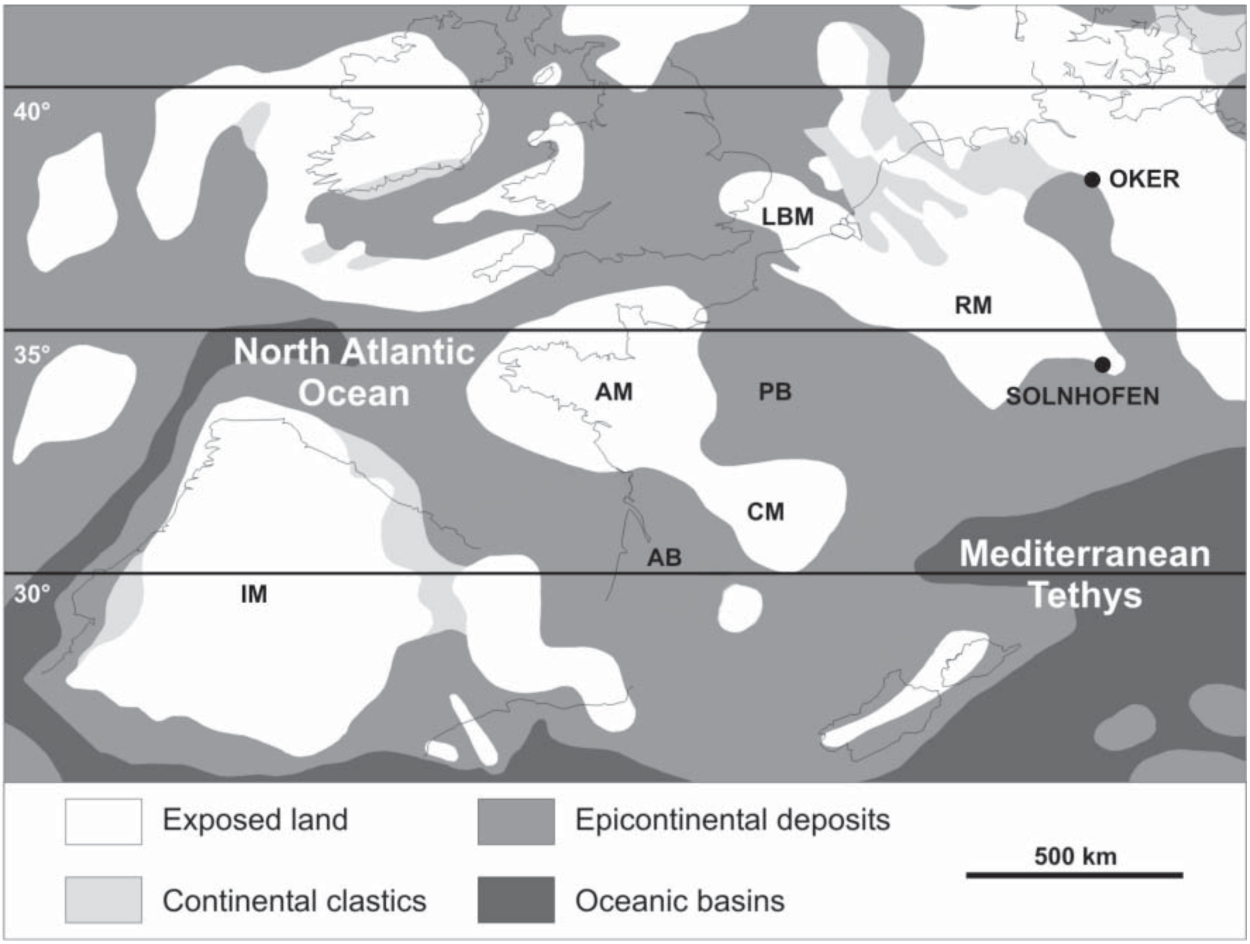

Fig. 1. Palaeoenvironmental map, showing the palaeogeographic situation of the Early Tithonian (Late Jurassic) of western Europe modified from Billon-Bruyat (2005). Abbreviations: AB = Aquitaine Basin; AM = Armorican Massif; CM = Central Massif; IM = Iberian Massif; PB = Paris Basin; LBM = London Brabant Massif; RM = Rhenish Massif.

ly with the "Dinosaur Park Münchehagen" ("Dinosaurierpark Münchehagen") carefully secures, collects and prepares the now large materials of the "Dinosaur Cemetry" of the Langenberg. For the future, a special "Jurassic Museum" in the Langenberg is planned in cooperation with the "Dinosaur Park Münchehagen".

2.2 "Obernkirchen Sandstone"

Together with a mudstone series and a few coal seams, the "Obernkirchen Sandstone" is part of a sequence called Bückeberg Member. It is developed in the so-called "German Wealden facies". Contrary to the western European Wealden which mainly extends from the early Valanginian to the late Barremian, the "German Wealden" is restricted to the late Berriasian and thus to the early Lower Cretaceous. The thickness of the "Obernkirchen Sandstone" varies from more than 140m in the Hannover/Deister/Osterwald region to less than 20m in the Bückeberg area. The whole Wealden sandstone sequence is dissected into irregular, cubic square stones.

The "Obernkirchen Sandstone" yields a lot of fossils; many of them have already been described in the pioneer time of palaeontological research, for example by F. A. Roemer (1836, 1839), who already mentioned vertebrate fossils as a (then lost) large dinosaur skeleton and a turtle, by Koch & Dunker (1837), by v. Meyer (1841, with the first record of a crocodile) and by Dunker (1846).

The fossil fauna consists of mainly limnic to brackish bivalves (in particular *Neomiodon*), gastropods, ostracods as well as remains of fish-like vertebrates, turtles, crocodiles and dinosaurs (bones, teeth, and in particular large tracks of *Iguanodon*, one specimen of the small dinosaur *Stenopelix valdensis* H. v. Meyer, 1859) and other reptiles as for example plesiosaurs.

The flora has been outlined by Mägdefrau

(1968). Remains of plants are common and rich in taxa (for example ferns, lycopods, horsetails, cycads, ginkgos and conifers) in the associated beds of the coal seams, but rather rare in the sandstone sequence in which the conifer *Sphenolepis* is predominating. The rhizomal bulbs of the sphenophyte *Equisetes burchardti* DUNKER, 1846 indicate that these remains were autochthonous. The occurrence of several beds with common roots illustrate that the vegetation covered the region largely for several times.

Judging from the succession of fossils, the area of sedimentation was at first a system of estuaries, rivers, lakes and swamps which finally became more brackish by the temporarily transgressing sea.

The earth historical development of the area around Bückeburg and Obernkirchen (the country of Schaumburg-Lippe) was the subject of the last brief article of the important German biostratigrapher and palaeontologist Professor Dr Hermann SCHMIDT (03.11.1892 - 02.01.1978) who published this manuscript in a local and short-lived scientific journal in 1973. A more detailed popular survey was contributed by HAMM (1954).

3 On the history of quarrying the "Langenberg Limestone" and "Obernkirchen Sandstone"

3.1 Langenberg quarry (Kalkwerk Oker, now: Rohstoffbetriebe Oker GmbH & Co)

Extensive limestone digging at the Langenberg started in 1871 when the first owner Adolph Willikens founded the "Kalkwerk Oker". In this early time the limestone was quarried with hammers and chisels. The factory was enlarged and distinctly improved after having received a licence to blast with gun powder in 1898. The products at that time were mainly agricultural lime as well as carbonate as a flux for the iron and steel production. Soon after this early period, the factory also started to produce slaked lime in special limekilns.

Under the new owner, Adolf Willikens jr. the factory was transformed into a joint-stock company in 1923 and widely modernized during the following years to keep pace with the drastically enlarged demand. In 1936 the area got a special connection to the railway and thus could supply customers even at longer distances. Further extension and modernisation followed between 1937 and 1943 when facilities for the production of slaked and unslaked lime for bricklayery purposes were installed and the limekilns were altered into high-powered works. The whole factory was not destroyed during World War II. Adolf Willikens died in 1944 and was succeeded in 1951 by Herbert von Pupka. The reopening of the production after the war started under very difficult conditions. The capacity of the stocks had again to be enlarged, a fleet of lorries was founded and further modernisation was accelerated. In 1960 the company was taken on lease by the newly founded "Rohstoffbetriebe Oker GmbH & Co" under the management of Herbert von Pupka. Soon after this time, in 1962, the area of quarrying was enlarged by the area of the former iron mine "Hansa". The annual mining increased up to 200.000 – 300.000 tons of limestones in 1982. One third of it was needed in the iron and steel industry of the nearby-situated Salzgitter area; a second third was used for agricultural purposes in Lower Saxony and Schleswig-Holstein; the last third was worked up to burn lime as building material.

In September 1982 the company got the permission for further quarrying within the eastern part of the Langenberg, but at fall of 1984, the extension in the planned area had to be cancelled due to a decision of the Superior Administration Court in Lüneburg. The eastern part of the Langenberg became now a nature reserve, and quarrying was restricted to fixed limits in northern and southern directions of the quarry, whereas the limekilns were shut down. As a consequence, the staff had to be reduced dramatically from former 80 persons to now 7.

In 1992 Fabian von Pupka became new manager of the "Rohstoffbetriebe Oker GmbH & Co". The actual products are still slaked lime used for building materials for underground and street constructions as well as agricultural lime. Main customers' region is northern Germany. The resources are estimated as being sufficient for the next 20 years.

Major future plans include the museological activities jointly with the "Dinosaur Park Münchehagen" as mentioned above.

3.2 Obernkirchen area

The area around Obernkirchen, in particular the Bückeberg, is well known for its sandstone quarrying and historical coal-mining.

The earliest documentary evidence for coal-mining on the Bückeberg – and beyond that in Lower Saxony – is an account-book of the provostry of Obernkirchen of 1498. There are a few seams in the whole sequence, of which only the main seam (with a thickness of up to 70cm) has been exploited. It lies at the base of the „Obernkirchen Sandstone“. In the Obernkirchen area coal-mining has been dropped several decades ago (and has only been revived in times of need), whereas stone-cutting still continues.

According to BRÜNING & SCHMIDT (1969), it is known from mediaeval documents that the “Obernkirchen Sandstone” was already quarried on the ridge of the Bückeberg soon after 1100. After management by a monastic site hut, a guild of stonecutters was founded in 1597. The light, fine-grained and weatherproof sandstone with its siliceous cementing material soon became a favourite building stone and famous as the so-called “Bremer Stein”. It was supra-regionally used, mainly for representative buildings. The cut stones were shipped down the river Weser and then exported from Bremen into several countries of the world, as for example to the Netherlands, Scandinavia and even to Russia.

4 Materials and methods

The major part of the considered specimens is deposited in the following collections: Dinosaurier-Freilichtmuseum Münchehagen (DFMMh) and Institute of Geology and Palaeontology, Hannover University (GPH). Additional material for comparison is housed in the Museum Goslar and in the Institute of Geology and Palaeontology, Clausthal University of Technology.

5 Systematic palaeontology

Crocodylomorpha WALKER, 1968
Crocodyliformes HAY, 1930
Mesoeucrocodylia WHETSTONE & WHYBROW, 1983
Neosuchia BENTON & CLARK, 1988
Family Atoposauridae GERVAIS, 1871

Genus *Theriosuchus* OWEN, 1878
(Fig. 2A-B, 3A-B, 4, 5)
Type species: *Theriosuchus pusillus* OWEN, 1878.

Diagnosis: Brevirostrine skull, small antorbital fenestra, slit-like and horizontally positioned external nares, external nares separated from each other by the nasals, shallow sulcus on the dorsal surface of the maxillary rostrum, proportionally long jugal, medial base of postorbital process formed by the ectopterygoid, median crest on the frontal and the parietal in later ontogenetic stages, frontal and parietal partially unfused in early ontogenetic stages, dorsal margin of the supratemporal foramen smaller than the orbit, lateral margin of squamosal bevelled ventrally, proportionally narrow quadrate with concave mandibular articular surface, secondary choanae bounded by the palatines rostrally and separated by a median septum of the pterygoid, mandibular symphysis not exceeding caudally beyond a point level with the sixth dentary tooth, ilium with short praeacetabular process and long postacetabular process, biserial dorsal shield comprising parasagittal osteoderm.

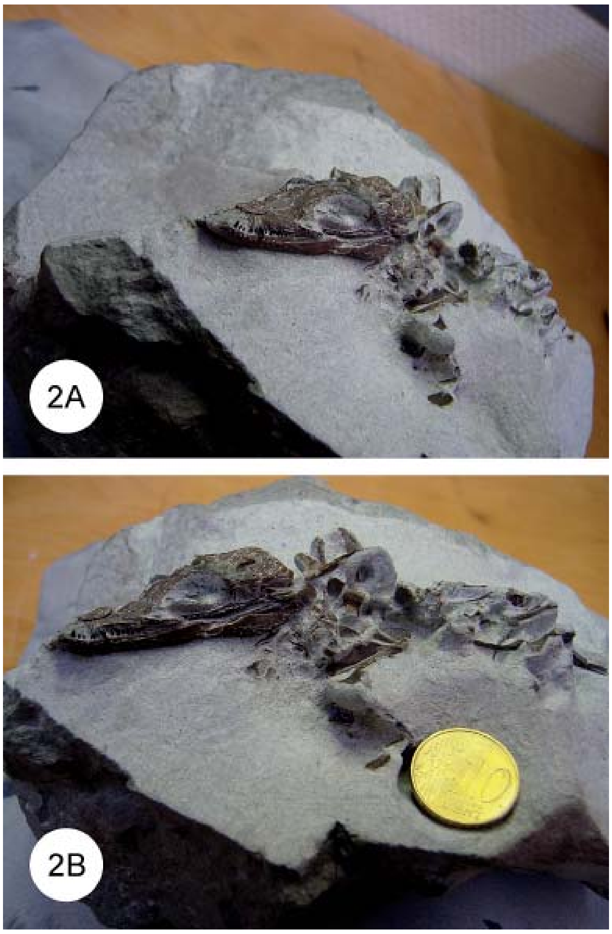

Fig. 2. *Theriosuchus* sp.: anterior part of a crushed skeleton (DFMMh 200) including the left half of a skull (preserved length = 4,7cm), 2 thoracic vertebrae, remains of a shoulder girdle, left radius and ulna, remains of both ilia, 2 femora, 1 humerus, some ribs and dermal plates (only questionably belonging to the same specimen). – **2A.** Anterior view mainly of the cranium. – **2B.** More lateral view of the whole specimen.

Material: DFMMh 200: anterior part of a crushed skeleton including the left half of skull, 2 thoracic vertebrae, remains of shoulder girdle, left radius and ulna, remains of both ilia, 2 femora,


```
                  +--------Montsecosuchus
                  |
                +--5          +---DFMMh 200
                |  |  +-----------7
                |  +--6          +--------Theriosuchus
  +------------------4    |
  |             |    +Alligatorium
  |             |
+----------2    |    +-Alligatorellus
|          |    +----3
|          |         +--Atoposaurus
|          |
|          +--------Araripesuchus
|
1-----Uruguaysuchus
|
+----------------------Notosuchus
```

requires a total of 42.000

between	and	length
-------	---	------
1	2	4.00
2	4	7.50
4	5	1.00
5	*Montsecosuchus*	3.00
5	6	1.00
6	7	4.25
7	**DFMMh 200**	1.25
7	*Theriosuchus*	3.00
6	*Alligatorium*	0.50
4	3	1.75
3	*Alligatorellus*	0.75
3	*Atoposaurus*	1.00
2	*Araripesuchus*	3.00
1	*Uruguaysuchus*	2.00
1	*Notosuchus*	8.00

Fig. 4. *Theriosuchus* sp.: damaged skull of specimen DFMMh 605, presumably a hatchling, in matrix. Preserved length = 29mm, posterior breadth = 19mm, breadth of condyles = 11mm, no ornaments at surface

1 humerus, some ribs and dermal plates, but it is not clear weather all extremity bones belong to the same specimen; DFMMh 605: damaged skull (presumably of a hatchling) in matrix, preserved length = 29mm, posterior breadth = 19mm, breadth of condyles =11mm, no ornaments at surface; DFMMh 325: 4 ventral osteoderms with irregular sculpture of shallow pits, but without keels (size of the largest = 4x4mm), 2 ribs, 1 piece of dorsal vertebrae; DFMMh 225, DFMMh 340, DFMMh 236: remains of dorsal osteoderms; DFMMh 279: femur, length = 20.5mm, proximal breadth = 4mm, distal breadth = 4mm; DFMMh 507: tooth remain.

Present characters: Snout very short (brevirostrine), external nares almost completely divided by nasals, orbits larger than supratemporal foramen, lateral margin of squamosals convex and bevelled ventrally.

Remarks: The characters listed above indicate that the material can be assigned to the genus *Theriosuchus*. The external nasal openings are almost completely divided by nasals and the lateral borders of the caudal skull table are convex and slightly ventrally bevelled. The dorsal armour is composed of rectangular, imbricating plates (osteoderms) with

Fig. 3 (left): Phylogenetic position of the Oker crocodile DFMMh 200. – **3A.** Tree from DOLMOVE made with Tree View (Roderik Page). – **3B.** Analysis with PARS-Discrete character parsimony algorithm, version 3.6a3.

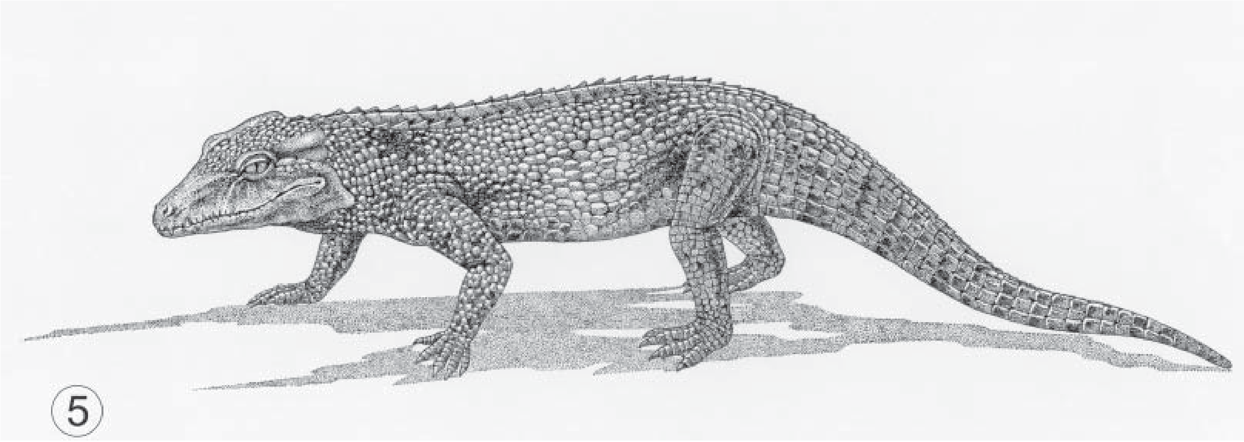

Fig. 5. Life reconstruction of *Alligatorellus* sp. (a small crocodile with a length of approximately 0,22m), shown as an example for a more terrestrial living crocodile like *Theriosuchus*.

a cranial process and the ventral plates are polygonal.

The dentition comprises 5 premaxillary, approximately 12 maxillary and more than a dozen mandibular teeth. The individual teeth are are slightly laterally compressed, lanceolate and most of them bear two carinae and a system of small longitudinal striae. The fourth mandibular tooth and the 3rd and 4th mandibular teeth are caniniform and enlarged. The greater, caudal part of the dentition teeth lies in a confluent sulcus along the internal surface of the jaws rather than to be implanted in true alveoli. Those teeth resemble most closely those of the type species *T. pusillus* and the species *T. guimarotae*, but can be distinguished from those of *T. ibericus* by a lack of serrated carinae (Brinkmann 1991 a, b, Salisbury 2002, Schwarz & Salisbury 2005). Similar atoposaurid teeth from Oker were described by Thies, Windolf & Mudroch (1997). However, distinctively laterally compressed teeth in the caudal maxillary and dentary region as in *T. pusillus* are lacking in the Oker specimens.

The results of the character analysis based upon DOLMOVE show a close relationship between the Oker specimen DFMMh 200 and *Theriosuchus*. But there are also significant differences concerning character 21. Contrary to the caudal ("dolichocephalous") orientation of the occipital surface arrangement as stated by Buscalioni & Sanz (1988a) for *Theriosuchus*, in Oker DFMMh 200 the orientation is evidently vertical. This could be the reason for the larger distance (3.00) of *Theriosuchus* from node 7 within the tree by PARS, whereas the distance of DFMMh 200 from node 7 is only 1.25. There is nothing known yet concerning possible ontogenetic changes of the occipital region in the Atoposauridae. The significant size differences between the Oker specimens and *Theriosuchus pusillus* indicate different ontogenetic stages, which might also be the reason for differences in tooth morphology. We therefore prefer not to separate the Oker specimen from *Theriosuchus pusillus* Owen, 1878 and tentatively assign the material to this species.

Family Goniopholidae Cope, 1875

Genus *Goniopholis* Owen, 1841

Type species: *Goniopholis crassidens* Owen, 1841, Early Cretaceous ("Wealden"), Sussex, England.

Diagnosis: Notch at premaxillo-maxillary suture at lateral margin of rostrum, short and broad premaxillae, external nares dorsally oriented and undivided, nasals excluded from external nares by premaxillae, broad interorbital plate, frontal forming only small portion of orbital margin, supratemporal foramen slightly larger or of similar size as orbit and nearly circular in outline, flat skull table.

Goniopholis simus Owen, 1878
(Fig. 6A-D, 7, 12B)

Present characters: Teeth trigonal and flattened with sharp lateral crests and some coarse longitudinal striae.

Material: DFMMh 352: ventral osteoderm; DFMMh 329, DFMMh 631, DFMMh 338, DFMMh 339, DFMMh 630, DFMMh 628, DFMMh 629, DFMMh 393, DFMMh 390, DFMMh 276-278, DFMMh 632, DFMMh 416(6.9.2001): tooth or tooth remains.

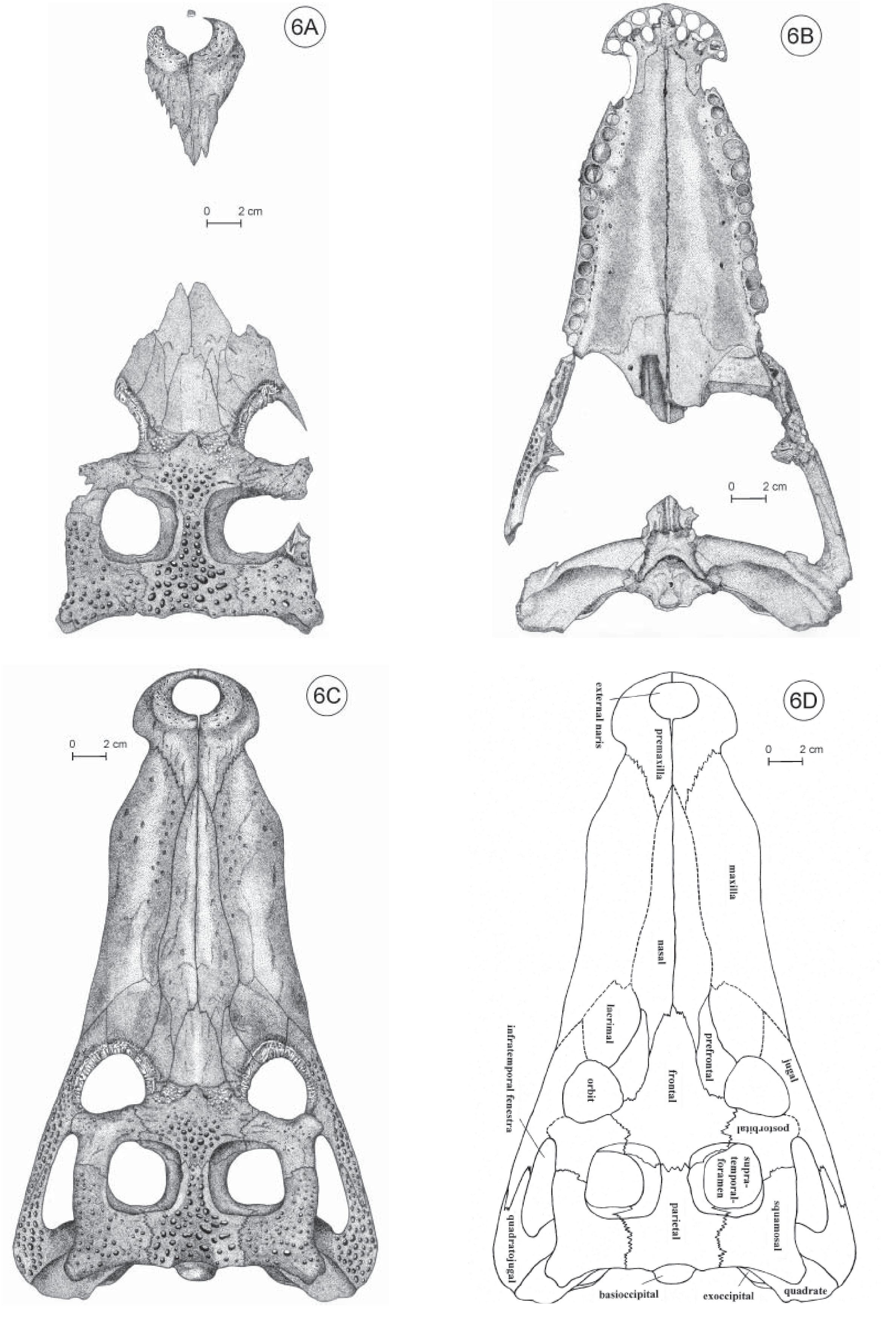

Fig. 6 Specimen of *Goniopholis simus* Owen, 1878, the "Obernkirchen Sandstone" hollow mould, private collection of Willi Adam, drawn after the silicon mould. – **6A.** Cranium, dorsal view. Length of the skull = 36,5cm. – **6B.** Cranium, ventral view. – **6C.** Cranium, reconstruction of the dorsal view. – **6D.** Cranium, terminology of the cranial elements.

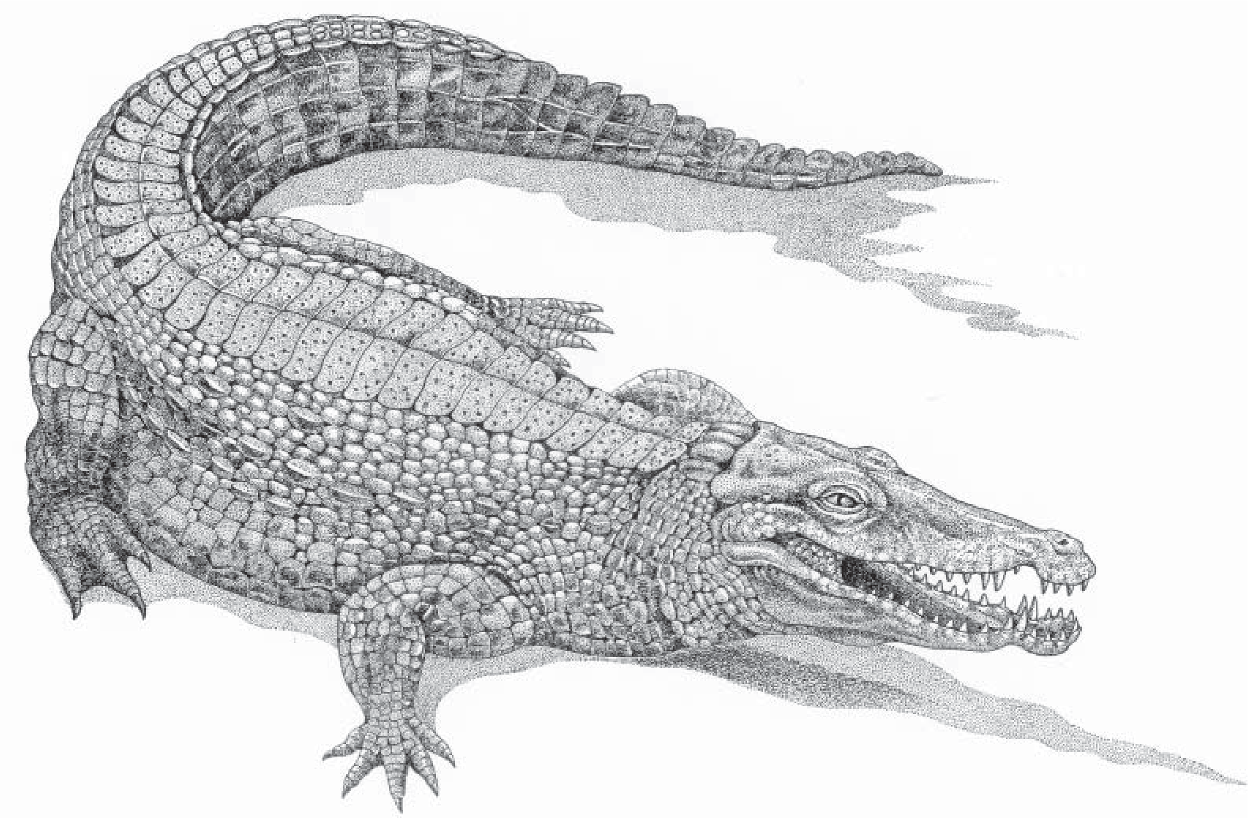

Fig. 7: Life reconstruction of *Goniopholis simus*. Length of the animal = approximately 2m (with the cranium length = approximately 40cm).

Remarks: In comparison with related material from the Late Jurassic of England, the present skull from the Berriasian of Obernkirchen is very similar in the dorsal skull-outline as well as in the position, shape and size oft the supratemporal fenestrae, orbits and the nasal opening. Contrary to the type species *Goniopholis crassidens* Owen, 1841 from the Wealden of Sussex, our material is not characterised by the distinctly stout teeth and the tapering morphology of the skull. Furthermore, in *Goniopholis crassidens* the supratemporal fenestrae are subcircular in shape and approximately twice as large as the orbits. In contrast, in our Berriasian specimen and in *Goniopholis simus* from Late Jurassic (see Salisbury 2002: text-fig. 5 and this article: fig. 6A-D) the orbits are triangular in shape with rounded corners and relatively similar in length to the rounded square supratemporal fenestrae. The shape of the orbits in *Goniopholis baryglyphaeus* Schwarz, 2002 from the Kimmeridgian of the Guimarota coal mine/Leira (Portugal) is long and oval and the prefrontals are larger than in *Goniopholis simus*. A survey of type specimens and synonymy of the crocodilians from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset/ Southern England, including *Goniopholis*, gives Salisbury (2002).

Suborder Thalattosuchia Fraas, 1902
Family Teleosauridae Cope, 1871

Genus *Machimosaurus* H. v. Meyer, 1838

Type species: *Machimosaurus hugii* (H. v. Meyer, 1837).

Diagnosis: Longirostrine with relatively short snout compared to other teleosaurids, large supratemporal fenestrae, massive and blunt conical teeth with strongly wrinkled enamel.

Machimosaurus hugii (H. v. Meyer, 1837)
(Fig. 8A-B, 12C-D)

Present characters: Anterior teeth long caniniform, posterior ones short and massive for food crushing, with a broad and rounded or flat crown; both types with small, but relatively prominent lateral seams; the enamel is delicately wrinkled in the crown; surface with 40 to 100 fine canals (according to Karl & Tichy, 2004).

Material: DFMMh 330, DFMMh 541: teeth (Karl & Tichy, 2004, Fig. 1), DFMMh 270, DFMMh 473, DFMMh 329, DFMMh 313, DFMMh 614, DFMMh 333, DFMMh 268, DFMMh 271, DFMMh 506, DFMMh 366, DFMMh 372, DFMMh 332, DFMMh 331, DFMMh 620, DFMMh 625, DFMMh 624, DFMMh 623: teeth, tooth remains.

Remarks: Remains of *Machimosaurus* are known from the Middle and Late Jurassic of Portugal, France, England, Switzerland (type locality), and Germany. The classic locality of *Machimosaurus hugii* is now situated in the urban area of Hannover in Lower Saxony/Northern Germany. From the Kimmeridgian of the Normandy (France) the species is recorded by Buffetaut (1982). The new material has been collected from Kimmeridgian sediments of the Langenberg quarry at Oker (E Goslar). According to Krebs (1967) and Steel (1973), *Machimosaurus hugii* is the only valid species of this genus. It is a teleosaur with a relatively short snout and very large supratemporal fenestrae, which possesses typically stout and conical teeth with a broad apex and strongly wrinkled tooth enamel. In the rostral region of the snout, the teeth can also become larger and more slender, being nearly caniniform, but still with the strongly wrinkled enamel. This wrinkled enamel results in a furrowed surface of the teeth, which is together with the stout and blunt conical tooth morphology typical for this species. The new material including only teeth and fragments of teeth

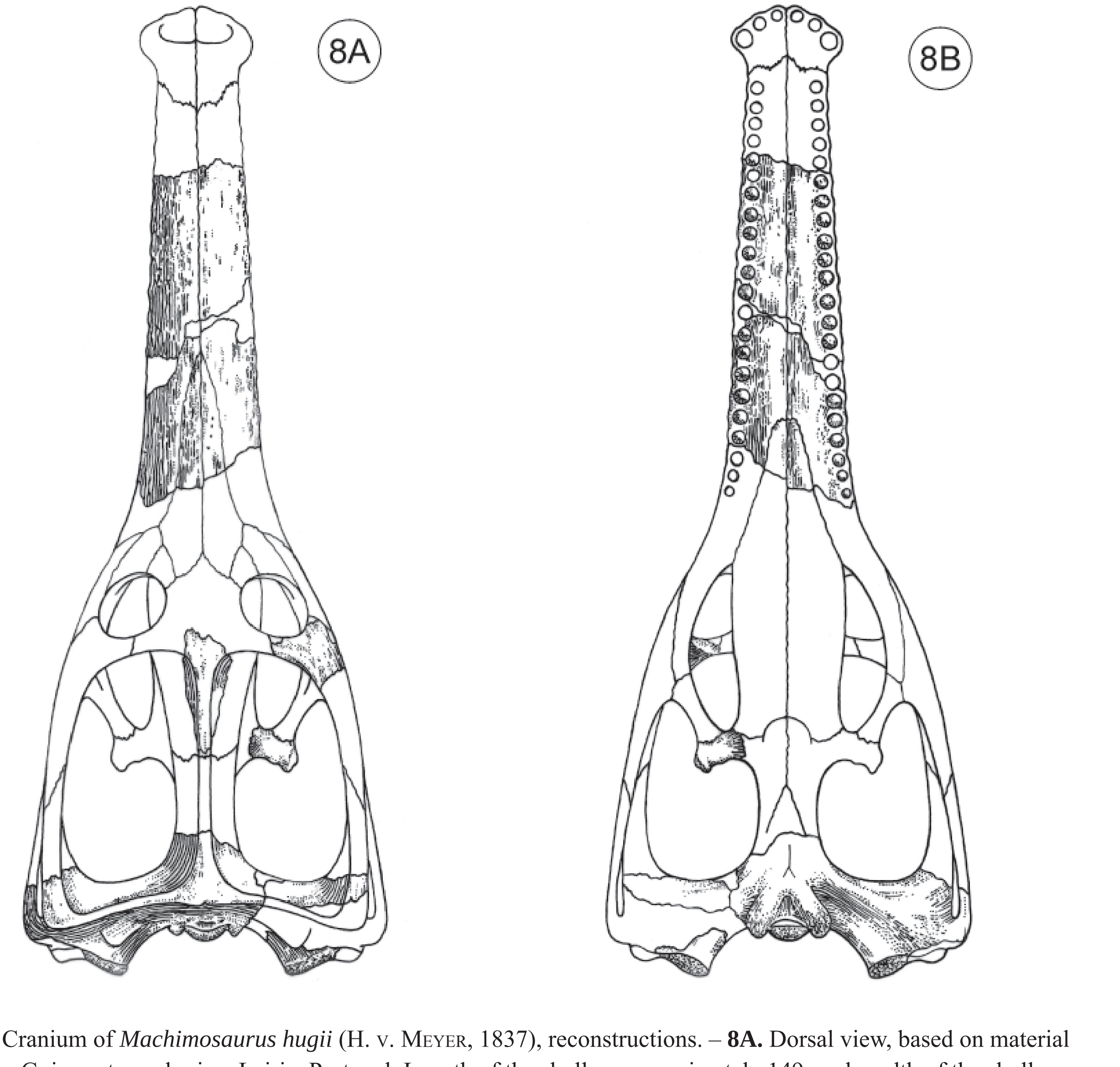

Fig. 8. Cranium of *Machimosaurus hugii* (H. v. Meyer, 1837), reconstructions. – **8A.** Dorsal view, based on material from the Guimarota coal mine, Leiria, Portugal. Length of the skull: = approximately 149cm, breadth of the skull = approximately 52cm, (total length of the animal: more than 9m.); modified after Krebs (1967: 52). – **8B.** Ventral view, based on material of the Guimarota coal mine, Leiria, Portugal; modified after Krebs (1967: 52).

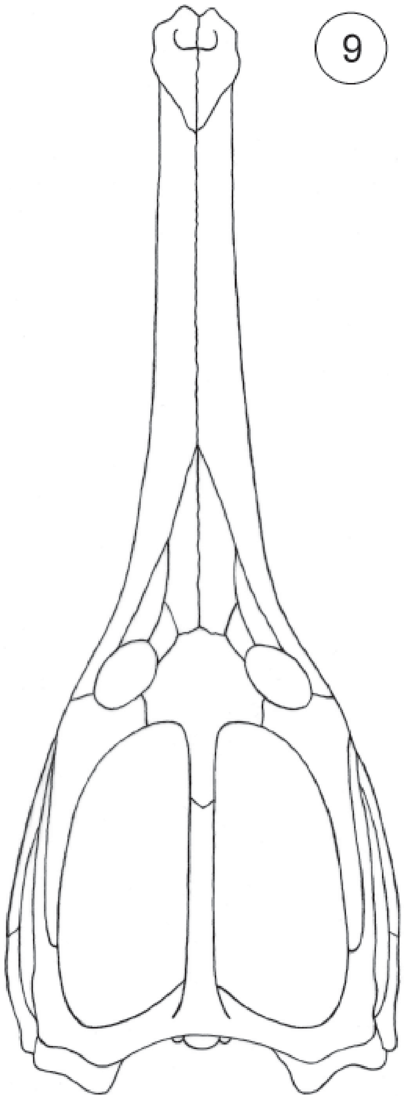

Fig. 9. Cranium of *Steneosaurus* sp., reconstruction, dorsal view. Length of the skull: approximately 88cm.

can, due to similar tooth morphology, be assigned to *Machimosaurus hugii*. This thalattosuchian species attained a presumable total length of about 9,5m with a skull length of about 1,5m..

Family Metriorhynchidae Fitzinger, 1843

Genus *Steneosaurus* Geoffroy, 1825
(Fig. 9, 10, 13A-E)

Type species: Crocodile de Quilly Cuvier, 1824 [= *Steneosaurus megistorhynchus* Eudes-Deslongchamps, 1866].

Diagnosis: longirostrine snout cranially rounded and caudally more flattened, broadened premaxillae deflected ventrally and with 4 or 5 premaxillary teeth, small antorbital opening, dorsally directed orbits, postorbital bar approximately at right angles to long axis of skull, small frontal, flat skull table longer than broad, large supratemporal foramina with rounded rectangular outline, alveolar borders without undulations, pterygoids with prominent lateral processes, teeth with a few striae, conical and slightly curved.

Steneosaurus aff. *brevirostris* Owen, 1842
(Fig. 12A)

Present characters: Teeth very long, caniniform, without lateral crests, but with some lateral striae.

Material: DFMMh 510: neural arch of caudal vertebra; DFMMh 353neural arch (?); DFMMh 330, DFMMh 281, DFMMh 474, DFMMh 334, DFMMh 335, DFMMh 609, DFMMh 327(9.3.2001), DFMMh 611, DFMMh 615(1999), DFMMh 616, DFMMh 618, DFMMh 619, DFMMh 621, DFMMh 622, DFMMh 272-275, DFMMh 392: teeth and tooth remains.

Remarks: Wincierz (1967) described a skeleton of *Steneosaurus* aff. *bollensis* (Jaeger, 1828) from the lower Toarcian of Hondelage near Braunschweig. The younger taxon *Steneosaurus jugleri* (H. v. Meyer, 1845) [*Sericodon*] was based upon teeth from the Portlandian of the Lindener Berg near Hannover and from Solothurn. Vertebrae from the Lindener Berg have been referred to the same species. *Steneosaurus picteti* (de Tribolet, 1873) was described from the Portlandian of Solothurn, too, based on vertebrae, ribs, osteoderms and teeth. However, the material, which is closest to our present specimens in both stratigraphical position and sedimentological conditions was described by Owen (1842) as *Steneosaurus brevirostris* from the Kimmeridgian of Shotover/ England.

Gen. et sp. indet. 1

Present characters: Insufficiently preserved for specific or generic determination.

Material: DFMMh 328, DFMMh 365: vertebral corpus; DFMMh 304: basisoccipital; DFMMh 242: remain of dorsal osteoderm; DFMMh 281a, DFMMh 337, DFMMh 610, DFMMh 368, DFMMh 612, DFMMh 626: tooth fragment.

Remarks: None.

Gen. et sp. indet. 2

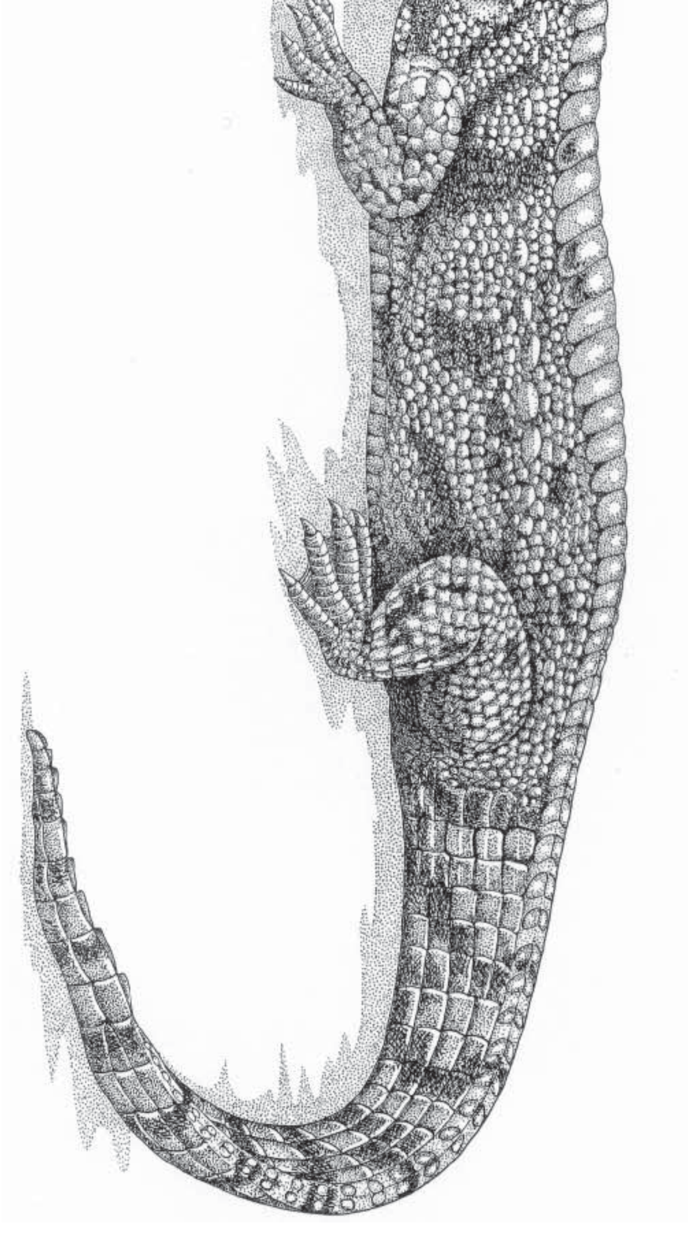

Fig. 10. Life reconstruction of *Steneosaurus* sp., length of the animal = approximately 4,8m.

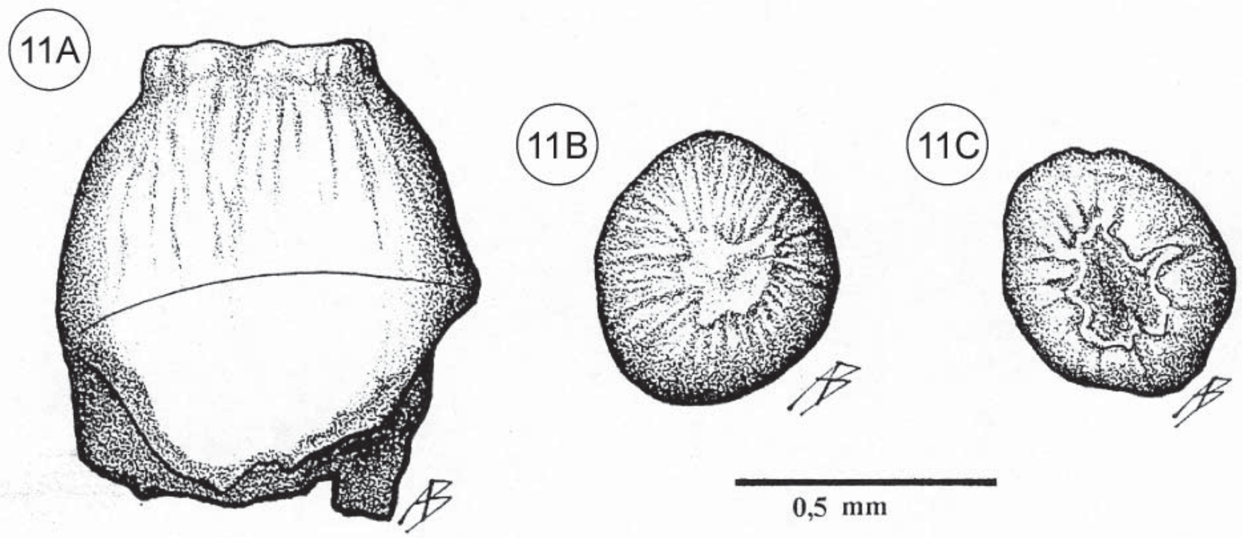

Fig. 11. Button-shaped teeth of gen. et sp. indet. (height = 2mm), ?embryonic teeth of either *Machimosaurus* or *Bernissartia*. – **11A**. Specimen GPH 2001-III-1 in lateral view. – **11B.** Specimen GPH 2001-III-2 in apical view. – **11C.** Specimen GPH 2001-III-3 in apical view. (Drawings with kind permission from Annette Broschinski.)

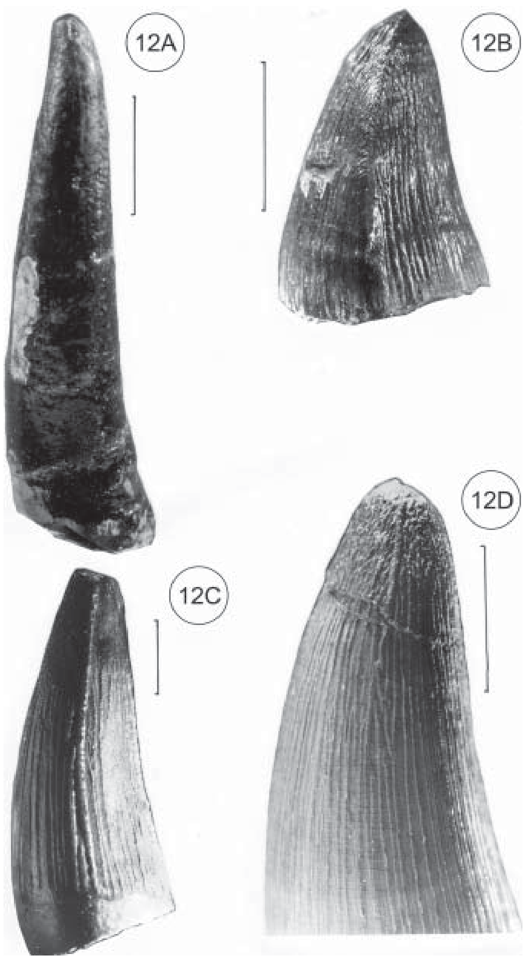

Fig. 12. Teeth of Oker crocodiles, scale bars = 1cm: **12A.** *Steneosaurus* aff. *brevirostris* Owen, 1842; DFMMh/FV 618. – **12B.** *Goniopholis simus* Owen, 1878; DFMMh/FV 268. – **12C.** *Machimosaurus hugii* H. v. Meyer, 1837; JMO 121 (coll. Udo Resch). – **12D.** *Machimosaurus hugii* H. v. Meyer, 1837; DFMMh/FV 541.

Fig. 13. Dorsal vertebra of *Steneosaurus* sp., specimen 865 of the Museum Goslar, length of corpus = approximately 8cm. – **13A.** Anterior view. – **13B.** Dextral view. – **13C.** Dorsal view. – **13D.** Posterior view. – **13F.** Sinistral view. no.

(Fig. 11A-C)

Present characters: According to THIES & BROSCHINSKI (2001) an outcrop of Kimmeridgian age near Oker (= Langenberg quarry) has yielded a few small teeth of probably crocodilian origin. As mentioned by these authors, a similar dental morphology is still unknown among crocodylomorphs and indicates a durophagous habit. The teeth are provisionally referred to as Mesoeucrocodylia fam., gen. et spec. indet.

Material: Institute of Geology and Palaeontology of Hannover University: GPH 2001-III-1 to 2001-III-3: remains of teeth.

Remarks: Compare with BRINKMANN (1991a, b). Due to the very small size of the teeth (height = 2 mm!), it is possible that these teeth represent embryonic dental arrangements of either *Machimosaurus* or *Bernissartia*.

6 Phylogenetic position of the Oker crocodiles

Several results of phylogenetic analyses show that Thalattosuchia (including *Steneosaurus*) are basal neosuchians (ORTEGA et al. 2000, BUSCALIONI et al. 2004) and possibly a sister taxon of more derived neosuchians as atoposaurids, *Goniopholis*, *Bernissartia* and eusuchians (WU et al. 2001). According to CLARK (1994: fig 5.3.), Thalattosuchia (*Pelagosaurus*, Teleosauridae, including *Machimosaurus*, and Metriorhynchidae) form together with *Pholidosaurus* and Dyrosauridae a clade of longirostrine mesoeucrocodylians. Furthermore, *Goniopholis* is probably the sister taxon to *Bernissartia* and Eusuchia (SALISBURY & WILLIS, 1997).

The material of the large crocodylomorphs of Oker does not permit any phylogenetic comparison; therefore the analysis is here focused on the better known atoposaurids. According to BUSCALIONI & SANZ (1988a) the monophyly of the Atoposauridae is based on the following apomorphic characters: anterior maxillary teeth enlarged; external mandibular fenestrae absent; antorbital fenestrae reduced or absent; squamosals not descendant and dental hypertrophy absent.

Previous phylogenetic analyses of this complex based on different characters came to largely divergent results, as briefly discussed here. According to BUSCALIONI & SANZ (1988a), a cladogram of atoposaurid interrelationships based on cranial characters shows an arrangement of sister groups with *Notosuchus* + *Uruguaysuchus* + *Araripesuchus* as the sister group of both *Atoposaurus* + *Alligatorellus* and *Theriosuchus* + *Alligatorium*, and *Montsecosuchus* as the basal taxon within Atoposauridae. An analysis based on postcranial characters results in a different cladogram, with Protosuchia as the sister group of *Orthosuchus* + *Theriosuchus*. The latter genus would be sister taxon of the joined node of *Alligatorellus* + *Alligatorium* + *Montsecosuchus*. In this case *Atoposaurus* would be the basal taxon. A third cladogram based on metric characters shows *Orthosuchus* as a sister taxon of two pairs of taxa and *Alligatorium* as basal taxon. *Atoposaurus* and *Alligatorellus* would have their common origin from a joined node at the basal line and be closer to *Alligatorium*. The node of the pair *Theriosuchus* + *Montsecosuchus* would be more distant from the basal line. Both genera would form the sister group of *Atoposaurus* + *Alligatorellus* and *Alligatorium*. A synthesis of the two versions of cladograms shows *Alligatorium* + *Alligatorellus* as sister group of *Montsecosuchus* and *Theriosuchus*. Thus, *Alligatorium* and *Alligatorellus* would be the most closely related taxa, and *Theriosuchus* would be either more distant or form a sister group relationship with *Montsecosuchus* (BUSCALIONI & SANZ 1988, but see also BUSCALIONI & SANZ, 1990a, b).

Concerning their carpal morphology, Atoposauridae are considered as sister group of the Thalattosuchia + Goniopholidae + Eusuchia (BUSCALIONI et al., 1997). In phylogenetic analyses on mesoeucrocodylian relationships, often only *Theriosuchus* is included and groups as basal neosuchian closely related to *Goniopholis* (BUSCALIONI & SANZ 1990c, ORTEGA et al. 2000).

For our following analysis we use the cranial characters in accordance with BUSCALIONI & SANZ (1988a).

Character analysis

1. Relation of frontal to supratemporal fossae - adjoining (0)/ - not adjoining (1);
2. Lacrimo-nasal suture - posterior to nasal (0)/ - lateral to nasal (1);
3. Maxillo-jugal suture - posterior to orbit (0)/ - anterior to orbit (1);
4. Maxillary posterior teeth - conical (0)/ - laterally compressed (1)/ - laterally compressed and denticulated (2);
5. Retroarticular process - slightly developed (0)/ - strongly developed (1);
6. Angular, ventral outline - straight (0)/ - dorsally

incurved (1)/ - ventrally incurved (2);
7. Maxillary festooning - absent (0)/ - slight (1)/ - strong (2);
8. Dorsal outline of snout - straight or convex (0) - concave (1);
9. Enlarged anterior maxillary teeth - absent (0) - anterior-2nd,3rd alveoli (1)/ - middle-4st,5th alveoli (2);
10. Premaxillo-maxillary space - present with a notch (0)/ - absent or slight (1)/ - diastema (2);
11. Dentition - homodont (0)/ - heterodont (1);
12. Premaxilla, number of teeth - less than five (0)/ - five (1);
13. Maxilla, number of teeth - less than 12 (0)/ - 12 to 18 (1);
14. External nares - paired (0)/ - single (1);
15. External mandibular foramen - present (0)/ - absent (1);
16. Antorbital fenestrae - present (0)/ - reduced or absent (0);
17. Postorbital pillar - exterior (0)/ - interior (1);
18. Dorso-lateral edge in squamosals - with a sulcus (0)/ - without a sulcus;
19. Orbito-supratemporal space - relatively long (0)/ - short (1);
20. Parieto-frontal surface - smooth (0)/ - with a ridge (1);
21. Occipital surface arrangement - vertical (0)/ - caudal (“dolichocephalous”) (1);
22. Ornamentation - tenuous (0)/ - well developed (1);
23. Pineal foramen - present (0)/ - absent (1);
24. Choana with septum - present (0)/ - absent (1);
25. Anterior outline of premaxillae - pointed (0) - wide (1);
26. Quadrate - fenestrated (0)/ - not fenestrated (1);
27. Supratemporal fossae - wide (0)/ - slit-like (1);
28. Postero-laterally descendant squamosals - present (0)/ - absent (1);
29. Direction of external nares - frontal (0)/ - dorsal (1);
30. Basioccipital ventral and anterior - present (0)/ - absent (1);
31. Thickness of postorbital bar - slender (0)/ - thick (1);
32. Dental hypertrophy - present (0)/ - absent (1);
33. Greatest quadrate hemicondyle - medial (0)/ - lateral (1);
34. Quadrate condyle development - slight (0)/ - pronounced (1).

Tab. 1: Data matrix for character analysis.

9 34	
Notosuchus	1000110000 0000100010 001010010? 0000
Uruguaysuchus	0?01110000 00101100?0 00?1001100 1001
Araripesuchus	111??10101 00100?0000 0110000100 1001
Atoposaurus	0???????01 01101?1?0? 11110101?0 1111
Alligatorellus	0101101101 0110111101 1111000??0 1111
Alligatorium	0101100101 111011?101 1111001 1?0 1011
Montsecosuchus	?10????00 0??01????? 1101011??? 1011
Theriosuchus	00111?0111 1111111101 1101101101 1011
DFMMh 200	??11?1?1?? 1?1?11?101 011?1??10? ?0??

Outtree from DOLMOVE (Joe Felsenstein):

(**DFMMh 200**, (*Theriosuchus*, (*Montsecosuchus*, (*Alligatorium*, (*Alligatorellus*, (*Atoposaurus*, (*Araripesuchus*, (*Uruguaysuchus*, *Notosuchus*))))))));

Outtree from PARS (Joe Felsenstein):

((((*Montsecosuchus* : 3.00, ((**DFMMh 200** : 1.25, *Theriosuchus* : 3.00) : 4.25, *Alligatorium* : 0.50) : 1.00) : 1.00, (*Alligatorellus* : 0.75, *Atoposaurus* : 1.00) : 1.75) : 7.50, *Araripesuchus* : 3.00) : 4.00, *Uruguaysuchus* : 2.00, *Notosuchus* : 8.00);

Tree from DOLMOVE made with TreeView (Roderick Page)(fig. 3A)

7 Palaeoecologic aspects of the Oker crocodiles

The crocodile fauna of Oker consists of different basal neosuchians, which are all only distantly related to each other.

Thalattosuchian remains are normally derived from shallow marine facies and they were most probably marine crocodiles and good swimmers. According to Billon-Bruyat et al. (2005), *Steneosaurus* is considered to belong to the autochthonous fauna of the well known coastal marine environments of Cerin, Canjeurs and Solnhofen. This interpretation is supported by the oxygen isotope composition in the teeth, with the $\delta^{18}O$ isotope as the indicator in their study. The slender, tubular rostrum and the uniform, slender and pointed teeth of *Steneosaurus* indicate that it was a fish-eater.

Based on the osteological characters of *Machimosaurus*, Krebs (1967) considered that the habitat of this genus was the open sea. Due to the find localities of *Machimosaurus*, the taxon can also be interpreted to have lived in a shallow lagoonal environment. In contrast to the pointed teeth of *Steneosaurus*, the bluntly rounded teeth of *Machimosaurus* indicate hard, but swimming prey. Thus, possible prey items could have been marine turtles or large ganoid fishes. Interestingly, Meyer (1994) describes shell elements of plesiochelyid turtles with bite-holes from the Jurassic limestone of Solothurn in Switzerland, which might have been caused by *Machimosaurus* (Karl & Tichy, 2004).

The constitutional morphology of the animals and the facies types of the Kimmeridgian at Oker and of the Berriasian at Obernkirchen suggest for *Goniopholis* a swamp-like environment, similar to recent mangrove forests. Remains of *Goniopholis* are mainly found in fresh water deposits with or without brackish influence. This crocodile was in habitus similar to modern crocodiles and could reach up to four meters in length. *Goniopholis* was a crocodile with an amphibic lifestyle, moving through the water by wriggling movements of the body, but being also capable of terrestrial locomotion (Salisbury & Frey 2000). *Goniopholis* was an opportunistic feeder that stood at the top of the food chain in the aquatic environments of its time. The taxon most probably fed on fishes and corpses of large terrestrial animals, such as dinosaurs.

From the heterodont teeth of *Theriosuchus*, Buscalioni & Sanz (1988b) as well as Brinkmann (1991a, b) supposed soft and various food. Possibly the small *Theriosuchus* did scavenge on carcasses and on corpses of small animals washed up along the drift line of the shore, or fed on insects and small vertebrates. The small size (not more than 1 meter), and the anatomy of the postcranial skeleton of *Theriosuchus* indicates that the taxon was capable of different terrestrial locomotor modes (Salisbury & Frey 2000). This might suggest more terrestrial habits, as it was also concluded for other atoposaurids (Buscalioni & Sanz 1988b, 1990b). However, *Theriosuchus* was also able to swim (Salisbury & Frey 2000) and therefore might not have been restricted to either a terrestrial or an aquatic, shallow marine environment as suggested by Thies et al. (1997).

As it is reconstructed, the locality where these crocodiles have been found was first a system of estuaries, rivers, lakes and swamps, and later became more brackish by the temporarily transgressing sea. This fits well with the reconstructed palaeoecological requirements of the Oker crocodile fauna.

Acknowledgements

The authors wish to express their sincerest thanks to the following persons: to Bernd Wolter ("Dinosaur Park Münchehagen" = DFMMh), to Herwig Zang and Dr. Agnes-M. Daub (Natural History Association Goslar, honorary curators of the Natural History Collections, Museum Goslar) as well as to Willi Adam, Obernkirchen, for loaning us their important specimens for our studies, and to Angelika Schwager (Bad Münder), to Dr. Annette Broschinski (Landesmuseum Hannover) for her permission to use her drawings (Fig. 11 in the present article), and to Fabian von Pupka (manager of the "Rohstoffbetriebe Oker GmbH & Co") for providing us with informations on the history of quarrying at the Langenberg and for his kind permission to EG & CB for students' excursions in the quarries belonging to his enterprise, to Jean-Paul Billon-Bruyat for his permission to use his palaeoenvironmental map (fig. 1).

8 References

Billon-Bruyat, Jean-Paul, Lécuyer, Christophe, Martineau, Francois & Mazin, Jean-Michel (2005): Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles and crocodilians. – Palaeogeography, Palaeoclimatology, Palaeoecology, **216**: 359-375, figs. 1-6; Amsterdam (Elsevier).

Brinkmann, Winand (1991a): Die Krokodilfauna aus der Unter-Kreide (Ober-Barremium) von Uña (Provinz Cuenca, Spanien). – Inaugural-Dissertation Fachbereich Geowissenschaften Freie Universtät Berlin. – : 1-182 , figs. 1-47, pls. 1-11; Berlin.

Brinkmann, Winand (1991b): Die Krokodilier-Fauna aus der Unter-Kreide (Ober-Barremium) von Uña (Provinz Cuenca, Spanien). – Berliner Geowissenschaftliche Abhandlungen, Reihe E, **5:** 1-123, figs. 1-48, pls. 1-10; Berlin.

Brüning, Kurt, & Schmidt, Heinrich [eds.] (1969): Niedersachsen und Bremen. – Handbuch der historischen Stätten, **2:** 1-602; 26 city maps, 14 maps; Stuttgart (Alfred Kröner Verlag).

Buffetaut, Eric (1982): Le Crocodilien *Machimosaurus* von Meyer (Mesosuchia, Teleosauridae) dans le Kimméridgien de L'Ain. – Bulletin de la Société Géologique de Normandie et des Amis du Muséum du Havre, **69** (1/2), #; Le Havre.

Buscalioni, Angela & Sanz, José Luis (1984): Los Arcosaurios (Reptilia) del Jurásico Superior-Cretácico Inferior de Galve (Teruel, España). – Revista Teruel, **71:** 9-28, figs. 1-4, pls. 1-2; Teruel.

Buscalioni, Angela & Sanz, José Luis (1988a): Phylogenetic relationships of the Atoposauridae (Archosauria, Crocodylomorpha). – Historical

Biology, **1:** 233-250, figs. 1-9; Chur, London, Paris, New York, Melbourne.

BUSCALIONI, Angela & SANZ, José Luis (1988b): Hypothetical behaviour scaling in a Lower Cretaceous crocodilian community of Galve (Teruel, Spain). – International Symposium on Vertebrate behaviour as derived from the fossil record: 65. – Museum of the Rockies; Montana State University.

BUSCALIONI, Angela & SANZ, José Luis (1990a): La familia Atoposauridae: una aproximatión a la historia de los cocodrilos enanos. – Trabajos Museo Geologico Barcelona, **1:** 77-89, figs. 1-4; Barcelona.

BUSCALIONI, Angela & SANZ, José Luis (1990b): *Montsecosuchus depereti* (Crocodylomorpha, Atoposauridae), new denomination for *Alligatorium depereti* VIDAL, 1915 (Early Cretaceous, Spain): Redescription and phylogenetic relationships. – Journal of Vertebrate Paleontology, **10** (2): 244-254; Norman/Oklahoma.

BUSCALIONI, Angela & SANZ, José Luis (1990c): The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). – Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **60:** 129-150; Brussels.

BUSCALIONI, Angela, ORTEGA, Francisco, PÉREZ-MORENO, Bernardino P. & EVANS, S. E. (1996): The Upper Jurassic maniraptoran theropod *Lisboasaurus estesi* (Guimarota, Portugal) reinterpreted as a crocodylomorph. – Journal of Vertebrate Paleontology, **16** (2): 358-362, figs. 1-3; Norman/Oklahoma.

BUSCALIONI, Angela, ORTEGA, Francisco, RASSKIN-GUTMAN, Diego & PÉREZ-MORENO, Bernardino P. (1997): Loss of carpal elements in crocodilian limb evolution: morphogenetic model corroborated by palaeobiological data. – Biological Journal of the Linnean Society, **62:** 133-144, figs. 1-5; London.

BUSCALIONI, Angela, PÉREZ-MORENO, Bernardino P. & SANZ, José Luis (2003): Pattern of biotic replacement in modern crocodiles during the Late Cretaceous. – Coloquios de Paleontologia, Vol. Ext. **1:** 77-93, figs. 1-5, tabs. 1-6; Madrid.

BUSCALIONI, Angela, SCHULP, Anne, JAGT, John W. M., HANNA, Samir S. & HARTMAN, Axel F. (2004): Late Cretaceous neosuchian crocodiles from the Sultanate of Oman. – Cretaceous Research, **25:** 167-275, figs. 1-5; London.

CLARK, James M. (1994): Chapter 5 – Patterns of evolution in Mesozoic Crocodyliformes. – In: FRAZER, Nicholas C. & SUES, Hans-Dieter (eds.): In the shadow of the Dinosaurs. Early Mesozoic tetrapods: 84-97, figs. 1-4; Cambridge.

DUNKER, [Rudolf] Wilhelm (1843-1844): Über den norddeutschen sogenannten Wälderthon und dessen Versteinerungen. – Programm der Höheren Gewerbeschule; Cassel.

DUNKER, [Rudolf] Wilhelm (1846): Monographie der Norddeutschen Wealdenbildung. Ein Beitrag zur Geognosie und Naturgeschichte der Vorwelt. – : 1-86, pls. 1-21; Braunschweig (Oehme & Müller).

FASTNACHT, Michael (2005): The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones. – Acta Palaeontologica Polonica, **50** (2): 273-288, figs. 1-18, appendix 1; Warszawa.

FELSENSTEIN, Joseph (1986): PHYLIP/ DOLMOVE-Interactive Dollo and Polymorphism Parsimony © Copyright 1986-2002 by the University of Washington. Written by Joseph FELSENSTEIN.

FELSENSTEIN, Joseph (1986): PHYLIP/ PARS-Discrete character parsimony © Copyright 1986-2000 by the University of Washington. Written by Joseph FELSENSTEIN.

FISCHER, Rudolf (1991): Die Oberjura-Schichtfolge vom Langenberg bei Oker. – Arbeitskreis Paläontologie Hannover, **19** (2): 21-36, figs. 1-8; Hannover.

GEOFFROY SAINT-HILAIRE, Etienne (1825): Recherches sur l'organisation des gavailas. – Memoires du Museum National d'Histoire Naturelle, **12:** 97-155 ; Paris.

GRAMANN, Franz, HEUNISCH, Carmen, KLASSEN, Horst, KOCKEL, Franz, DULCE, Gesine, HARMS, Franz-Jürgen, KATSCHOREK, Tanja, MÖNNIG, Eckhard, SCHUDACK, Michael, SCHUDACK, Ulla, THIES, Detlev & WEISS, Michael (1997): Das Niedersächsische Oberjura-Becken – Ergebnisse interdisziplinärer Zusammenarbeit. – Zeitschrift der Deutschen Geologischen Gesellschaft, **148** (2): 165-236, figs. 1-18, tab. 1, pl. 1; Stuttgart.

HAMM, Friedrich (1954): Niedersachsens Erdgeschichte. – : 1-104, figs. 1-30, pl. 1; Hannover.

KARL, Hans-Volker & TICHY, Gottfried (2004): The structure of fossil teeth of chelonophagous crocodiles (Diapsida: Crocodylia). – Studia Geologica Salmanticensia, **40:** 115-124, figs. 1-4; Salamanca.

KOCH, Carl Ludwig, & DUNKER, [Rudolf] Wilhelm (1837): Beiträge zur Kenntnis des norddeutschen Oolithgebildes und dessen Versteinerungen. – : 1-64, pls. 1-7; Braunschweig (Oehme & Müller).

KOKEN, Ernst (1886): Über das Vorkommen fossiler Crocodiliden in den Wealdenbildungen Norddeutschlands und über die Systematik der mesozoischen Crocodiliden. – Zeitschrift der Deutschen Geologischen Gesellschaft, **38:** 664-670; Berlin.

KOKEN, Ernst (1887): Die Dinosaurier, Crocodilien und Sauropterygier des Norddeutschen Wealden. – Geologische und Palaeontologische Abhandlungen, **3:** 309-411; Jena.

KOKEN, Ernst (1896): Die Reptilien des deutschen Wealden (Nachtrag). – Geologische und Palaeontologische Abhandlungen, **7:** 119-126, Taf. 1; Jena [mit Abb. v. *Goniopholis*].

KREBS, Bernard (1967): Der Jura-Krokodilier *Machimosaurus* H. v. MEYER. – Paläontologische Zeitschrift, **41** (1/2): 46-59, figs. 1-4; Stuttgart.

KUHN, Oskar (1936): Crocodilia. – Fossilium Catalogus I: Animalia, **75:** 1-144; 's-Gravenhage.

LOOK, Ernst-Rüdiger (1985): Geologie, Bergbau und Urgeschichte im Braunschweiger Land. – Geologisches Jahrbuch Reihe A, **88:** 3-452, figs. 1-181, tabs. 1-18, 1 geol. map; Hannover.

MÄGDEFRAU, Karl (1968): Paläobiologie der Pflanzen. – 4. edition. – : 1-549, figs. 1-395; Jena (VEB Gustav Fischer Verlag).

MEYER, Christian (1994): 145 Millionen Jahre vor unserer Zeit. Das Leben in einer tropischen Meereslagune. – : 1-71; Schild, Solothurn.

MEYER, Hermann von (1837): Mitteilungen, an Professor Bronn gerichtet. – Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde, **4:** 413-418; Stuttgart [*Madrimosaurus* (sic!) *hugii*].

MEYER, Hermann von (1838): Briefliche Mitteilungen an Professor Bronn. – Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde, **1838:** 668; Stuttgart.

MEYER, Hermann von (1841): *Pholidosaurus schaumburgensis* ein Saurus aus dem Sandstein der Wald-Formation Nord-Deutschlands. – Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde, **4:** 443-445; Stuttgart.

ORTEGA, F., GASPARINI, Z., BUSCALIONI, Angela & CALVO, J. O. (2000). A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). – Journal of Vertebrate Paleontology, **20** (1): 57-76; Norman/Oklahoma.

OWEN, Richard (1841): A description of a portion of the skeleton of the *Cetiosaurus*, a gigantic extinct saurian reptile occurring in the oolitic formations of different portions of England. – Proceedings of the Geological Society of London, **3:** 457-462; London.

OWEN, Richard (1878): Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement No VIII. Crocodilia (*Goniopholis, Petrosuchus*, and *Suchosaurus*). – Palaeontological Society, Monograph, **32:** 1-15, pls. 1-6; London.

PAPE, Hansgeorg (1970): Die Malmschichtfolge vom Langenberg bei Oker (nördl. Harzvorland). – Mitteilungen aus dem Geologischen Institut der Technischen Universität Hannover, **9:** 41-134, figs. 1-15, tab. 1, pls. 1-14; Hannover.

ROEMER, Friedrich Adolph (1836): Die Versteinerungen des norddeutschen Oolithen-Gebirges. – [I-VI,] 1-218, pls. 1-16; Hannover (Hahn'sche Hofbuchhaltung).

ROEMER, Friedrich Adolph (1839): Die Versteinerungen des norddeutschen Oolithen-Gebirges. Ein Nachtrag. – I-IV, 1-59, pls. A and 17-20; Hannover (Hahn'sche Hofbuchhandlung).

SALISBURY, Steven W. (2002): Crocodilians from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset, Southern England. – In: MILNER, Andrew R. & BATTEN, David J. (eds.): Life and environments in Purbeck times. – Special Papers in Palaeontology, **68:** 121-144, figs. 1-16, tab. 1; London.

SALISBURY, Steven W. & FREY, Eberhard (2000): A biomechanical transformation model for the evolution of semi-spheroidal articulations between adloining vertebral bodies in crocodilians. – In: GRIGG, Gordon C., SEEBACHER, Frank & FRANKLIN, Craig E. (eds.): Crocodylian biology and evolution: 85-134, figs. 1-29; Chipping Norton, New South Wales (Surrey Beatty & Sons).

SALISBURY, Steven W., FREY, Eberhard, MARTILL, David M. & BUCHY, Marie-Céline (2003): A new crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil. – Palaeontographica, Abteilung A, **270** (1-3): 3-47, figs. 1-9; Stuttgart.

SALISBURY, Steven W. & WILLIS, Paul M. A. (1997): A new crocodylian from the Early Eocene of southeastern Queensland and a preleminary investigation of the phylogenetic relationships of crocodylids. – Alcheringa, **21** (3): 218-226, figs. 1-17; Adelaide.

SALISBURY, Steven W., & WILLIS, Paul M. A., & PEITZ, Sabine, & SANDER, P. Martin (1999): The crocodilian *Goniopholis simus* from the Lower Cretaceous of north-western Germany. – In:

Unwin, David N. (ed.): Cretaceous fossil vertebrates. – Special Papers in Palaeontology, **60:** 121-148, figs. 1-12, tab. 1; London.

Sander, P. Martin, Mateus, Octávio, Laven, Thomas & Knötschke, Nils (2006): Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. – Nature, **441:** 739-741, Abb. 1-2; London.

Schmidt, Hermann (1973): Zur geologischen Geschichte des Schaumburger Landes. – Ballerstedtiana, **1:** 5-8; Bückeburg und Stadthagen (Schaumburg-Lippischer Heimatverein e. V.).

Schwarz, Daniela (2002): A new species of *Goniopholis* from the Upper Jurassic of Portugal. – Palaeontology, **45** (1): 185-208, figs. 1-7; London.

Schwarz, Daniela & Fechner, Regina (2004): *Lusitanisuchus*, a new generic name for *Lisboasaurus mitracostatus* (Crocodylomorpha: Mesoeucrocodylia), with a description of new remains from the Upper Jurassic (Kimmeridgian) and Lower Cretaceous (Berriasian) of Portugal. – Canadian Journal of Earth Sciences, **41**: 1259-1271, figs. 1-6, Appendix A; Vancouver.

Schwarz, Daniela & Salisbury, Steven W. (2005): A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. – Geobios, **38:** 779-802; Lyon.

Selenka, Emil (1867): Die fossilen Krokodilinen des Kimmeridge von Hannover. – Palaeontographica. Beiträge zur Naturgeschichte der Vorwelt, **16** (3. Lieferung): 137-144, pls. 9-11; Cassel.

Steel, Rodney (1973): Crocodylia. - In: Kuhn, Oskar (ed.): Handbuch der Paläoherpetologie. Encyclopedia of Paleoherpetology, **16:** 1-116, figs. 1-33; Stuttgart, Portland-USA (Gustav FischerVerlag).

Steel, Rodney (1975): Die fossilen Krokodile. - Die Neue Brehm-Bücherei, **488:** 1-76, figs. 1-47; Wittenberg-Lutherstadt (A. Ziemsen Verlag).

Sturm, Helmut & Brauckmann, Carsten (1999): Seltene und weniger bekannte Fossilien aus dem Malm bei Hildesheim. – Arbeitskreis Paläontologie Hannover, **27** (2): 53-65, figs. 1-10; Hannover.

Thies, Detlev & Broschinski, Annette (2001): Teeth of a small durophagous crocodile from the Late Jurassic (Kimmeridgian) of North Germany. – Geologische Beiträge Hannover, **2**: 65-70, figs. 1-5; Hannover.

Thies, Detlev, Windolf, Raymund & Mudroch, Alexander (1997): First record of Atoposauridae (Crocodylia: Metamesosuchia) in the Upper Jurassic (Kimmeridgian) of Northwest Germany. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **205** (3): 393-411, figs. 1-10, tabs. 1-2; Stuttgart.

Wincierz, Josef (1967): Ein *Steneosaurus*-Fund aus dem nordwestdeutschen Oberen Lias.- Paläontologische Zeitschrift, **41** (1/2): 60-72, pls. 5-6; Stuttgart.

Wu X.-C., Russell, A. P. & Cumbaa, S. L. (2001): *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. – Journal of Vertebrate Paleontology, **21** (3): 492-514; Norman/Oklahoma.

Zihrul, Bernd (1990): Mikrobiostratigraphie, Palökologie und Mikropaläontologie in Gesteinen des Unteren und Mittleren Malm am Langenberg bei Goslar/Oker. – Clausthaler Geowissenschaftliche Dissertationen, **38:** 1-220, figs. 1-14, tabs. 1-7, pls. 1-16; Clausthal-Zellerfeld.

Adressen der Autoren:
Hans-Volker Karl, Institut für Geographie, Geologie & Mineralogie, Abt. Paläontologie der Universität Salzburg, Hellbrunner Straße 34, A-5020 Salzburg, e-mail: hvkarl@web.de
Elke Gröning & Carsten Brauckmann, Institut für Geologie und Paläontologie der TU Clausthal, Leibnizstraße 10, D-38678 Clausthal-Zellerfeld, e-mail: Elke.Groening@tu-clausthal.de , Carsten.Brauckmann@tu-clausthal.de
Daniela Schwarz, Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, daniela.schwarz@bs.ch
Nils Knötschke, Dinosaurier-Park Münchehagen, Alte Zollstr. 5, 31547 Rehburg-Loccum palaeo_nils@hotmail.com