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REVISION OF THE GENUS *ENALIOSUCHUS* KOKEN, 1883 (ARCHOSAUROMORPHA: METRIORHYNCHIDAE) FROM THE EARLY CRETACEOUS OF NORTHWESTERN GERMANY

[Revisión del género* Enaliosuchus *Koken, 1883 (Archosauromorpha: Metriorhynchidae) del Cretácico Inferior del NW de Alemania]

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RESUMEN: El material-tipo de *Enaliosuchus schroederi* Kuhn, 1936 del Cretácico Inferior bajo (base del Valanginiense inferior) de las arcillas de Sachsenhagen (SSW del "Steinhuder Meer", Sajonia Inferior, Alemania del noroeste) es revisado detalladamente por primera vez bajo aspectos modernos. Consiste en un cráneo (sin la punta del hocico), la mandíbula inferior y las tres vértebras cervicales anteriores que quedaron fijas al cráneo durante el proceso de recogimiento. La conclusión principal de este estudio es que los especímenes más viejos enteros de *Enaliosuchus* no pueden ser determinados exactamente más que como

Metriorhynchus sp. (en nomenclatura abierta). Para una clasificación sistemática más detallada serían necesarios una revisión y análisis anatómico de todos los cráneos hasta ahora conocidos de *Metriorhynchus,* en vistas occipital y palatinal.

Palabras clave: Cretácico inferior, Alemania noroeste, Archosauromorpha, Crocodylia, Metriorhynchidae, *Metriorhynchus* sp., sinónimos, *Enaliosuchus macrospondylus*, *Enaliosuchus schroederi*, análisis de las características, revisión.

ABSTRACT: The type material of *Enaliosuchus schroederi* Kuhn, 1936 from the lower Early Cretaceous (lower Early Valanginian) of the former clay pit of Sachsenhagen (SSW of the "Steinhuder Meer", Lower Saxony, northwestern Germany) is revised in detail for the first time under modern aspects. It consists of a skull (without the tip of the snout) with lower jaw and the anterior three cervical vertebrae which were still attached to the skull during the collecting process. The main conclusion of this study is that the whole older materials of *Enaliosuchus* cannot be determined more precisely than as *Metriorhynchus* sp. (in open nomenclature). For a more detailed systematic classification, a revision and anatomical analysis of all hitherto known skulls of *Metriorhynchus* in both, occipital and palatinal views would be necessary.

Key words: Lower Cretaceous, northwestern Germany, Archosauromorpha, Crocodylia, Metriorhynchidae, *Metriorhynchus* sp., synonymy, *Enaliosuchus macrospondylus*, *Enaliosuchus schroederi*, character analysis, revision.

INTRODUCTION

KOKEN (1883) based his fossil crocodile genus *Enaliosuchus* with the type species *Enaliosuchus macrospondylus* upon very poor materials, e.g. the remains of atlas, axis and a few vertebrae, however without selecting a type-specimen. The preserved characters of the materials may haven been appropriate for defining a new genus during the 19th century, but they are completely insufficiant due to modern state of knowledge.

The specimens were collected from the "Hils of the Osterwald". In this case, "Hils" does not mean the Hils Mountain within the Leine region (S Hildesheim) but the "Hils clay" of the lower Early Cretaceous in the Osterwald Mountain S Springe (SW Hannover). In earlier stages of the history of geological research in Lower Saxony, the "Hils clay" was allocated to the "Neokom" of northern Germany; according to the recent subdivision of the Early Cretaceous, the "Hils clay" encloses a maximum time of sedimentation approximately from the Valanginian up to the early Aptian, however with largely diachronic lower boundary. The exact type stratum of *Enaliosuchus macrospondylus* could possibly be restricted to the latest Valanginian, if the dating by KOKEN (1883: 792) as "beds of *Ammonites (Olcostephanus) marginatus*" (= "Astierien-Schichten" of the older literature) is correct.

Typical remains of a metriorhynchid crocodile (skull with tip of the snout lacking and lower jaw in connection as well as three cervical vertebrae,

originally directly in connection with the skull) from the lower Early Valanginian ("*Platylenticeras* beds") of the former clay pit W Sachsenhagen ("Papesche Ziegeleitongrube" in KEMPER, 1961) were described by SCHRÖDER (1923); he considered them to be almost identical with the genus *Enaliosuchus* Koken. But he also points out the somewhat more robust atlas of the Sachsenhagen crocodile when compered with *E. macrospondylus*" which he explained by the "probably higher individual age" of the former specimen.

Based upon the description, figure and discussion - evidently inclusive the slight differences in the atlas when compared with *E. macrospondylus* as pointed out by SCHRÖDER (1923) - but without any more detailed reasons, KUHN (1936: 76) separated the Sachsenhagen specimen on specific level and named it "*Enaliosuchus* schröderi n. sp." The spelling of the epitheton "schröderi" does not correspond with the rules of the "International Code of Zoological Nomenclature" (which do not allow diacritic marks) and must be corrected into "schroederi".

After a longer time of uncertainty about the place where the Sachsenhagen crocodile was deposited, SICKENBERG (1961) re-discovered it within the "Museum für Geschichte, Landes- und Volkskunde" in Minden (Northrhine-Westphalia). This author also gave a brief comment on the history of research of this specimen. More recently, it was additionally mentioned and figured by KAUFMANN *et al.*, (1980). A modern detailed taxonomic revision has never been published yet. This lack of research should be closed in the present paper.

CHARACTER ANALYSIS

ACTUAL SYNONYMS OF SOME TAXA USED BY KOKEN (1883)

A. MESOSUCHIA

1. *Machimosaurus hugii* (H. V. Meyer, 1937), syn. *Machimosaurus mosae* Sauvage, 1878.

2. *Pelagosaurus typus* Bronn, 1841, syn. *Teleosaurus temporalis* Deslongchamps, 1853.

3. *Steneosaurus bollensis* (Jaeger, 1828), syn. *Mystriosaurus tiedemanni* Kaup, 1841. *Mystriosaurus longipes* Bronn, 1843, *Mystriosaurus mandelslohi* Kaup, 1841.

B. EUSUCHIA

1. *Osteolaemus tetraspis* Cope, 1861, syn. *Crocodilus frontatus* Murray, 1862.

2. *Diplocynodon ebertsi* (Ludwig, 1877), syn. *Crocodilus ebertsi* Ludwig, 1877.

3. *Diplocynodon darwini* (Ludwig, 1877), syn. *Alligator darwini* Ludwig, 1877.

CHARACTER DISTRIBUTION

KOKEN's (1883) very detailed description of *Enaliosuchus macrospondylus* is based upon details of the anteriormost cervical vertebrae which, however, are no more diagnostic for a crocodile genus due to the present state of knowledge. Helpful for a revisional valuation of the original description is the comparative table of characters (KOKEN, 1883: enclosure between pp. 808-809) which, transferred into a modern terminology, enables us to prepare a character analysis. In this case the characters used by KOKEN (1883) correspond with the following ones (put in brackets are those taxa which share the same characters with *Enaliosuchus*):

1. Proatlas inserted *(Pelagosaurus typus)*.

2. Body of atlas developed as dens epistrophei *(Osteolaemus tetraspis, Alligator mississippiensis, ?Diplocynodon darwini, Steneosaurus bollensis)*.

3. Neurapophyses of atlas widely separated *(Crocodilus frontatus, Alligator mississippiensis)*.

4. Hypapophysis of atlas present *(Osteolaemus tetraspis, Steneosaurus bollensis, Alligator mississipiensis)*.

5. Diapophysis present *(Pelagosaurus typus, Teleosaurus cadomensis, Steneosaurus bollensis, Pelagosaurus typus)*.

6. Parapophysis present *(Diplocynodon darwini, Machimosaurus hugii, Pelagosaurus typus, Teleosaurus cadomensis, Steneosaurus bollensis)*.

7. Epistropheus ventrally depressed, without median keel *(Machimosaurus hugii, Pelagosaurus typus)*.

From this list it becomes evident that *Enaliosuchus* has not a single character of its own (autapomorphy). On the contrary, their distribution shows nothing more than a very general complex of characters typical for the Mesosuchia or the Crocodylia on the whole. Moreover, several "characters" of the genus *Metriorhynchus* are insufficiantly known. Only after consideration of typical characters of the skull of the Metriorhynchidae the problems can be dissolved, and the family can clearly be grouped with the Mesosuchia. These charcters are as follows:

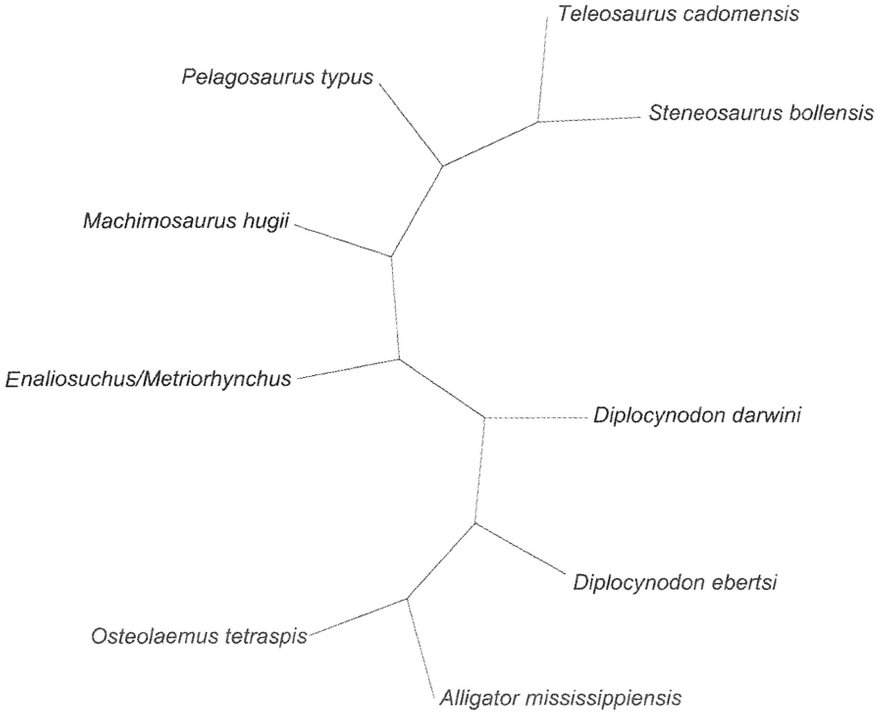
8. Prefrontalia enlarged to a roof-like shape *(Steneosaurus bollensis)*.

9. Supratemporal fenestra expanded *(Machimosaurus hugii, Pelagosaurus typus, Teleosaurus cadomensis, Steneosaurus bollensis)*.

10. Contact of premaxilla and nasale absent *(Machimosaurus hugii, Pelagosaurus typus, Teleosaurus cadomensis, Steneosaurus bollensis)*.

DATAMATRIX

Osteolaemus tetraspis	0	1	1	1	?	?	0	0	0	1
Alligator mississippiensis	0	1	1	1	?	?	0	0	0	1
Diplocynon ebertsi	?	0	?	?	?	?	0	0	0	1
Diplocynon darwini	?	?	0	?	?	1	0	0	0	1
Enaliosuchus/Metriorhynchus	1	1	1	1	1	1	1	1	1	0
Machimosaurus hugii	?	0	?	?	?	1	1	0	1	0
Pelagosaurus typus	1	0	0	1	1	1	1	0	1	0
Teleosaurus cadomensis	0	0	?	?	1	1	?	0	1	0
Steneosaurus bollensis	?	0	?	1	1	1	?	1	1	0



TREE BY TREEVIEW (Roderic Page) based on Outtree by DOLMOVE (Joseph FELSENSTEIN)

OUTTREE BY DOLMOVE (Joseph FELSENSTEIN)

(*Steneosaurus bollensis*, (*Teleosaurus cadomensis*, (*Pelagosaurus typus*, (*Machimosaurus hugii*, (*Enaliosuchus/Metriorhynchus*, (*Diplocynodon darwini*, (*Diplocynodon ebertsi*, (*Alligator mississipiensis*, *Osteolaemus tetraspis*))))))));

OUTFILE BY PARS (Joseph FELSENSTEIN)

Discrete character parsimony algorithm, version 3.6a3, shows 4 trees in all found:

(*Diplocynodon darwini*: 1.00, ((*Teleosaurus cadomensis*: 0.00, (*Pelagosaurus typus*: 1.00, *Machimosaurus hugii*: 0.00, (*Steneosaurus bollensis*: 0.00, *Enaliosuchus/Metriorhynchus*: 1.00):1.00):1.50):2.50, *Diplocynodon ebertsi*: 0.00):1.00, *Alligator mississippiensis*: 0.00, *Osteolaemus tetraspis*: 0.00)[0.2500].

(*Diplocynodon darwini* :1.00, ((*Teleosaurus cadomensis* :0.00, *Machimosaurus hugii*: 0.00, (*Pelagosaurus typus*: 1.00, (*Steneosaurus bollensis*: 0.00, *Enaliosuchus/Metriorhynchus*: 1.00):1.00):1.00):3.00, *Diplocynodon ebertsi*: 0.00):1.00, *Alligator mississippiensis*: 0.00, *Osteolaemus tetraspis*: 0.00)[0.2500].

(((*Teleosaurus cadomensis*: 0.00, *Machimosaurus hugii*: 0.00, (*Pelagosaurus typus*: 0.33, (*Steneosaurus bollensis*: 0.00, *Enaliosuchus/Metriorhynchus*: 1.33):1.33):1.00):3.00, *Diplocynodon darwini*: 0.33, *Diplocynodon ebertsi*: 0.00): 1.67, *Alligator mississippiensis*: 0.00, *Osteolaemus tetraspis*: 0.00)[0.2500];

(((*Teleosaurus cadomensis*: 0.00, (*Pelagosaurus typus*: 0.33, *Machimosaurus hugii*: 0.00, (*Steneosaurus bollensis*: 0.00, *Enaliosuchus/Metriorhynchus*: 1.33):1.33):1.50):2.50, *Diplocynodon darwini*: 0.33, *Diplocynodon ebertsi*: 0.00):1.67, *Alligator mississippiensis*: 0.00, *Osteolaemus tetraspis*: 0.00)[0.2500].

All treefiles show only one classification of *Enaliosuchus/Metriorhynchus* within the Mesosuchia.

DISCUSSION

In general it can be concluded that all those characters previously pointed out as typical for *Enaliosuchus macrospondylus* are corresponding much better to the genus *Metriorhynchus*. Even the synonymy of *Mystriosaurus bollensis* (Jaeger, 1828), originally described as *Crocodilus bollensis*, shows already that "macrospondyly" is common within the Thalattosuchia: This character was originally used for example to name and characterize the genus *Macrospondylus* H. V. Meyer, 1831. Although this generic name was occasionally used by previous authors (compare synonymy in KUHN, 1936: 44-50; STEEL, 1973) it soon became generally accepted that *Macrospondylus* is synonymous with *Mystrisaurus* Kaup, 1835 which again is now regarded as younger synonym of *Steneosaurus* Geoffroy, 1825.

In addition to the formal doubts about the justification of a separate species *Enaliosuchus schroederi* Kuhn, 1936, as already emphasized by SICKENBERG (1961), neither the morphological similarities to the extremely inappropriate type species *Enaliosuchus macrospondylus* nor their (possible) differences can really be verified.

The following changes are suggested on the base of results from the character analysis:

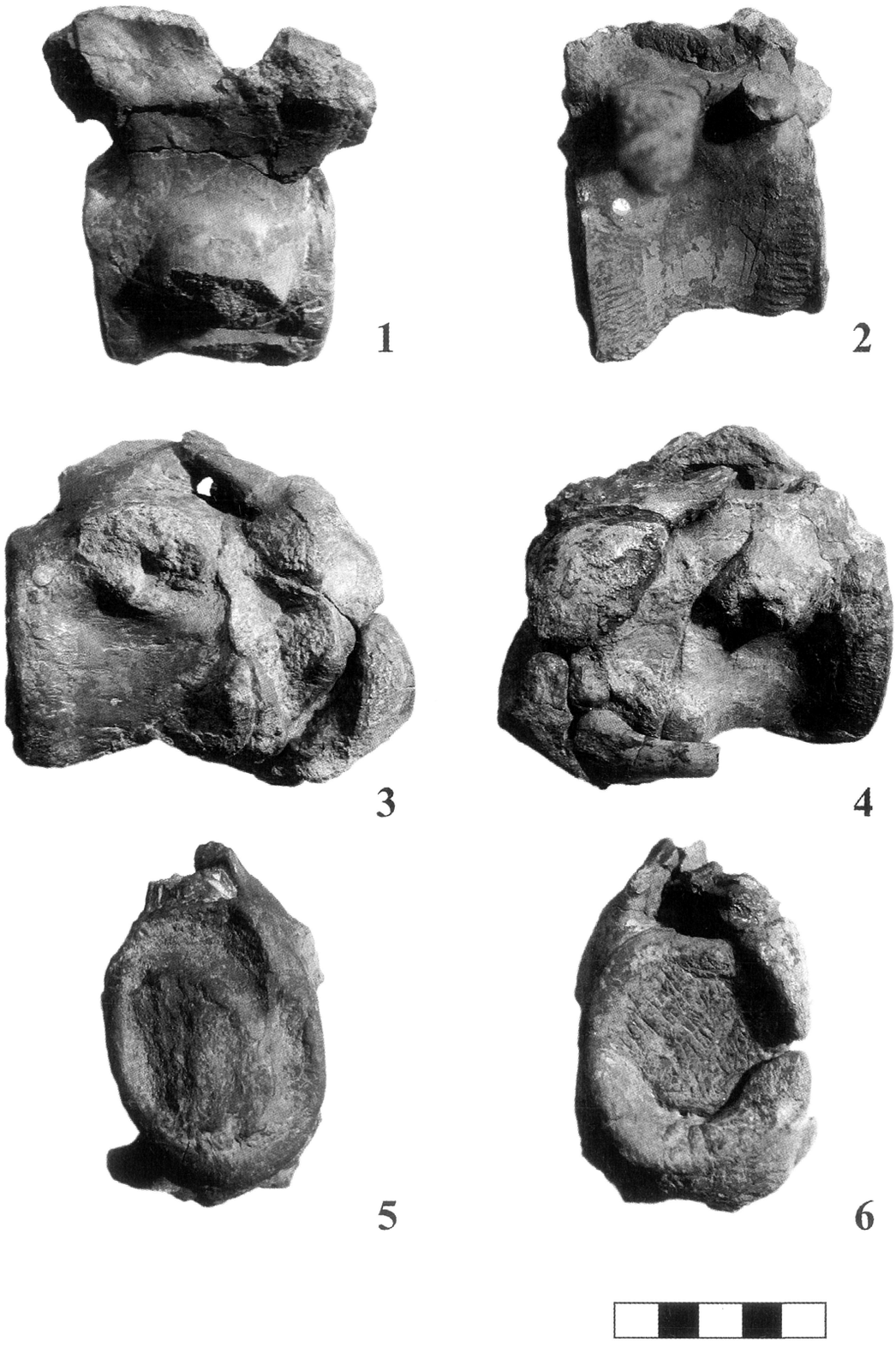


Plate 1. Type materials of Enaliosuchus macrospondylus *Koken, 1883: vertebrae, deposited in the palaeontological collection of the "Museum für Naturkunde der Humboldt-Universität Berlin", number MNHUB #.*

1. The re-examination of the characters used by KOKEN (1883) to establish *Enaliosuchus* are completely insufficient to define a separate genus. They are rather features which are generally typical for the Crocodylia as well as for the Metriorhynchidae; therefore *Enaliosuchus* Koken, 1883 is in fact a *nomen dubium*; due to both, its stratigraphical and paleogeographic occurrence it is here regarded additionally as a possible younger synonym of *Metriorhynchus* H. V. Meyer, 1830.

2. Establishing a separate species *Enaliosuchus schroederi* Kuhn, 1936 for the Sachsenhagen specimen was completely unnecessary.

3. It cannot be excluded that the present materials of "*Enaliosuchus*" ["*E. macrospondylus*" and "*E.* schroederi"] are closely related or even conspecific, but due to the present knowledge, a generic assignment can only be proposed for the fragmentary Sachenhagen specimen and is to be restricted to *Metriorhynchus* sp.

4. Basic requirement for a more detailed systematic classification is a detailed revision and anatomical analysis of all known skulls of *Metriorhynchus* in both, occipital and palatinal views which cannot be done in the present article. Furthermore, in most flattened specimens the palatinal view is not preserved. Therefore the whole material previously allocated to *Enaliosuchus* should be determined until further notice suitably as *Metriorhynchus* sp.

CLASSIFICATION

In accordance to the character analysis, the systematics grouping of the materials in question is as follows:

Legion Archosauromorpha Von Huene, 1946
Supercohort Crurotarsi Sereno & Arcucci, 1990
Cohort Crocodylotarsi Benton & Clark, 1988
Magnorder Suchia Krebs, 1974
Superorder Crocodylomorpha Walker, 1968
Grandorder Crocodyliformis Hay, 1930
Microrder Mesoeurocrocodylia Whetstone & Whybrow, 1983
Order Mesosuchia emend. Huxley, 1875
Suborder Thalattosuchia emend. Fraas, 1901
Family Metriorhynchidae Fitzinger, 1843
Genus *Metriorhynchus* H. V. Meyer, 1830

Type species: *Metriorhynchus geoffroyi* H. V. Meyer, 1832; genus first published 1830 without proposed species.

Description: According to STEEL (1973) *Metriorhynchus* differs from *Geosaurus* in the absence of serrations on the dental carinae, and the enamel

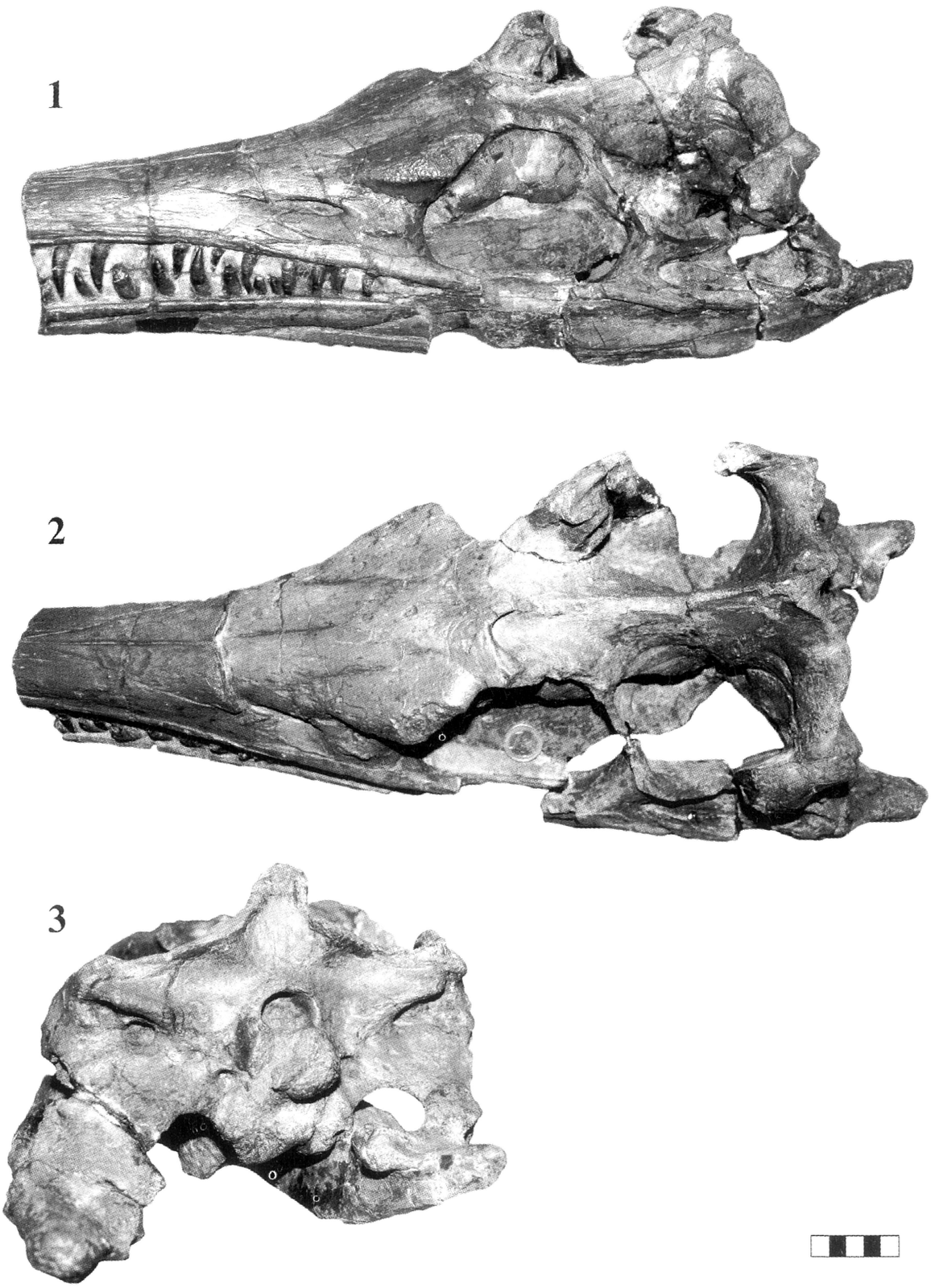


Plate 2. Original materials of SCHRÖDER, 1923 and Enaliosuchus schroederi *KUHN, 1936, deposited in the palaeontological collection of the "Mindener Museum für Geschichte, Landes- und Volkskunde", number MMGLV #.*

is generally raised into a varying number of fine longitudinal ridges. This condition is also present in the Valanginian specimen from Sachsenhagen discussed here. For further characters see STEEL (1973: 45-49).

Type horizon and locality of the type species: Oxfordian of Honfleur in France.

Known distribution: As far as hitherto known, *Metriorhynchus* occurs in Oxfordian and Kimmeridgian strata of England and France, and according to STEEL (1973) the genus is presumably ancestral to the Kimmeridgian and Portlandian metriorhynchids of the same area [*Geosaurus* Cuvier, 1824, *Dakosaurus* Quenstedt, 1856 and *Cricosaurus* Wagner, 1858]. The Valanginian materials from northwestern Germany are the stratigraphically youngest and palaeogeographically the most eastern records of this genus.

***Metriorhynchus* sp.**

SYNONYMS:

?*Enaliosuchus macrospondylus* Koken, 1883

LOCALITY: Osterwald S Springe (SW Hannover, Lower Saxony, northwestern Germany). In the original description there are no more detailed specification of the locality in this rather large region.

HORIZON: "mariner Hils" = "Hils-Ton" ["Hils clay"], lower Early Cretaceous, most probably latest Valanginian, if the dating given by KOKEN (1883: 792: "Niveau des *Ammonites* (*Olcostephanus*) *marginatus*" = "Astierien-Schichten" of the older literature on the Early Cretaceous in northwestern Germany) is correct.

MATERIAL: atlas, axis and a few further vertebrae, deposited in the "Museum für Naturkunde der Humboldt-Universität Berlin", number MNHUB # (KUHN, 1936; STEEL, 1973).

?*Enaliosuchus schroederi* Kuhn, 1936

LOCALITY: former clay pit W Sachsenhagen ("Papesche Ziegeleitongrube" in KEMPER, 1961), approximately 6 km SSW of the southern lakeside of the "Steinhuder Meer" (Lower Saxony, northwestern Germany). Exploitation in the clay pit started in 1904. In the southern part (= "older part") of the pit the "Platylenticeras beds" cropped out (KAUFMANN *et al.*, 1980: 18) from which part also "*Enaliosuchus* schroederi" was collected.

HORIZON: lower Early Valanginian, "*Platylenticeras* beds".

MATERIAL: MMGLV #: skull withot tip of the snout and lower jaw in connection as well as three cervical vertebrae, originally directly in

connection with the skull (KUHN, 1936; SCHRÖDER, 1923; SICKENBERG, 1961; STEEL, 1973).

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