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FIRST REMAINS OF THE HEAD OF *STENEOSAURUS* (CROCODYLOMORPHA: TELEOSAURIDAE) FROM THE LATE JURASSIC OF OKER (LOWER SAXONY, GERMANY)

[Primeros restos cefálicos de* Steneosaurus *(Crocodylomorpha: Teleosauridae) del Jurásico Superior de Oker (Baja Sajonia, Alemania)]

Hans-Volker KARL (*)

Elke GRÖNING (**)

Carsten BRAUCKMANN (**)

Nils KNÖTSCHKE (***)

(*): Geocenter of the University Göttingen. Dpt. Geobiology. Goldschmidtstrasse, 3. D-37077 Göttingen. Correo-e: hkarl@uni-goettingen.de or hvkarl@web.de

(**): Institute of Geology and Palaeontology. Clausthal University of Technology. Leibnizstrasse, 10. D-38678 Clausthal-Zellerfeld. Correo-e: Elke.Groening@tu-clausthal.de, Carsten.Brauckmann@tu-clausthal.de

(***): Dinosaur Park Münchehagen. Alte Zollstrasse, 5. D-31547 Rehburg-Loccum. Correo-e: palaeo_nils@hotmail.com

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RESUMEN: Se describen dos restos cefálicos del cocodrilo marino *Steneosaurus brevirostris* Owen, 1842, del Jurásico Superior, provenientes del Kimmeridgiense del monte Langenberg cerca de la comunidad de Oker, Baja Sajonia, Alemania. Se trata de fragmentos de un rostrum y una mandíbula inferior y representan el primer hallazgo de partes de la cabeza en esta localidad. La comparación con materiales parecidos de *Steneosaurus jugleri* (V. Meyer, 1845) y *St. picteti* (De Tribolet, 1873), casi contemporáneos, hace suponer que las últimas dos especies son sinónimas con *St. brevirostris*.

Palabras clave: Crocodylomorpha, Neosuchia, *Steneosaurus brevirostris*, Jurásico Superior, Kimmeridgiense, Oker, Alemania noroccidental.

ABSTRACT: Two remains of the head region of the Late Jurassic marine crocodile *Steneosaurus brevirostris* Owen, 1842 are described from the Kimmeridgian of the Langenberg near Oker, Lower Saxony, Germany. They consist of fragments of a rostrum and a lower jaw (mandible) and represent the first record of parts of the head from this locality. A comparison with similar materials of the nearly contemporary *Steneosaurus jugleri* (V. Meyer, 1845) and *St. picteti* (De Tribolet, 1873) suggest that the latter two species are synonymous with *St. brevirostris*.

Key words: Crocodylomorpha, Neosuchia, *Steneosaurus brevirostris*, Late Jurassic, Kimmeridgian, Oker, Lower Saxony, northwestern Germany.

INTRODUCTION

As already documented by KARL *et al.* (2006) in their compilation on Late Jurassic and Early Cretaceous crocodiles from northwestern Germany, *Steneosaurus* remains from the "Kimmeridge" of Oker (close to the northern slope of the Harz Mountains in Lower Saxony/Germany) were previously restricted to isolated teeth and vertebrae. In the meantime the prospecting team of the "Dinosaur Park Münchehagen" discovered and prepared the first fragmentary rostrum and a part of the lower jaw (mandible) which can be assigned to the species *Steneosaurus brevirostris* Owen, 1842.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The geology and biostratigraphy as well as the history of quarrying in the Langenberg section have already been published in detail by KARL *et al.* (2006). Therefore, here we only need to repeat the most important data:

The large quarry of the "Rohstoffbetriebe Oker GmbH & Co" is situated at the western slope of the Langenberg, between Oker and Schlewecke. According to FISCHER (1991), it exposes a nearly 200 m 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 (see figure 1). 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).

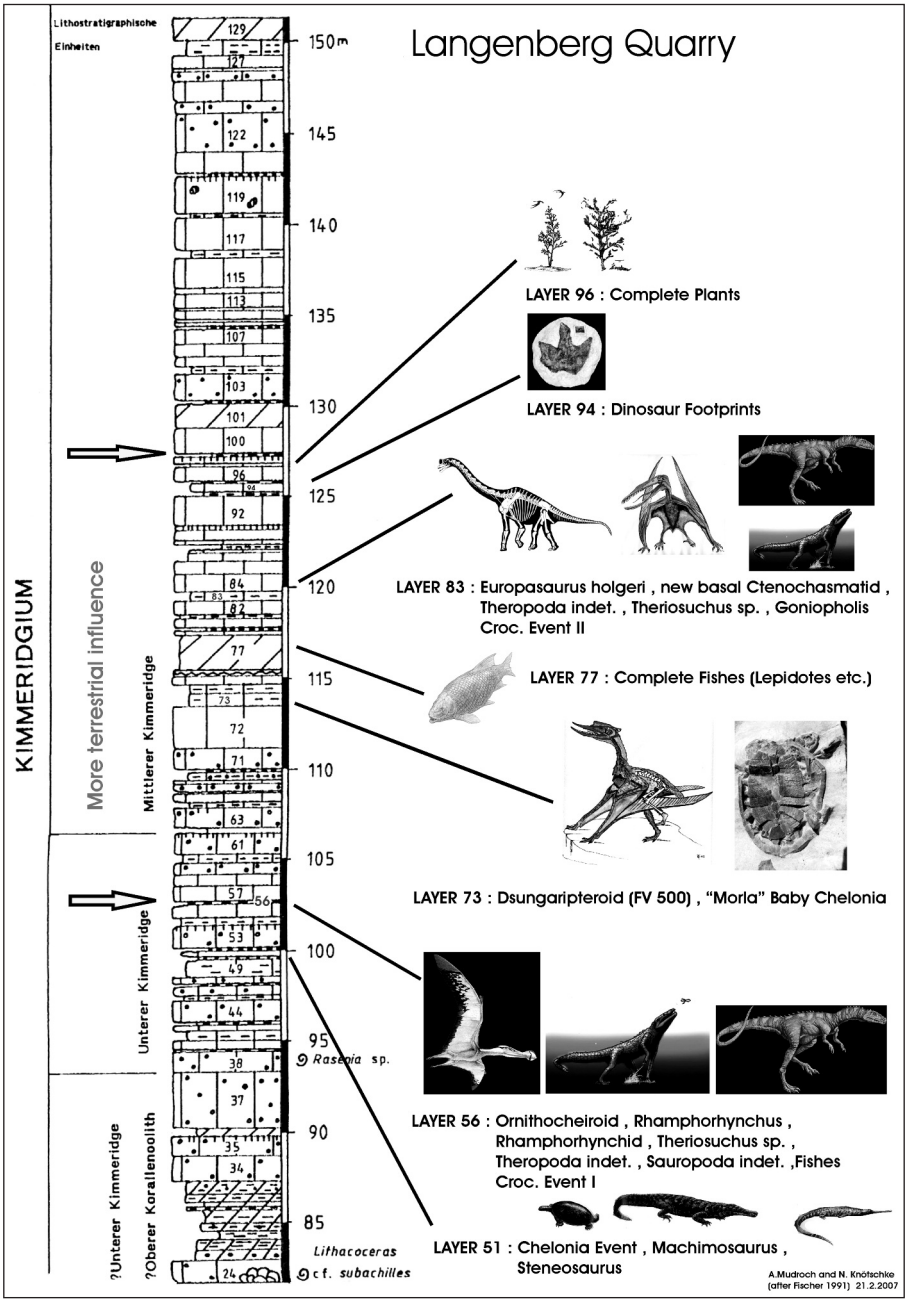


Figure 1. The Kimmeridgian part of the Langenberg section of Oker, Lower Saxony, northwestern Germany, prepared by Mudroch & Knötschke, using basic data published by FISCHER *(1991).*

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", "Northern Border Fault of the Harz Mountains"). 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).

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 (SANDER *et al.*, 2006). Other vertebrate fossils (mainly fishes, but also crocodiles, turtles, etc.) are present; more recently, FASTNACHT (2005) presented a detailed description of a dsungaripterid pterosaur and KARL *et al.* (2007) for the plesiochelid and hylaeochelid turtles.

In the meantime a team of palaeontologists jointly with the "Dinosaur Park Muenchehagen" ("Dinosaurier-Freilichtmuseum 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 Muenchehagen".

MATERIALS

The specimens described in the present contribution are deposited in the collections of the "Dinosaur Park Muenchehagen" ("Dinosaurier-Freilichtmuseum Münchehagen"), numbers DFMMh FV 870 and DFMMh FV 878.

SYSTEMATIC PALEONTOLOGY

Legion Archosauromorpha von Huene, 1946

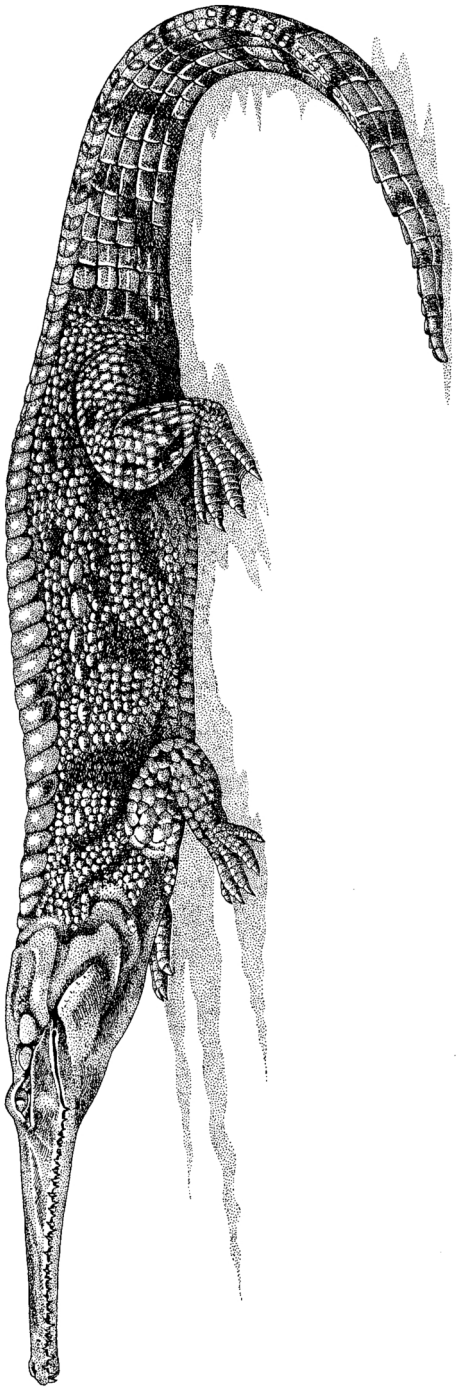


Figure 2. Life reconstruction of Steneosaurus *sp.; length of the animal = approximately 4,8 m. Drawing: Elke Gröning, from* Karl *et al. (2006).*

Superorder Crocodylomorpha Walker, 1968

Order Neosuchia Benton & Clark, 1988

Suborder Thalattosuchia emend. Fraas, 1901

Family Teleosauridae Geoffroy Saint-Hilaire, 1831

Subfamily Teleosaurinae Geoffroy Saint-Hilaire, 1831 (sensu Lydekker, 1887)

Genus Steneosaurus Geoffroy Saint-Hilaire, 1825

TYPE SPECIES: "Crocodile de Quilly" Cuvier, 1824 = *Steneosaurus megistorhynchus* (Deslongchamps, 1866) (fide DESLONGCHAMPS, 1866; LYDEKKER, 1888; KUHN, 1936).

NOMENCLATURAL REMARKS (based mainly on STEEL, 1973): When establishing *Steneosaurus* "pour les reptiles fossils connus jusqu'à ce jour sous le nom de Gavials d'Honfleur", GEOFFROY SAINT-HILAIRE (1825) proposed two species, *Steneosaurus rostro-major* [correct spelling according to ICZN, article 32.5.2.3.: *St. rostromajor*] and *Steneosaurus rostro-minor* [correct spelling: *St. rostrominor*], the former being CUVIER's "gavial à museau plus allongé" and the latter his "gavial à museau plus court". However none of these two species is appropriately defined. In fact, *St. rostrominor* belongs to *Metriorhynchus geoffroy* V. Meyer, 1832, and thus to the type species of a different genus. Furthermore, CUVIER's "gavial à museau plus allongé" (and thus *Steneosaurus rostromajor*) is unfortunately based upon a combination of two species: *Steneosaurus edwardsi* (Deslongchamps, 1866) [snout; Early Oxfordian] and *Metriorhynchus superciliosus* (Deslongchamps, 1866) [skull; Oxfordian]. The species name *Steneosaurus megistorhynchus* was attributed to GEOFFROY SAINT-HILAIRE by DESLONGCHAMPS (1866) who subsequently (1869) reiterated his opinion that *Steneosaurus megistorhynchus* should replace the doubtful *St. rostromajor*, and both LYDEKKER (1888) and KUHN (1936) accepted *St. megistorhynchus*.

But this discussion does not really dissolve the nomenclatural problem because it neglects that only after a definite selection of a type specimen (snout or skull) of *St. rostromajor* it could be decided whether it is appropriate for a clear definition of this species. If the latter appears to be true, *St. rostromajor* could become either the older synonym of *Steneosaurus edwardsi* or *Metriorhynchus superciliosus*. In the former case *St. megistorhynchus*, in the latter case *Metriorhynchus superciliosus* will be a younger synonym of *St. rostromajor*. To our present knowledge we cannot decide whether a type specimen of *St. rostromajor* has already been selected or not. If not, this procedure would be a first step in a revision of the original materials of the species names discussed.

CHARACTERS (from STEEL, 1973: 26-28): *Steneosaurus* is characterized by a snout varying in relative length and of more or less rounded cross-section anteriorly, becoming flattened in the posterior part. The obliquely truncated

premaxillae are markedly deflected at their expanded extremity and each contains 4 or 5 teeth. Orbit of regular shape and upwardly directed, but frequently more laterally placed than in *Teleosaurus*. A small antorbital fenestra is present and the postorbital bar is approximately at right angles to the long axis of the skull so that the posterior border of the orbit is situated well in advance of the supratemporal opening. Infraorbital bar deep and upper temporal arcade lacking sculpture. Frontal bone small and skull table greatly flattened and isodiametric with the length acceeding the breadth. The supratemporal fenestrae are very large, elongate and of trapezoid shape with rounded angles. In comparison with the orbits they are of greater size than in *Teleosaurus*. Alveolar border without undulations and the palatal vacuities are large and the pterygoids bear prominent lateral processes. Internal nares rounded and situated in advance of the temporal fenestrae, they are rather smaller than in *Teleosaurus*. Teeth slanting outwards at an angle and displaying two longitudinal carinae. Number of caudal vertebrae: approximately 40.

KNOWN DISTRIBUTION: Early to Late Jurassic of Europe, Early Jurassic of South America, Middle Jurassic of Madagascar, and Jurassic of Morocco (STEEL, 1973).

PALAEOECOLOGICAL REMARKS: According to BILLON-BRUYAT *et al.* (2005) *Steneosaurus* shows nearly the same range of $\delta^{18}O$ values (19,9‰ to 21,9‰) as the "fish" *Lepidotes* and other Pycnodontiformes from five collecting sites in lithographic limestone in western Europe. This fact suggests that at least these Osteichthyes were embedded in sediments close to the shore, but originally lived offshore in deeper and cooler water. *Steneosaurus* was their possible predator.

Steneosaurus brevirostris Owen, 1842

SYNONYM: *Steneosaurus* aff. *brevirostris* Owen, 1842, KARL, GRÖNING, BRAUCKMANN, SCHWARZ & KNÖTSCHKE, 2006: 69, fig. 12A.

LOCALITY AND HORIZON: For general data see chapter "Geological and stratigraphical setting". The blocks which yielded the specimens described in the present article were already broken off; thus the exact position within the sequence is not clearly known. Due to their thickness and lithology they could have had their origin perhaps in bed 53 (see figure 1).

PREVIOUS MATERIALS FROM OKER: KARL *et al.* (2006) listed fragmentary materials related to that taxon in "open nomenclature" under *Steneosaurus* aff. *brevirostris*, as for example DFMMh FV 510: neural arch of caudal vertebra; DFMMh FV 353 neural arch (?); DFMMh FV 330, DFMMh FV 281, DFMMh FV 474, DFMMh FV 334, DFMMh FV 335, DFMMh FV 609, DFMMh FV 327(9.3.2001), DFMMh FV 611, DFMMh FV 615(1999), DFMMh FV 616, DFMMh FV 618, DFMMh FV 619, DFMMh FV 621, DFMMh FV 622, DFMMh FV 272-275, DFMMh FV 392: teeth (complete and fragmentary); MG 865 trunk vertebra (Museum Goslar).

MAIN CHARACTERS (based on the teeth): Teeth very long, caniniform, without lateral crests, but with some lateral striae.

MORPHOLOGY OF THE NEW SPECIMENS

(1) Fragment of the rostrum: dfmmh fv 870

Measurements (in mm): Preserved length = 73; preserved width = 16. Width of external nasal opening = 8. Length of teeth-bearing sections: left row = 71; right row = 61.

Preservation: Fragment of rostrum threedimensionally preserved. Several transversal fractures: Rostrum therefore dorsally with slight concave vaulting. Posterior part broken off. Anterior part fractured, only left side of premaxilla largely present.

Dentition: Not a single tooth completely preserved, 4 teeth of the right rostral side broken off within their alveoles. Left row: 3 alveoles within the premaxilla, 9 alveoles within the maxilla. Right row: 1 alveole, flanked by 2 fragmentary replacementary teeth at the posterior end of the premaxilla; 8 alveoles within the maxilla.

Fragment of the lower jaw: dfmmh fv 878

Measurements (in mm): Preserved length = 184. Length of preserved mandibular symphysis = 51. Length of complete preserved postsymphysal right branch of mandible = 130. Length of intramandibular window: 47. Length of preserved dental = 83. Length of surangular = 117. Length of angular = 109. Height of right posterior branch of mandible at the posterior end of intramandibular window = 16. Length of teeth-bearing sections: left row = 66; right row = 60.

Preservation: Excellently three dimensional preservation. Only few fractures. At least the anterior two thirds of mandibular symphysis broken off. Right posterior branch of mandible complete, left posterior branch only preserved by the anterior third.

Angle between the two postsymphysal branches of the mandible = 50º.

Dentition: Left row: 12 alveoles, 2., 4., 6., 7., 8., 10. and 12. alveole (seen from the anterior part) with teeth (7., 8. and 10. tooth completely preserved). Right row: 11 alveoles, (from anterior) 1., 2., 4., 6. and 8. alveole with teeth (1. tooth completely preserved and with a length of 3,8 mm the largest one).

CHARACTER ANALYSIS

(1) Snout short [0] or snout long [1];

(2) Snout anteriorly flattened [0] or more or less rounded in cross section [1];

(3) Teeth slender, with sharply pointed crowns [0] or blunt with rounded crowns [1];

(4) Mandibular symphysis shorter than 50% of length of jaw [0] or of same length or more than 50% [1];

(5) Nares of premaxillars directing anteriorly [0] or dorsally [1].

DATAMATRIX

Steneosaurus leedsi 10110, *Steneosaurus durobrivensis* 01000, *Steneosaurus brevirostris* 00010, *Steneosaurus jugleri* 00010, Langenberg 00010.

OUTFILE BY DOLMOVE (Joseph FELSENSTEIN)

(Langenberg, (*Steneosaurus jugleri*, (*Steneosaurus brevirostris*, (*Steneosaurus durobrivensis*, *Steneosaurus leedsi*))));

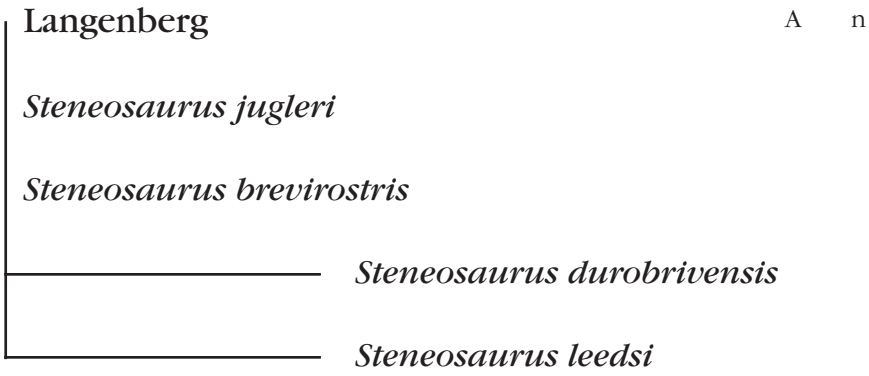
OUTFILE BY PARS (Joseph FELSENSTEIN)

Discrete character parsimony algorithm, version 3.6a3, shows 1 common tree:

(Langenberg: 0.00, *Steneosaurus jugleri*: 0.00, *Steneosaurus brevirostris*: 0.00, *Steneosaurus durobrivensis*: 2.00, *Steneosaurus leedsi*: 2.00);

TREE BY TREEVIEW (Roderic Page)

DISCUSSION



extensive list of *Steneosaurus* species was provided by KREBS (1962). Similar and closely related species have been documented from several Jurassic sections in Germany and Switzerland.

A comparison of all the previously distinguished Jurassic species of *Steneosaurus* suggests that the total number seems to be too large. Most of them have been based upon incomparable fragmentary materials. Therefore we do not wonder that the number has been strongly reduced after revisions by modern methods. For example, WESTPHAL (1961, 1962) minimized the number of Late Liassic crocodiles from Germany and Great Britain to only five species in three genera: *Pelagosaurus typus*, *Platysuchus multiscrobiculatus*, *Steneosaurus bollensis*, *Steneosaurus brevior* and *Steneosaurus gracilirostris*. WINCIERZ (1967) recorded *Steneosaurus* aff. *bollensis* from the Late Liassic of Hondelage near Brunswick in the Subhercynian Basin.

ADAMS-TRESMAN (1987) analyzed the Middle Jurassic (Callovian) Teleosauridae *Steneosaurus* and *Mycterosuchus* of Central England by using 12 cranial measurements and 8 quotients and could restrict the number to two clearly distinct species: *Steneosaurus leedsi* Andrews, 1909 and *St. durobrivensis* Andrews, 1909.

The first species is characterized by: Elongated, slender rostrum; preorbital length 72% or more of total length of skull. Considerable variation in degree of separation of nasals and premaxillae; this distance accounts for 45-62% of length of rostrum. Teeth slender, with sharply pointed crowns, forty or more in each maxilla. Mandibular symphysis c. 58% of length of jaw.

The second species differs by: Short rostrum; preorbital length c. 60% or less of total length of skull. Nasals and premaxillae separated by 36-56% of total length of rostrum. Teeth blunt, rounded at tips; crowns become increasingly blunt as size of skull increases; twenty-eigth to thirty teeth in each maxilla; mandibular symphysis c. 40% of length of jaw.

More interesting for comparison with the present materials of *St. brevirostris* are the following nearly contemporaneous Late Jurassic European species [in brackets: the material on which the species are based]:

1. *Steneosaurus blumenbachi* Deslongchamps, 1868 [upper jaw segment];

2. *Steneosaurus bouchardi* Sauvage, 1872 [incomplete skull, lower jaw, vertebrae, dermal plates, teeth];

3. *Steneosaurus jugleri* (V. Meyer, 1845) [teeth, vertebrae];

4. *Steneosaurus megarhinus* (Hulke, 1871) [slender rostrum];

5. *Steneosaurus morinicus* Sauvage, 1872 [lower jaw fragment, 2 vertebrae];

6. *Steneosaurus picteti* de Tribolet, 1873 [vertebrae, ribs, dermal plates, teeth];

7. *Steneosaurus recurvirostris* Lennier, 1889 [maxillary portion of upper jaw, imperfect lower jaw].

Plate 1. Steneosaurus brevirostris *Owen, 1842, FV 870, fragment of the rostrum. 1 = palatinal view, 2 = lateral view of right side, 3 = dorsal view, 4 = lateral view of left side; scale bar 3 cm.*

This list clearly shows that the diagnostic characters of certain distinguished species are based upon completely different parts of the skeleton and are therefore not comparable. Furthermore, the intraspecific variation in the Late Jurassic species of *Steneosaurus* is still poorly known.

As shown above, *Steneosaurus jugleri* (V. Meyer, 1845) [originally described under the generic name *Sericodon*] was at first only based upon teeth from the "Kimmeridge" (instead of "Portlandian" as incorrectly indicated by STEEL 1973: 29) of the Lindener Berg in Hannover (Lower Saxony, northwestern Germany) and from the Tithonian ("Portlandien") of Solothurn (northwestern Switzerland). SELENKA (1867) added vertebrae and parts of the head [nearly complete skull, rostrum, fragmentary lower jaw] from the Lindener Berg to the same species which seems to be identical with *St. brevirostris*.

Steneosaurus picteti (De Tribolet, 1873) was originally described from the Tithonian ("Portlandien") of Neuchâtel, western Switzerland, based on vertebrae, ribs, dermal plates, and teeth. V. HUENE (1926) allocated to the same species materials consisting of lower jaws, vertebrae, occiput, teeth and a femur from the Tithonian ("Portlandian") of Solothurn, too. The lower jaw (and thus the only comparable material) differs only minimally from the Langenberg specimen and from the Hannover materials grouped by SELENKA (1867) with *St. jugleri*. Since both species, *St. picteti* and *St. jugleri*, seem to be associated in Switzerland, we suppose that the slight differences between them are only caused by intraspecific variation which has not yet been studied in detail.

The only further species of the same stratigraphical age ("Kimmeridge") in a similar facies and with comparable parts of the head (an imperfect skull and lower jaw) is *Steneosaurus brevirostris* Owen, 1842, as described from the Late Jurassic (Kimmeridgian) of Shotover in England. It is therefore directly comparable with both, the new specimens from Oker, and with *St. jugleri* (at least the Hannover specimens). Because *Steneosaurus jugleri* and even *St. picteti* are extremely similar, we cannot exclude that they are junior synonyms of *Steneosaurus brevirostris*.

Therefore we now prefer to group the Oker specimens with *Steneosaurus brevirostris*.

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Plate 2. Steneosaurus brevirostris *Owen, 1842, FV 878, fragment of the lower jaw (mandible). 1 = ventral view, 2 = dorsal view, 3 = lateral view of left side, 4 = lateral view of right side, 5 = frontal view; scale bar 3 cm.*

& CB want to express their sincerest thanks to the late Professor Dr. Bernard Krebs (1934-2001) for inspiring us during his teaching activities at the Free University of Berlin and his most helpful and exact data on *Steneosaurus* species published in his contribution of 1962.

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