

New remains of *Machimosaurus hugii* von Meyer, 1837 (Crocodylia, Thalattosuchia) from the Kimmeridgian of Germany

Jeremy E. Martin^{*, 1} and Peggy Vincent²

¹ School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, United Kingdom.

E-mail: j.e.martin@bristol.ac.uk

² Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany. E-mail: pvincent@mnhn.fr

Abstract

Received 16 August 2012

Accepted 12 March 2013

Published 5 August 2013

Key Words

Crocodylia

Germany

Kimmeridgian

Machimosaurus

Thalattosuchia

The fourth complete skull of the marine crocodylian *Machimosaurus* von Meyer, 1837 is hereby described together with an associated complete mandible and disarticulated postcranial elements from the Kimmeridgian of Neuffen, Germany. Although the genus has been described fairly recently on the basis of two nearly complete skulls, their state of preservation did not allow a thorough examination of the entire skull anatomy. Here, we add new information with the description of nicely preserved cranial and mandibular elements of a single individual attributable to *Machimosaurus hugii* von Meyer, 1837. The diagnosis is updated for the genus and for the species *M. hugii* and challenges the validity of the second species *M. mosae* (Liénard, 1876). Moreover, previous assumption that *Steneosaurus obtusidens* Andrews, 1913 is a junior synonym of *Machimosaurus hugii* is not supported by our observations. Notably, *M. hugii* differs from *S. obtusidens* by a lower tooth count, the morphology of the dentition, the shape of the supratemporal fenestrae and the absence of an antorbital fenestra. Comparative anatomy and a phylogenetic analysis show that *Machimosaurus* is more closely related to the genus *Steneosaurus* than to *Teleosaurus cadomensis* (Lamouroux, 1820).

Introduction

The holotype of the thalattosuchian *Machimosaurus hugii* von Meyer, 1837 from the Lower Kimmeridgian strata of Soleure, Switzerland has been erected on the basis of teeth. Due to their characteristic morphology bearing a set of pronounced vertical ridges on the enamel surface, the genus *Machimosaurus* von Meyer, 1837 is easily recognizable in Late Jurassic strata of Europe (Sauvage & Liénard 1879; Krebs 1967, 1968; Buffetaut 1982; Hua et al. 1993; Hua 1999; Karl et al. 2006). However, only three relatively complete specimens have been reported so far. *Machimosaurus mosae* (Liénard, 1876, unpublished work) from the Kimmeridgian near Verdun, Meuse, France was originally described on fairly complete material (Sauvage & Liénard 1879), but has since been lost (Hua 1999). Krebs (1967, 1968) also described skull fragments he attributed to *Machimosaurus hugii* from the Kimmeridgian of Guimarota, Portugal and attempted an accurate recon-

struction of the skull. Buffetaut (1982) described the first complete skull attributable to the type species, *Machimosaurus hugii* from the Kimmeridgian of Montmerle, Ain, France. The third nearly complete specimen (BHN2R 1100) has been referred to *Machimosaurus mosae* and was found in the Kimmeridgian of Pas-de-Calais, France (Hua 1999). Although relatively complete, the two remaining specimens bear damage or in the case of *M. hugii* from Montmerle, the mandible in occlusion precludes any palatal observation to the exception of the anterior part of the rostrum. Therefore, many details of the anatomy of *Machimosaurus* remain unknown.

The genus *Machimosaurus* is restricted to the Late Jurassic, the oldest record being possibly represented by fragmentary remains from the Upper Oxfordian strata near Hannover, Germany (Krebs 1968). Although a few thalattosuchians such as *Peipehsuchus teleorhinus* Young, 1948 from the Late Jurassic deposits of China and a yet undescribed taxon from Late Jurassic strata

* Corresponding author

of Thailand were reported from strictly continental deposits (Martin et al. 2011), *Machimosaurus* from the Portuguese lignite deposits of the Guimarota coal mine represents a rare occurrence in a brackish environment (Krebs 1967, 1968). While *Machimosaurus* remains have mostly been discovered in European deposits, a single record exists from the Late Jurassic strata of Ethiopia (Bardet & Hua 1996).

Here, we describe one additional specimen referable to *Machimosaurus hugii* from the Kimmeridgian of Baden-Württemberg in southern Germany. The specimen consists of a complete skull and mandible with associated postcranial elements. The state of preservation and the disarticulated nature of the skeleton render possible observations of yet unknown areas and provide new anatomical information about the genus *Machimosaurus*.

Abbreviations

Anatomical Abbreviations. an, angular; ar, articular; bo, basioccipital; bsph, basisphenoid; ca, caudal vertebra; ch, choana; cqg, cranioquadrate groove; den, dentary; dep, depression; ec, ectopterygoid; eo, exoccipital; en, external nares; fic, foramen intermandibularis caudalis; fo, foramen ovale; fr, frontal; if, incisive foramen; j, jugal; lac, lacrimal; ltf, lower temporal fenestra; meu, median Eustachian foramen;

mmf, medial mandibular fossa; mx, maxilla; n, nasal; oc, occipital condyle; of, occipital foramen; on, otic notch; or, orbit; otf, orbito-temporal foramen; p, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; po, postorbital; pre, prearticular; pro, prootic; psan, surangular process; pt, pterygoid; prf, prefrontal; q, quadrate; qj, quadrato-jugal; san, surangular; so, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; sqs, squamosal flat surface; stf, supratemporal fenestra; XII, cranial nerve twelve.

Institutional Abbreviations. BHN2R, Muséum d'Histoire Naturelle de Boulogne-sur-Mer, France; M.J., Serviços Geológicos, Lisbon, Portugal; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMSS, Staatliche Naturhistorische Sammlungen, Dresden, Germany.

Systematic paleontology

Order **Crocodylia** Gmelin, 1789

Suborder **Thalattosuchia** Fraas, 1901

Family **Teleosauridae** Geoffroy Saint-Hilaire, 1831

Genus ***Machimosaurus*** von Meyer, 1837

Machimosaurus hugii von Meyer, 1837

Figures 1–9

Holotype. SMSS Nr. 96, isolated teeth from Soleure (Switzerland).

Emended diagnosis. Teleosaurid crocodylian with a robustly built longirostrine skull and possessing blunt conical teeth bearing numer-

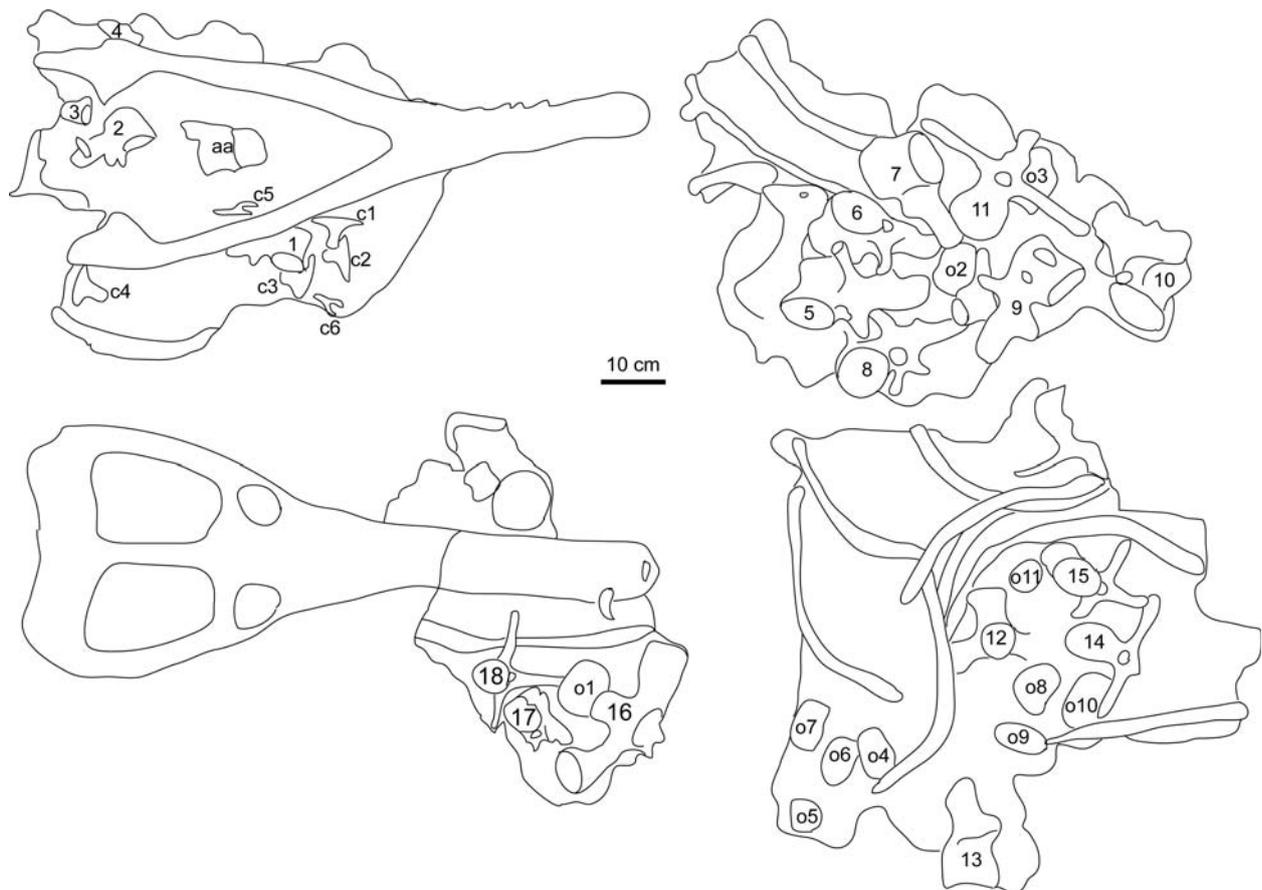


Figure 1. Sketch of the four blocks containing the skeletal elements of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen. Dimensions are provided in Tables 3, 4 and 5 for the bones labeled with numbers (vertebrae), with the letter 'o' (osteoderms) and with the letter 'c' (cervical ribs).

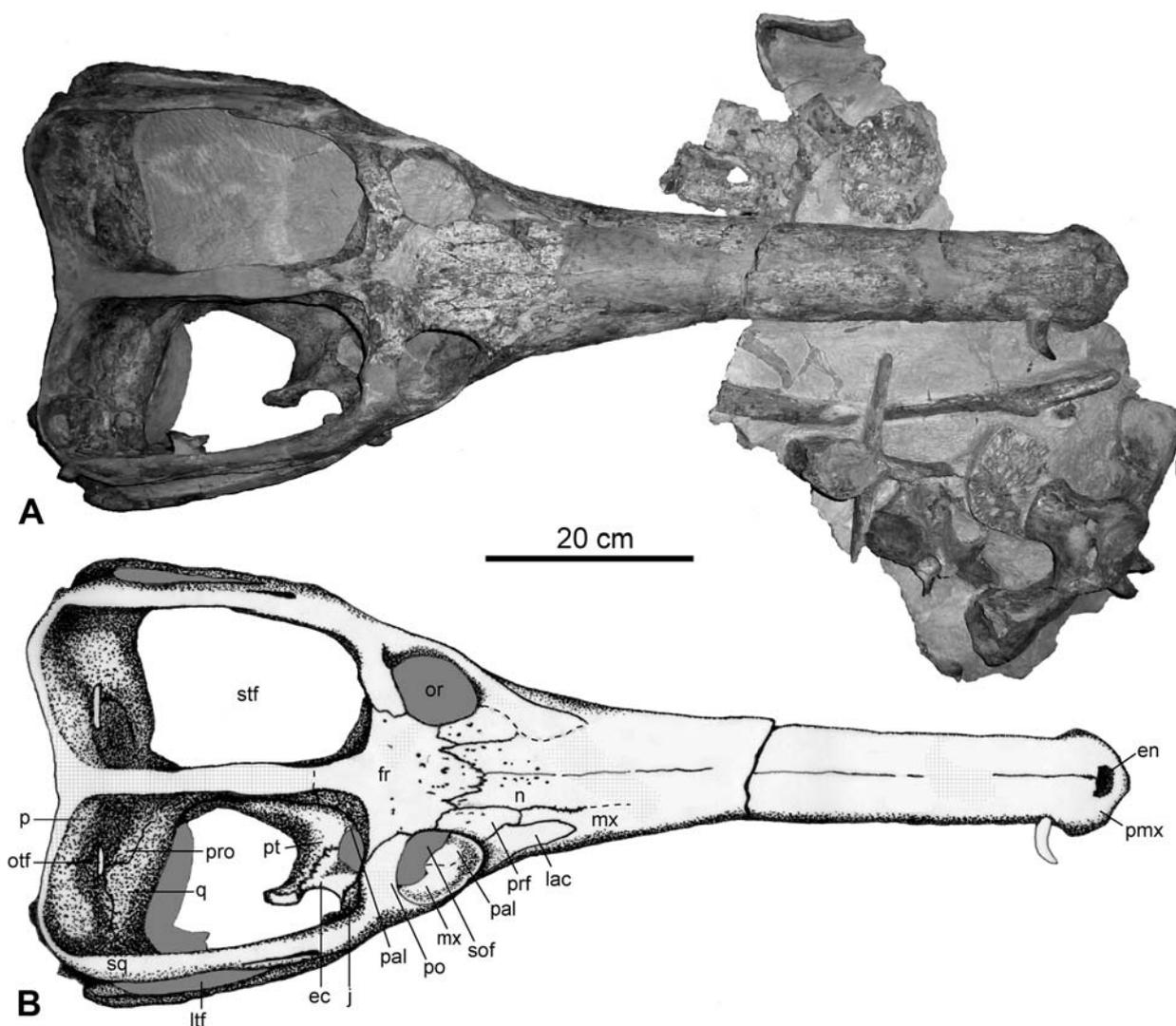


Figure 2. Photograph (A) and interpretive drawing (B) of the dorsal side of the skull of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. Cross-hatching indicates restored area.

ous vertical and well-marked striae on the surface of the enamel; carinae barely visible but affecting both the dentine and the enamel. Differs from other teleosauroids by the lack of an antorbital fenestra and a comparatively smaller number of alveoli (22 maxillary and 18–22 dentary alveoli).

Referred specimens. SMNS 91415, a complete skull and jaws with associated parts of the postcranial skeleton, Kimmeridgian of Neuffen, Germany; no number, Musée de Verdun, France, a mandible from the Kimmeridgian of Haudainville, Meuse, France (Basse de Menorval 1961–62; Maubeuge 1963, 1968); M.J. 501.155, skull fragments, teeth and associated postcranial elements from the Kimmeridgian of Guimarota, Leiria, Portugal (Krebs 1967, 1968); no number, Musée de l'Ain, Bourg-en-Bresse, complete skull with mandible and associated vertebrae from the Kimmeridgian of Montmerle, Ain, France (Buffetaut 1982); Lafaurie Private Collection, a mandible and associated postcranial elements from the Kimmeridgian of Gigouzac, Lot, France (Hantzpergue et al. 1982); BHN2R 1100, a complete skeleton from the Kimmeridgian of Ambleteuse, Pas-de-Calais, France (Hua 1999).

Locality and age. Am Hörnle Quarry, Neuffen, Baden-Württemberg, Germany. *Ataxioceras hypselocyclum* Zone (Weisser Jura γ 2), Lower Kimmeridgian, Late Jurassic (see Simon et al. 2011). Specimen found by E. Schlipf in 1974 and prepared by P. Riederle.

Description

The skeleton of SMNS 91415 is disarticulated and incomplete (Fig. 1). The skeletal elements are spread on a surface covering approximately 4 m² and are now prepared as four large blocks of limestone. The bones are therefore partially covered by the sediment on one face. SMNS 91415 comprises a complete skull (Figs 2–4), complete mandibular rami (Fig. 5), a portion of the shoulder girdle, 18 vertebrae, 19 ribs and 11 osteoderms (Fig. 9).

Skull

General description and openings. Skull and alveolar dimensions are reported in Tables 1 and 2 respectively. The skull possesses a long rostrum, which is straight and narrow with parallel edges and is slightly expanded at the tip. It is longer than the orbital and skull table region. Ornamentation is well developed between the orbits. Elsewhere, the rostrum displays shallow longitu-

Table 1. Dimensions of the skull and mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from Neuffen, Germany.

Characteristics	SMNS 91415 (cm)
Length of skull (from tip of premaxilla to basioccipital condyle)	93.5
Maximal width of skull (across quadrates)	39.7
Length of snout (in front of orbits to premaxillae)	54.7
Maximal width of snout at tip of nasals	10.4
Maximal length of naris (fossa inc.)	2.7
Maximal width of naris (fossa inc.)	6
Diameter of orbit	6 (left) 6 (right)
Width between medial hemicondyles	21
Interorbital width	8.4
Length of cranial table (through center of supratemporal fenestrae)	28.4
Width of cranial table (across centers of supratemporal fenestrae)	32.8
Maximal length of supratemporal fenestra	26 (left)
Maximal width of supratemporal fenestra	13.6 (left)
Interfenestral width	2
Length of ventral border of infratemporal fenestra	19.5
Length of incisive foramen	2
Width of incisive foramen	0.3
Length of long axis of suborbital fenestra	10.5 (left)
Length of short axis of suborbital fenestra	4.6 (left)
Interfenestral width of palatines	4.8 (left)
Width of choanae	8 x 8
Width across basioccipital ventral surface	8.5
Occipital condyle width	4
Mandible length (parallel to symphysis)	95.4
Symphysis length	48.6
External mandibular fenestra length	19.5 (left)
External mandibular fenestra height	5.2 (right)
Glenoid fossa width	8.8 (right)
Retroarticular process length	12.8 (left)
Width at level of 13th dentary tooth	9.5

dinal furrows but the bones of the skull table are smooth. The skull underwent restoration along a fracture in the anterior region of the snout and on the dorsal surface of the posterior region of the snout. The dorsal surface of the interfenestral bar is completely restored, as is the area for the supraoccipital. The anterior corner of the left orbit, most of the right postorbital, and a portion of the left postorbital are also restored. Fractures on the occipital surface have been restored as well as most of the ventral surface of the basisphenoid. The orbits are perfectly circular. Their diameter is slightly smaller than the width of the rostrum. In dorsal view, the supratemporal fenestrae are anteroposteriorly stretched and more than five times larger than one orbit. From an

occipital view, the lateral arches of the skull table are positioned more ventrally than the interfenestral bar.

Only the left suborbital fenestra is completely prepared (Fig. 3). The suborbital fenestra is small with a surface area comparable to that of the choanae. The suborbital fenestra is narrower than the width of the paired palatines, is longer than wide and possesses an acute anterolateral incision. The palatine contributes to the medial margin of the suborbital fenestra and the maxilla contributes to the lateral margin of the anterolateral incision. The medial margin of the suborbital fenestra is exclusively built by the palatine and is nearly straight. The lateral margin accommodates the ectopterygoid and the maxilla. A small contribution of the pterygoid to the suborbital fenestra occurs posteriorly.

The orbitotemporal foramen is visible on both sides of the posterior wall of the supratemporal fenestrae but details of sutures are best visible from the right surface (Fig. 7C). This foramen fully faces anteriorly and is thus not visible from a dorsal view. Here, the floor of the supratemporal fossa is built by the quadrate and faces dorsally. The orbitotemporal foramen is wider than high, its floor is gently convex and its dorsal margin consists of a lamina of the squamosal and parietal. The squamosal makes the dorsal and lateral contour of the orbitotemporal foramen. The parietal makes the dorsomedial and possibly the medial contour of the foramen, but the parietal is damaged here and its contact with the prootic cannot be properly assessed. The prootic contributes to most of the ventral margin of the orbitotemporal foramen and nearly excludes the quadrate from reaching this foramen. However, the quadrate exhibits a minor participation in the ventrolateral corner of the orbitotemporal foramen.

The foramen ovale is best observed at the base of the posteromedial corner of the right supratemporal fenestra (Fig. 7C). It is large and circular and is bounded dorsally by the prootic and laterally then ventrally by the quadrate, which sends an elongate process on the dorsal surface of the pterygoid. The foramen ovale opens anteromedially as a groove. Inside of it, the laterosphenoid penetrates deeply within the foramen ovale and builds its ventral margin for the trigeminal nerve (V). The anterior basisphenoid process is difficult to discern but seems to be visible ventral to the laterosphenoid, where a longitudinal groove underlines it.

Premaxilla. The premaxilla completely surrounds the external naris. This opening almost faces anteriorly. Dorsally, it is visible as a crescent slit located at the tip of the premaxilla. It is undivided. The premaxilla possesses three alveoli. The first is separated from the second alveolus by a short diastema. The largest is the third. The premaxillary-maxilla suture is square-like in ventral view and reaches the middle of the third alveolus. Ahead of it, a slit-like incisive foramen is identifiable but filled with sediment. This foramen is longer than wide and is barely visible. The premaxillary tooth row is separated from the anterior area of the maxillary

Table 2. Alveolar dimensions (in cm) of the premaxillae, maxillae and mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from Neuffen, Germany.

skull	left tooth row: anteroposterior length	left tooth row: mediolateral length	right tooth row: anteroposterior length	right tooth row: mediolateral length
pmx 1	1.4	1.4	1.1	1
pmx 2	~1.6	~1.9	1.5	1.1
pmx 3	–	–	1.8	1.8
mx 1	–	–	~1.1	1
mx 2	–	–	1.4	1.4
mx 3	–	–	1.2	1.3
mx 4	–	–	~1.7	2
mx 5	–	–	–	–
mx 6	–	–	–	–
mx 7	–	–	–	–
mx 8	–	–	–	–
mx 9	–	–	–	–
mx 10	–	–	~1.4	?
mx 11	1.8	1.7	1.7	1.8
mx 12	1.9	~1.7	1.8	1.5
mx 13	–	–	1.5	1.5
mx 14	–	–	1.7	~1.8
mx 15	–	–	1.6	1.5
mx 16	–	–	1.7	1.6
mx 17	1.8	1.6	1.5	1.4
mx 18	1.7	1.6	1.4	1.4
mx 19	1.6	1.3	1.4	1.3
mx 20	1.4	1.2	1.2	1.2
mx 21	1.3	1.1	1.2	1.2
mx 22	1.1	0.9	1.2	1.2
mandible	left tooth row: anteroposterior length	left tooth row: mediolateral length	right tooth row: anteroposterior length	right tooth row: mediolateral length
den1	~1.5	~1.6	1.6	1.7
den2	~1.5	~1.2	1.7	1.6
den3	1.1	1.5	1.5	1.8
den4	1.8	2	1.9	2
den5	1.1	1.1	1.3	1.4
den6	~1.3	~1.4	1.3	1.3
den7	~1.5	~1.3	~1.3	~1.1
den8	~1.5	~1.4	~1.5	~1.3
den9	~1.5	~1.4	~1.5	~1.7
den10	1.6	1.6	1.8	1.6
den11	~1.7	~1.5	~1.6	~1.6
den12	~1.7	~1.5	~1.6	~1.7
den13	~1.7	~1.8	1.8	2
den14	~1.8	~1.8	2	2
den15	–	–	2	2
den16	~2	~2	–	–
den17	~1.9	~1.6	1.7	1.9
den18	~1.8	–	1.7	1.7
den19	1.8	1.6	1.6	1.7
den20	1.7	1.5	1.4	1.6
den21	1.6	1.4	1.6	1.5
den22	–	–	1.2	1.1

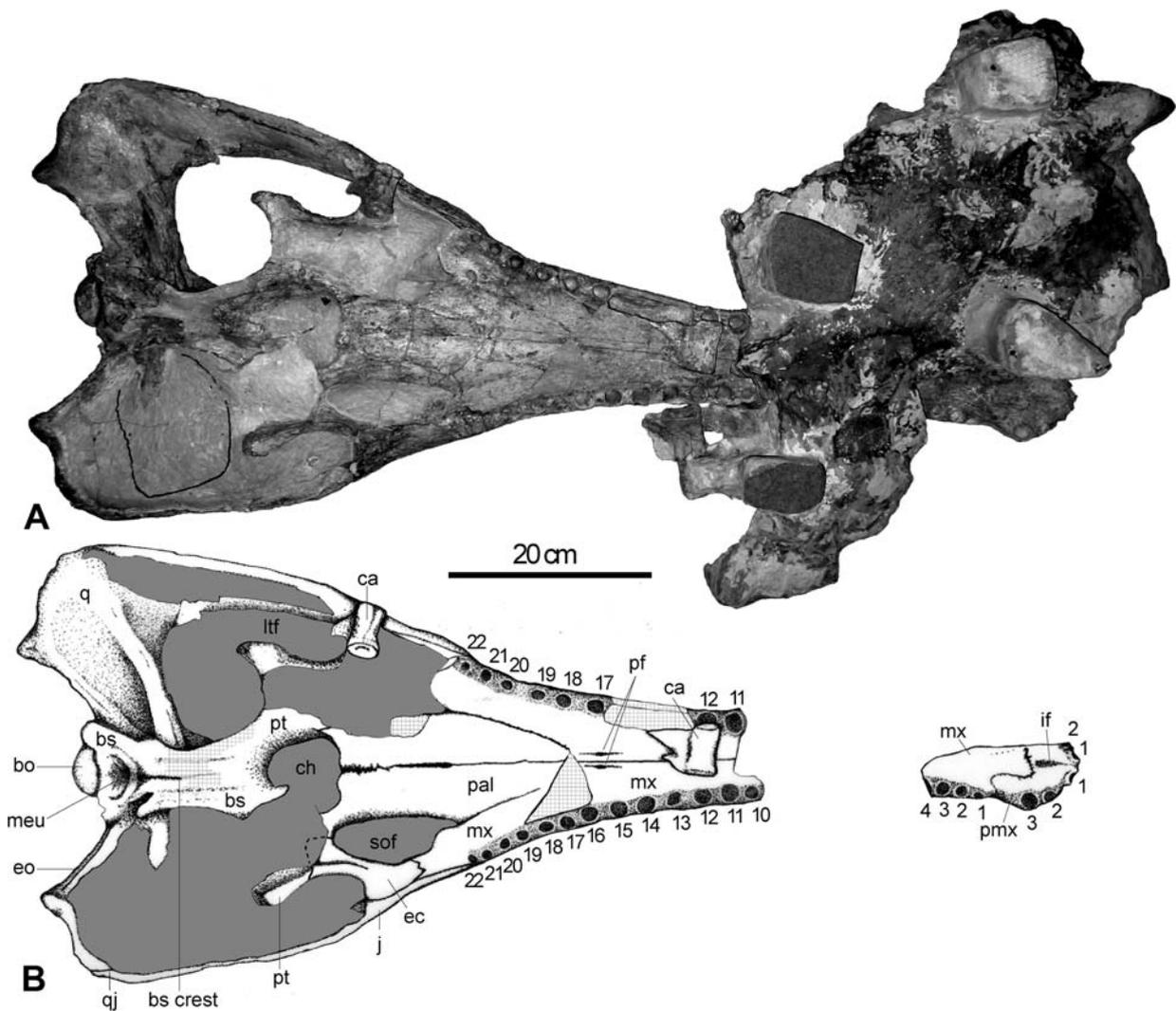


Figure 3. Photograph (A) and interpretive drawing (B) of the ventral side of the skull of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. Cross-hatching indicates restored area. Numbers refer to alveolar positions.

tooth row by a wide diastema. At this level, the last premaxillary alveolus is shifted laterally relative to the first maxillary alveolus. No notch was detected.

Maxilla. The maxillae build most of the rostrum length and their margins are parallel to each other. They are D-shaped in cross section. Relatively deep and well-spaced foramina occur on the lateral surfaces of the maxillae above the tooth row. The left maxilla allows a precise count of the number of alveoli: alveoli 1–4 are visible in ventral view. Then, sediment hides the count but it is possible to spot five alveoli in lateral view thanks to the shape of their collar. Finally, 13 alveoli are visible in ventral view. The total maxillary alveolar count is 22. The maxillary tooth row ends just in front of the anterior level of the suborbital fenestra. Posterolaterally, the maxilla sends a long and pointed process within the jugal at about mid-length of the suborbital fenestra. Here, the maxilla contacts the anterior-most tip of the ectopterygoid. The occlusal pits are located between the posterior maxillary alveoli and are shifted close to the level of the lingual alveolar margin.

Nasal. The anterior extension of the paired nasals on the rostrum cannot be assessed. However, there is no evidence of a nasal suture on the anterior portion of the rostrum, indicating that nasal and premaxilla are not in contact. The bones only preserve their posterior portion. The nasals are medially divided by the frontal. The nasals send a short posterior triangular projection between the frontals and the prefrontals.

Lacrimal. The right lacrimal is nearly complete, missing its anterior region only. However, the anterior region of the left lacrimal indicates that it reaches further anteriorly than the prefrontal and is about twice as long. On the dorsal surface of the right lacrimal, the suture with the prefrontal presents a smooth groove entering the orbit. The lacrimal makes the entire anterior margin of the orbit and is inflated above the maxillary surface. Its contact with the jugal is destroyed on both sides but the maxilla and lacrimal remain adjacent to each other below the anterior level of the orbit. Here, the jugal sends an anterior pointed process within the maxilla. The lacrimal-maxilla contact is horizontal as

observed from both sides and here, no evidence for an antorbital fenestra was detected.

Prefrontal. Both prefrontals are complete. The bone is longer than wide, half of the bone extending slightly beyond the anterior margin of the orbit. Its anteromedial tip is pointed. The bone makes the anteromedial corner of the orbit. The prefrontal is bordered medially by the nasal, although its posterior and posteromedial margins are built by the frontal. The prefrontal contacts the lacrimal on the anterior orbital margin.

Frontal. The unpaired frontal is a wide bone that makes the posteromedial margin of the orbit. This bone possesses a short pointed anterior process that terminates at the anterior level of the orbits. It sends another process between the medial end of the prefrontal and the posterolateral tip of the nasal. Posteriorly, the frontal penetrates deep in between the supratemporal fenestrae as a flat and quadrangular bar. The contact with the parietal is only visible on the left supratemporal medial wall, where a strongly interdigitated suture is visible. The anteromedial corner of the supratemporal fenestra has a nearly perpendicular angle. Here, the frontal consists of a beveled fossa that overhangs the medial margin of the supratemporal fenestra. The frontal suture with the postorbital is well discernible on both sides. This suture is not straight but its posterior end is located more laterally than its anterior end.

Postorbital. The dorsal surface of the left postorbital is nearly complete. Its anterior margin flushes with the lateral margin of the skull table. In lateral view, the postorbital sends a long and pointed posterior process beneath the squamosal. This process extends along the entire length of the lower temporal arch. Anterodorsally to the otic notch, the postorbital is pinched between the squamosal (dorsally) and the quadrate (ventrally). The right postorbital bar is best preserved. It builds the anteriormost corner of the lower temporal fenestra, is slightly concave laterally and anteriorly flushes with the postorbital. The distance between the lower temporal fenestra and the orbit is therefore considerable, being 10 cm long. Medially, the jugal builds the anteroventral portion of the lower temporal fenestra and the basal portion of the postorbital bar. The jugal excludes the ectopterygoid from the postorbital bar. The suture between the postorbital and the jugal is a straight line.

Parietal. Most of the parietal dorsal surface is not preserved. The lateral surface of the parietal is vertical between the supratemporal fenestrae. The parietal bar is thin and anteroposteriorly elongate. On the posterior margin of the supratemporal fenestra, the parietal contributes only to the dorsal margin of the orbitotemporal foramen.

Squamosal. The squamosal builds the posterolateral corner of the supratemporal fenestrae. Its shape is that of a bar with a convex dorsal margin in lateral view. The squamosal is restricted to the dorsal portion of the skull table. The posterolateral vertical corner of the squamosal bears a concave surface, located just above the quadrate margin of the otic notch (described as the

squamosal flat surface by Pol & Gasparini 2009, fig. 10). Visible on the right lateral side, an acute anterior process of the squamosal wedges within the postorbital (Figs 4C, D). The squamosal is excluded from any participation with the lower temporal fenestra by an ascending anterior process of the quadrate. More anteriorly, the dorsal margin of the lower temporal fenestra is built by the postorbital. Here, the postorbital bears on its lateral side an elongate depressed surface.

Jugal and quadratojugal. The jugal is incompletely preserved. It prevents the postorbital from contacting the ectopterygoid. The jugal makes most of the lower arcade of the lower temporal fenestra, except the posterior margin and the posterior corner, which is built by the quadratojugal. The quadratojugal reaches the posterior tip of the quadrate. In lateral view, the lateral quadrate hemicondyle is therefore not visible. The quadratojugal ascends along the posterior margin of the lower temporal fenestra.

Laterosphenoid. This bone is partly visible anterior to the foramen ovale (see above). Its anterior ascending process is not visible. The laterosphenoid appears to be damaged as seen through the right supratemporal fenestra, thus its contact with the foramen ovale is difficult to differentiate with the underlying and also damaged basisphenoid (Fig. 7C).

Quadrate. Both quadrates are preserved. The quadrate branch is short and the quadrate is therefore not visible in dorsal view. A large circular depression (diameter equals 28 mm) affects the dorsal surface of the quadrate at the level of both hemicondyles (Figs 4A, B). The medial quadrate hemicondyle is dorsoventrally deflected and projects more posteriorly than the lateral hemicondyle. Its articular surface is concave. In lateral view, the quadrate lateral hemicondyle seems to be obscured by a posterior projection of the quadratojugal. The quadrate contributes to the posterodorsal margin of the lower temporal fenestra. Dorsal to this fenestra, it expands both anteriorly and posteriorly for supporting the squamosal. The otic notch is enclosed by the quadrate both anteriorly and dorsally. The lateral quadrate hemicondyle is dorsoventrally thin but is mediolaterally expanded. Its articular surface is convex. In ventral view, the quadrate branch appears more expanded laterally than posteriorly. Ventrally, the right quadrate is almost entirely visible but is fractured. The medial contact with the pterygoid and basisphenoid is therefore unclear. Crest A of Iordansky (1964) for insertion of mandibular adductor muscles is massive and runs close to the anterior margin of the quadrate with the quadratojugal.

Exoccipital. The exoccipital builds the occipital surface of the skull. Its contact with the overlying squamosal is best observed on the right side. Medially, the exoccipital is tall above the foramen magnum. It is unknown whether it contacts the parietal but the exoccipital rapidly decreases in height laterally and ends as a robust and posteriorly projecting paroccipital lamina, which overhangs the dorsomedial corner of the cranio-

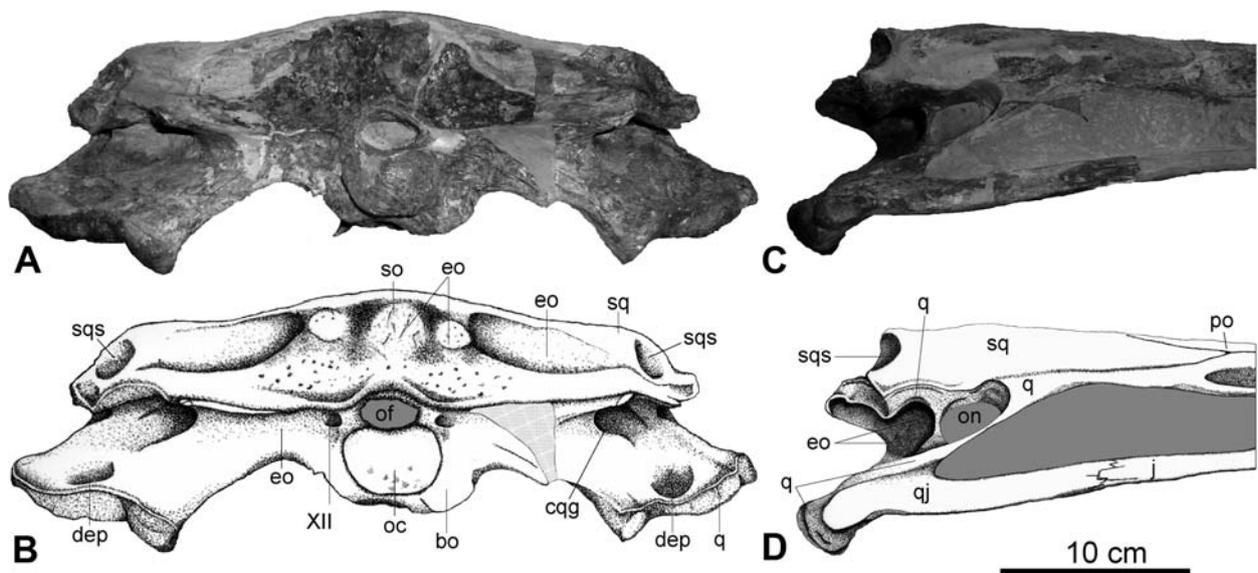


Figure 4. Photograph and interpretive drawing of the occipital region in posterior (A, B) and right lateral (C, D) views of the skull of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. Cross-hatching indicates restored area.

quadrate canal. The squamosal lateral process reaches further laterally than the lateralmost tip of the exoccipital. The cranioquadrate canal is large and opens lateroventrally below the paroccipital process. Anteriorly, and visible in lateral view, a thin vertical wall for the exoccipital separates the cranioquadrate canal from the anteriorly located otic notch. The otic notch is laterally open. Just above it, the posterodorsal process of the quadrate is overhanging the otic notch. The exoccipital sends a wide lamina over the dorsal surface of the quadrate branch, therefore hiding most of the dorsal surface of this bone except the lateralmost area, where the circular depression of the quadrate is present. The ventral margin of the exoccipital sends a lateral pointed process on the ventral branch of the quadrate, almost tapering to the level of the medial hemicondyle. The left hypoglossal foramen for cranial nerve XII is preserved. It is a large foramen (7 mm in diameter) that opens in line with the foramen magnum. More laterally at about the same level opens the smaller foramen vagus. The foramen caroticum posterius (7 mm in diameter) opens just above the exoccipital-basioccipital suture, but does not take part in it. It faces ventrally and is not visible from an occipital view.

Supraoccipital. The supraoccipital is only visible posteriorly but its suture with the exoccipital is unclear. Two spatulate vertical processes support the supraoccipital.

Basioccipital. The basioccipital builds the ventral margin of the foramen magnum. The foramen magnum is ovoid being wider than tall. The basioccipital condyle is larger than this foramen and circular in outline. The basioccipital plate is wide and dorsoventrally short. Although the left margin of the basioccipital plate appears abraded, the plate displays two distinct although weakly developed lateral pendulous protrusions. As

visible from the right side, the exoccipital-basioccipital suture is nearly horizontal.

Basisphenoid. The basisphenoid is facing ventrally and is anteroposteriorly elongate, extending anteriorly for about 8.5 cm. Its ventral surface is concave and hosts a median crest. The median Eustachian foramen opens at the basisphenoid-basioccipital suture in a large ovoid fossa (22 mm in diameter). Just anterior to the median Eustachian foramen, the posterolateral surface of the basisphenoid is excavated and ventrally connects to the pterygoid wing. However, sutures are difficult to identify. Dorsally, this excavation connects to a deep fossa, which is still encased in the sediment.

Pterygoid. The right pterygoid wing is complete but some of its ventral surface is hidden by sediment whereas most of the left wing is not preserved. The pterygoid hosts the posterolateral and posterior margins of the choanae. The posterior margin of the choanae flushes with the pterygoid. The pterygoid wing is positioned far anteriorly relative to the basioccipital. The choanae are large being nearly as wide as the palatines. The dorsal surface of the pterygoid wing is concave and the well-preserved right ventral surface seems convex (but some sediment hides this feature). The posterior outline of the pterygoid wing is concave in ventral view. The torus transiliens is small and rounded in lateral view. It expands dorsally above the wing. It is mediolaterally thin but becomes thick at its dorsal margin. The lateral margin of the torus transiliens bears a set of large foramina, which are more concentrated along the posterior edge. Medially, the pterygoid is restricted to the posteriormost corner of the suborbital fenestra.

Ectopterygoid. The ectopterygoid consists of a bent lamina that closes the lateral and posterolateral margin of the suborbital fenestra. Anteriorly, the ectopterygoid

does not reach the postorbital but connects to the jugal. These bones share a straight suture, which is parallel to the lateral margin of the skull. In ventral view, the lateral margin of the ectopterygoid has a markedly concave outline.

Palatine. The palatine is a robust bone that participates in the medial wall of the suborbital fenestra. It sends a posterior process that contributes to the anterior and anterolateral margins of the choanae. However, the choanae do not penetrate between the suborbital fenestrae. The palatine ventral surface is slightly inclined anteriorly. The medial palatine suture bears a trough, hosting an elongate foramen measuring 30 mm in length. Posteriorly, the palatine medial suture becomes grossly indented and is disjoint in the last 20 mm, just before entering the choanae. The palatine anterior process has the shape of a broad triangle and ends well ahead of the anterior margin of the suborbital fenestra

at the level of the 17th maxillary alveolus. The palatine takes part exclusively in the medial margin of the suborbital fenestra, whereas anteriorly and anterolaterally, the maxilla takes part in the suborbital fenestra.

Vomer. The vomer is not visible in the palatal region.

Mandible

General description. The mandible is complete, lacking only the posteriormost tip of the right retroarticular process (Figs 5, 6). The mandible is almost devoid of any ornamentation, except in the anterior region of the dentary where foramina similar to those of the maxilla occur. The external mandibular fenestra is extremely large being about four times longer than tall and covering most of the postdentary surface, it lies far anterior to the glenoid fossa. The medial mandibular fossa is

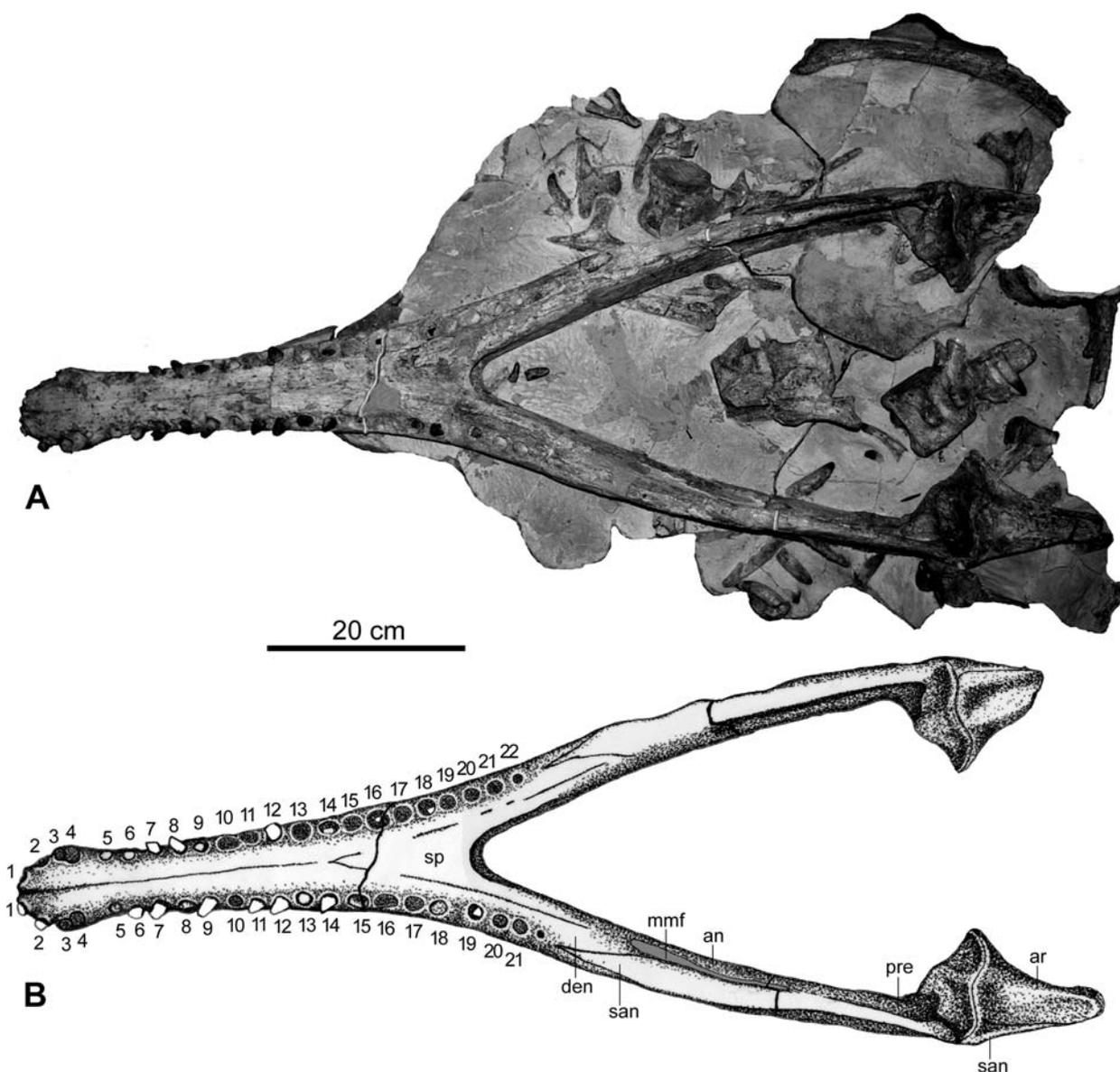


Figure 5. Photograph (A) and interpretive drawing (B) of the mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) in occlusal view, from the Kimmeridgian of Neuffen, Germany. Numbers refer to alveolar positions.

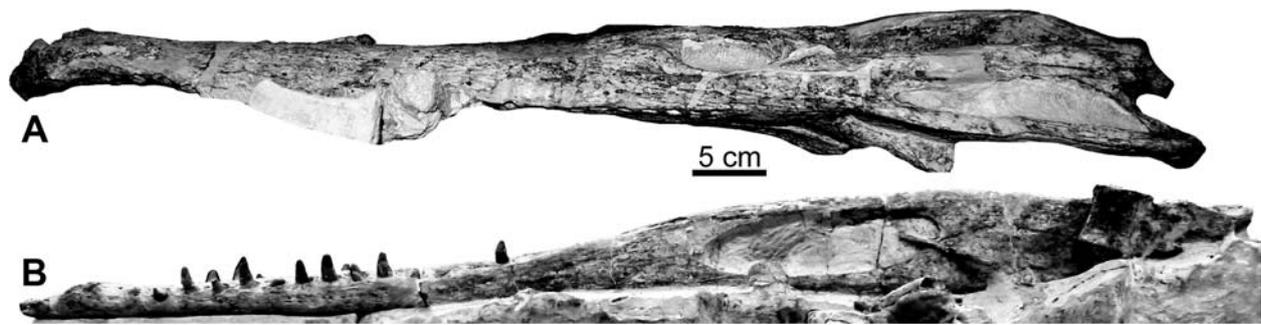


Figure 6. Left lateral views of the skull and associated mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany.

about as long as the external mandibular fenestra. It is bounded dorsally and posteriorly by the surangular, and anteriorly and ventrally by the splenial (Fig. 7B). The splenial sends a posterior process that prevents the angular to reach the medial mandibular fenestra.

Dentary. The dentary is anteriorly spatulated with a moderate lateral expansion at the level of the largest alveoli. A medial bifurcation affects the anteriormost region of the dentary medial suture. A total of 21 alveoli are present on the left dentary whereas 22 are present on the right dentary. The first two alveoli are facing anterodorsally. All subsequent alveoli are facing dorsally with a minor inclination of the tooth row. This is because the dentary is not exactly horizontal medio-laterally, but its edges are slightly inclined. The third and fourth dentary alveoli are confluent and elevated above the tooth row level (Fig. 7A). They are the largest of all the dentary alveoli. The mandibular symphysis is long and extends to the level of the 20th alveolus. The last two alveoli are positioned behind the posterior level of the symphysis. The dentary builds the anterior margin of the external mandibular fenestra and sends out two short posterior laminae, one dorsally and another ventrally along this fenestra. In front of the external mandibular fenestra, the external surface of the dentary presents a groove, anteriorly perforated by a foramen.

Splenial. The splenial has a long participation in the posterior portion of the symphysis. Anteriorly, it reaches the level of the 14th alveolus. Posterior to its contribution with the symphysis, the splenial becomes narrow. It does not take part in the medial wall of the last dentary alveoli. In the absence of a preserved coronoid, the splenial makes the anterior margin and the anterodorsal corner of the medial mandibular fossa.

Coronoid. The coronoid preserves its ventral portion only. A long lamina builds the entire ventral margin of the medial mandibular fossa and its posterior tip reaches the anterior elongate process of the articular at the posterior level of the medial mandibular fossa. Ventral to this lamina, at about midway of the medial mandibular fossa, there is a small elongate foramen. Its dorsal margin is made by the coronoid. Its ventral margin is made by the angular.

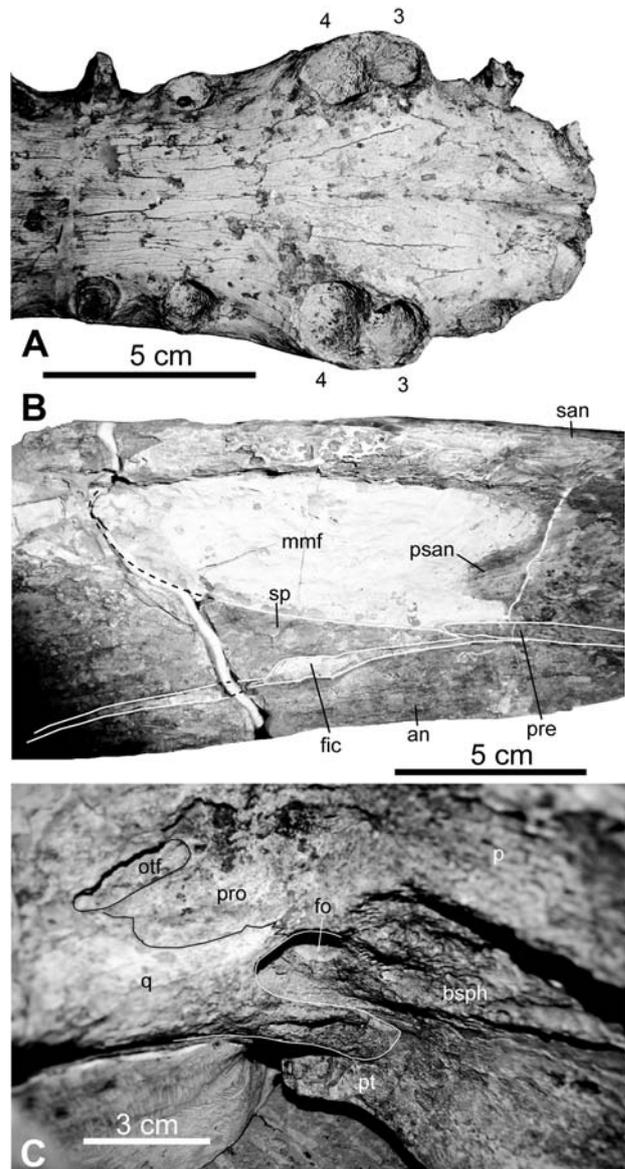


Figure 7. Selected details of anatomy of the skull and mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. **A.** Detail of the anterior portions of the dentaries in occlusal view showing the confluent alveoli 3 + 4; **B.** Sutural relationships around the right medial mandibular fossa; **C.** Organization on the postero-medial wall of the right supratemporal fenestra from an antero-lateral view.

Surangular. In its anterodorsal region, the surangular wedges between the lateral and medial surfaces of the posterior dentary and reaches what seems to be an occluded last alveolus. Posterior to the external mandibular fenestra, the angular and surangular meet along a wavy suture. Posteriorly, this suture does not end at the tip of the retroarticular process but in the middle of it. The dorsal margin of the surangular consists of a thin rod. There is no distinct enlarged surface attachment for the *M. adductor mandibulae externus superficialis* and *medius*. Medially, the surangular occupies most of the vertical space, just posterior to the medial mandibular fossa. The surangular sends an anterior rounded lamina in the medial mandibular fossa (Fig. 7B).

Angular. In lateral view, the angular contributes to the ventral and posteroventral margin of the external mandibular fenestra. Its surface is extensive when compared to the smaller surface area occupied by the surangular. The ventral surface of the angular cannot be observed. In medial view, the angular is restricted to the ventral margin of the mandible. It consists of an elongated lamina extending from the anterior level of the medial mandibular fossa back to the foot of the articular. Here, the angular does not contact the surangular because the anterior process of the articular projects anteriorly and separates the angular from the surangular. From a dorsal view, the angular is more medially shifted than any other bones at the base of the mandible. However, the absence of any major anchor for musculature is noticeable.

Articular. The articular is fixed to the posteromedial end of the mandible. The glenoid fossa faces anterodorsally, the medial one being twice as large as the lateral one. The retroarticular process is elongate and somewhat posterodorsally concave. It has a triangular shape in dorsal view. Its medial margin has an excavated profile and ends with a strong medial projection, located posteromedially from the glenoid fossa. The retroarticular process bears a strong anteroposterior keel on its dorsal surface separating the lateral and medial grooves. The foramen aereum is large and opens on the brow behind the medial glenoid fossa.

The foot of the articular is short; its medial surface bears an ovoid depression and does not extend anteriorly.

Prearticular. A prearticular seems visible on both mandibular rami and is confined to the base of the articular on the medial side. This bone sends a thin elongate rod far anteriorly from the articular foot and eventually floors the medial mandibular fenestra. This extension of the prearticular reaches a posterior rod-like process of the splenial (Fig. 7B) and prevents the angular from reaching the medial mandibular fenestra.

Dentition. Several teeth are still encased in the mandible (Table 1) and many others are in close association to the skeleton. The dentition is homodont. Complete teeth display a robust conical morphology. The apex is rounded, even on unworn teeth. Here, the enamel surface is not smooth but presents numerous

wrinkles ('surface chagrinée' of Buffetaut 1982). The crown is circular in cross section. Several pronounced vertical striae ornate the enamel but their number is variable. A large tooth presents 17 vertical striae on its lingual surface. The anterior and posterior carinae are barely discernible from other vertical striae. The 8th left dentary tooth is broken and reveals the enamel-dentine junction in cross section. The vertical striae characterize the enamel outer surface only but do not affect the dentine. Therefore, the enamel-dentine junction is perfectly circular to the exception of the mesiodistal carinae, which originate from the underlying dentine (Figs 8A, B).

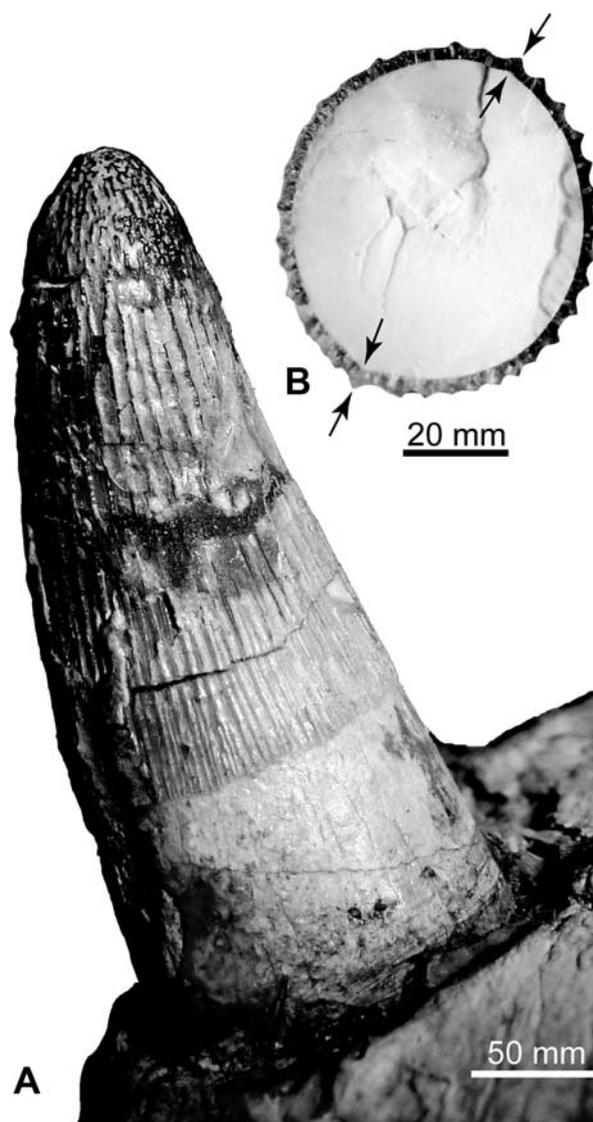


Figure 8. The dentition of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. **A.** Complete tooth from the dentary in distal view; **B.** Cross section of a broken tooth crown from the dentary with arrows pointing to the mesiodistal carinae. Note that contrary to the ornamented enamel, these carinae are also present in the dentine.

Postcranial skeleton

Measurements are listed under Tables 3, 4 and 5. Elements of the postcranial skeleton are disarticulated and randomly concentrated around the skull and mandible. Appendicular elements have not been recovered and to the exception of one coracoid, the postcranial material consists of the atlas-axis complex, 18 vertebrae, 7 cervical ribs, 12 ribs and 11 osteoderms. The neural arches are completely fused to all the centra, indicating that the specimen is an adult. All vertebrae are amphicoelous.

Atlas-Axis. The fused atlas-axis complex is well preserved and can be observed from its right side. The atlantal arch is not complete but the neural canal can partly be observed in anterior view. In lateral view, the odontoid, atlantal arches and intercentrum are not discernible because of the advanced degree of fusion. The sutures are however visible in anterior view (Figs 9C, D). The anterior surface is convex with the intercentrum making a large contribution to the ventral area. In lateral view, dia- and parapophyses occupy a considerable space. The axis is one third larger than the atlas. It possesses a very large and protruding diapophysis, which is anteroposteriorly elongated. The axis neural arch is short and gently slopes anteriorly for the length of the axis. Posteriorly, it projects beyond the margin of the centrum.

Cervical vertebrae and ribs. Other than the atlas-axis complex, 7 cervical vertebrae are preserved (e.g. Fig. 9B). The anterior and posterior margins of these vertebrae are thick, giving an hourglass shape outline to the cen-

Table 4. Dimensions (in cm) of the cervical ribs of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from Neuffen, Germany as distributed on the blocks (Figure 1).

ribs	length
C1	9
C2	8.4
C3	8.4
C4	>7.5
C5	~9.5
C6	–

Table 5. Dimensions (in cm) of the osteoderms of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from Neuffen, Germany as distributed on the blocks (Figure 1).

osteoderms	length	width
O1	3.1	2.4
O2	–	–
O3	6.1	4.2
O4	~8.7	6.6
O5	8.5	>5
O6	8.8	5
O7	~6	5.5
O8	9.2	–
O9	9.5	~5.5
O10	~10	~7.7
O11	~5.5	~2.8

Table 3. Dimensions (in cm) of the vertebrae of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from Neuffen, Germany. **ch**, centrum height; **cl**, centrum length, **cw**, centrum width; **d/p d**, dia/parapophysis distance; **nsh**, neural spine height; **nsl**, neural spine length; **pltp**, proximodistal length of transverse process; **altpt**, anteroposterior length of transverse process.

vertebrae	type	measured side	ch	cw	cl	d/p d	nsh	nsl	pltp	altpt
1	cervical	posterior	6.2	5.5	6.1	3	?	–	–	–
2	cervical	anterior	6.2	6.4	6.2	3	~7.5	–	–	–
3	caudal	no	~2.8	~2.5	4.4	–	–	–	–	–
4	caudal	no	3.9	3.4	4.7	–	6.5	–	–	–
5	posterior cervical	anterior	6.7	6	6	4.5	7.2	4.2	–	–
6	posterior cervical	posterior	6.8	6.4	6.1	~4.5	~6.5	~4.1	–	–
7	dorsal	both	~7 post	6.5 ant	6.9	–	–	–	8.4	5.1
8	posterior cervical	anterior	6.3	6.4	>5.9	3	~8	~4.5	–	–
9	posterior cervical	posterior	6.4	5.8	6.2	3.3	7.9	3.8	–	–
10	dorsal	posterior	7.6	6.8	7.9	–	5.5	5.4	5.8	4.6
11	dorsal	posterior	7.4	6.3	6.9	–	6	~6	10.8	~4
12	dorsal	anterior	~7	6.5	7.4	–	5	>6	11.7	5.1
13	dorsal	posterior	7	>5.5	7.6	–	–	–	11.8	5.1
14	dorsal	post	9	6.1	7.3	–	–	–	12	4.3
15	dorsal	posterior	7.5	~6.4	7.9	–	–	–	12.3	5
16	sacral	anterior	6.1	7.4	6.8	–	5.7	6.4	–	–
17	cervical	anterior	5.6	6	6	3.3	~8	–	–	–
18	anterior caudal	posterior	6.2	5.1	6.1	–	–	–	–	–

trum. The centrum is as tall as wide. In lateral view, the ventral margin is slightly concave. No hypapophysis was detected. The dia- and parapophysis consist of massively built tubera, which are separated from each other by a marked concavity of the centrum. The diapophysis is circular in outline and takes place at the suture between the centrum and the neural arch. The parapophysis consists of an anteroposteriorly elongate process. The neural spine is nearly as tall as the centrum and is rectangular in outline. Its dorsal tip is not pointed but is convex. The prezygapophysis tapers anteriorly beyond the level of the centrum, while the postzygapophysis remains at the same level as the posterior margin of the centrum. Pre- and postzygapophyses are vertically oriented. Seven disarticulated cervical ribs are preserved. They are T-shaped in dorsal and ventral views, their anterior process being slightly shorter than their

posterior process. The capitulum and tuberculum are ovoid and thick in comparison to the shaft of the rib.

Dorsal vertebrae and thoracic ribs. Seven dorsal vertebrae are preserved (e.g. Fig. 9A). As with the cervical vertebrae, the anterior and posterior margins are thick. One of them displays its posterior face (Fig. 9E). The surface of the centrum is concave and is taller than wide. Its outline is not symmetric but is wider near the base. The ventral margin of the centrum is concave. The transverse process is robust, horizontal and projects far laterally. Just above the circular neural canal, the small postzygapophyses are inclined at about 45°. The neural arch is not tall compared to that of the cervical vertebrae. It is however more anteroposteriorly expanded with a flat and thick distal margin. Twelve thoracic ribs are present but a few of them are complete (e.g. Fig. 9M). They are robust and strongly curved.

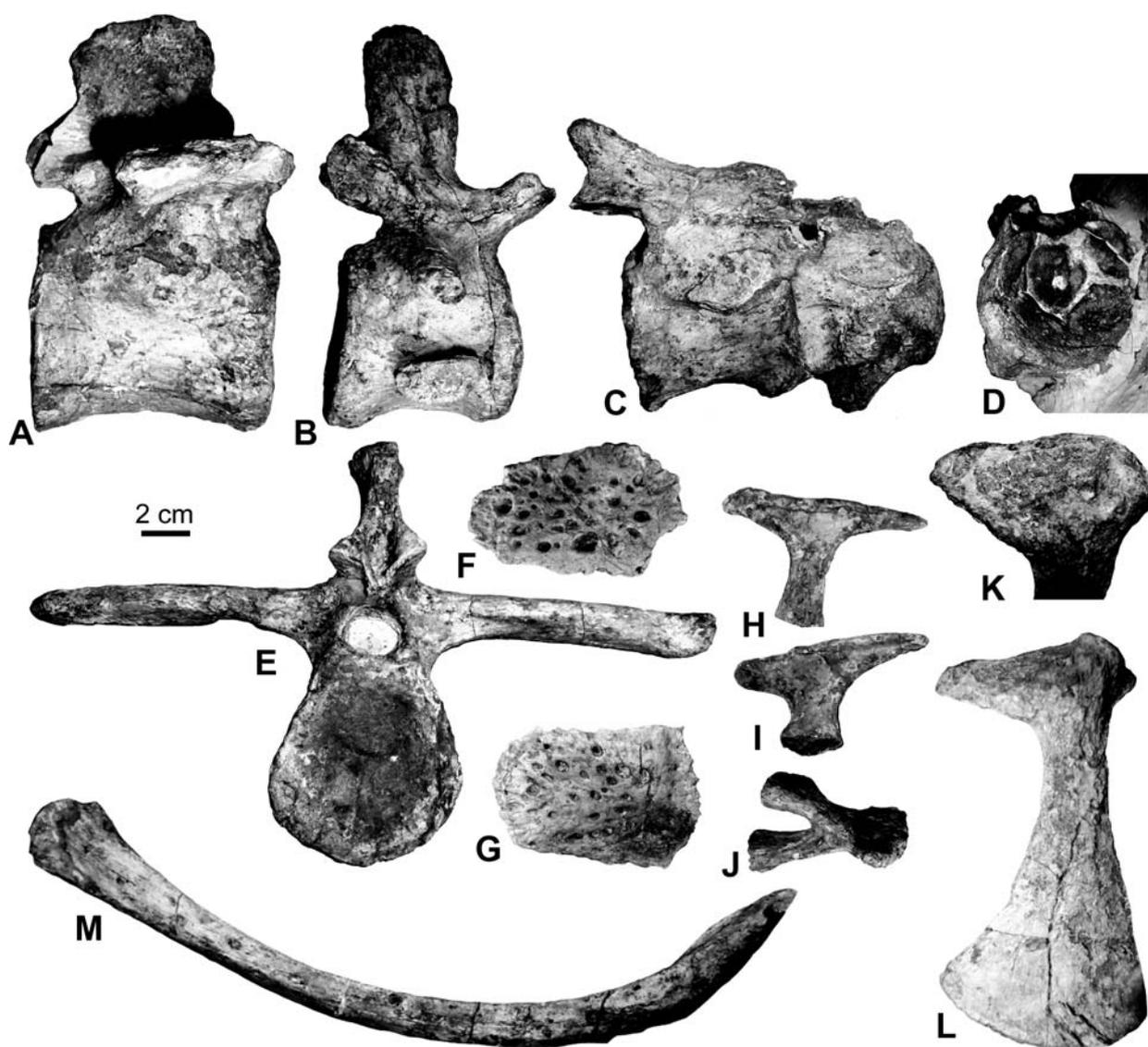


Figure 9. Selected postcranial elements associated to the skull and mandible of *Machimosaurus hugii* von Meyer, 1837 (SMNS 91415) from the Kimmeridgian of Neuffen, Germany. **A.** Anterior dorsal vertebra in right lateral view; **B.** Cervical vertebra in right lateral view; **C.** Atlas-axis complex in right lateral view; **D.** Atlas in anterior view; **E.** Mid-dorsal vertebra in posterior view; **F, G.** Dorsal osteoderms; **H, I.** Cervical ribs; **J.** Cervical rib in anterior view; **K.** Proximal portion of the left coracoid in anterior view; **L.** Left coracoid in lateral view; **M.** Thoracic rib.

Proximally, a faint crest runs on the posterior margin of the shaft.

Sacrum. One sacral vertebra is preserved. The centrum is circular in outline and its surface is flat. The robust sacral ribs are fused to the centrum and their distal tip is wide. These ribs bend ventrally toward their distal tip, which reaches the ventral level of the centrum. The neural canal is wider than tall. The neural arch is about as tall as that from other dorsal vertebrae.

Caudal vertebrae. Three caudal vertebrae are preserved. The centrum anterior and posterior surface is rectangular in outline, being taller than wide. The centrum is anteroposteriorly elongate. The neural arch is tall and bent posteriorly.

Coracoid. The left coracoid is preserved and shows its lateral surface. The proximal region is medially inclined, making an angle of nearly 90° with the coracoid blade. The posterior proximal area constitutes the glenoid fossa, which is slightly concave and supported by a thick bony basis. Just anterior to it opens the large coracoid foramen. This foramen is placed in the large excavated lateral surface of the proximal head of the coracoid. The coracoid blade is elongate and flares distally. Its posterior margin is nearly straight whereas its anterior margin is broadly concave, with a maximum concavity between the blade and the proximal margin.

Osteoderms. Eleven osteoderms are visible (e.g. Figs 9F, G). Their dimensions are reported in Table 5. They are all disarticulated. Their external surface is flat and no articular facet was detected. They are rectangular to oval in outline. The ornamentation of the osteoderms consists of large subcircular and widely spaced pits. The margin of the osteoderms tends to show fewer pits than the central area.

Discussion

Taxonomic content of the genus *Machimosaurus*

The specimen SMNS 91415 can be attributed with confidence to the genus *Machimosaurus* on the basis of tooth morphology. Because of the wide occurrence of the conical tooth morphology in crocodylians, it may not be recommended to consider tooth morphology as a diagnostic character. *Machimosaurus* has been erected on isolated teeth (von Meyer 1837) and subsequent recoveries of more complete specimens including the above-described specimen, justify the use of dental morphology as an exception for this genus. The teeth are short, stout with a blunt apex. Each tooth bears marked apicobasal ridges on the enamel surface and the mesiodistal carinae are not discernible from these ridges. The characteristic teeth of *Machimosaurus* can be distinguished from those of all other crocodylians, even from those of *Steneosaurus obtusidens* Andrews, 1913, which have been described with prominent ridges on the enamel surface (see below).

The taxonomic content of the genus *Machimosaurus* has been reduced to a single species by Krebs (1967, 1968) who argued that *Machimosaurus mosae* Sauvage & Liénard, 1879 was not valid because he viewed these remains as an assemblage of different reptiles. Although Krebs (1967, 1968) did not detail the reasons for such a conclusion, he also designated the fragmentary remains from the Kimmeridgian of Guimarota, Portugal, as the neotype of *Machimosaurus hugii*. This act should be considered invalid in reference to the code of nomenclature (Art. 75; ICZN 1999). The holotype of *Machimosaurus hugii* still consists of isolated teeth from Soleure, Switzerland (von Meyer 1837). Hua (1999), being the most recent work on the subject, resurrected *Machimosaurus mosae* Sauvage & Liénard, 1879 and therefore recognised a total of two species. Comparison of the relatively complete skeleton described by Hua (1999) with other remains of *Machimosaurus hugii* reveals that *Machimosaurus mosae* does not offer much difference from *Machimosaurus hugii*. Recognising two species of *Machimosaurus* is based on differences in alveolar counts, general proportions of the skull and ornamentation of the osteoderms as highlighted by Hua (1999).

Alveolar count in SMNS 91415 consists of three alveoli per premaxilla, 22 alveoli per maxilla and 21 to 22 alveoli on each dentary. Buffetaut (1982) was the first to describe the then only known complete skull and mandible of *Machimosaurus hugii* from the Kimmeridgian of Montmerle, Ain, France and observes three premaxillary alveoli and because the rostrum is not visible in palatal view, proposes 21 alveoli for the maxillary count and 24 or 25 dentary alveoli. However, due to the state of preservation, this estimation is uncertain (Buffetaut 1982). Except for the premaxillary count, which is identical in all specimens referred to *Machimosaurus*, Hua (1999) gives a count of 17 maxillary alveoli in the specimen of *Machimosaurus mosae* from Pas-de-Calais. But in that specimen, this count is only an estimate because the maxillary tooth rows are incomplete posteriorly. In this specimen, the only reliable counts are those of the dentaries (19 alveoli), which are indeed smaller than in SMNS 91415. The same number of dentary alveoli has been reported in a specimen from the Kimmeridgian of Gigouzac, Lot, southern France (Hantzpergue et al. 1982; revised count in Hua 1999). Because alveolar count variability in extant crocodylians can sometime be in excess of one to two, we tentatively interpret the diminutive number of alveoli of the specimens from Pas-de-Calais and Lot in terms of intraspecific variability and not as a significant difference warranting the recognition of a separate species. Hua (1999) recognized the specimen from Gigouzac as belonging to *Machimosaurus mosae* but this specimen is regarded here as belonging to *Machimosaurus hugii* instead.

Hua (1999) also highlights that *M. mosae* possesses a more robust rostrum compared to that of *M. hugii* from Montmerle, but we disagree. Indeed, as recognised by

Table 6. Dimensions (in cm) and ratios of selected teleosaurid taxa including the most complete skulls of *Machimosaurus*. **a**, total skull length from anterior tip of premaxilla to posterior margin of supraoccipital; **b**, rostrum length taken from anterior tip of premaxilla to anterior margin of orbits; **c**, maximum width between lateral edges of quadrate condyles; **d**, interorbital width; **e**, maximal width across one supratemporal fenestra; **f**, length of supratemporal fenestra. * According to Buffetaut (1982) the posterior surface is made of plaster and does not deserve to be described. **1**, this study; **2**, Buffetaut (1982); **3**, Hua (1999); **4**, R3168 in Andrews (1913); **5**, R3220 in Andrews (1913); **6**, R3701 in Andrews (1913)

	a	b	b/a	c	c/a	d	d/a	e	e/a	f	f/a	ma	da
<i>M. hugii</i> ¹	93.5	54.7	0.59	39.7	0.42	8.40	0.09	13.60	0.15	26.00	0.28	22	21–22
<i>M. hugii</i> ²	100	58	0.58	33*	0.33	8.00	0.08	14.00	0.14	30.00	0.30	?21	?24–25
<i>M. hugii</i> ³	96.5	56.2	0.58	43.0	0.45	8.60	0.09	16.30	0.17	25.10	0.26	?	19
<i>S. obtusidens</i> ⁴	116	71	0.61	37.5	0.32	8.50	0.07	14.00	0.12	33.00	0.28	?	28
<i>S. leedsii</i> ⁵	81	59	0.73	18.0	0.22	3.50	0.04	7.30	0.09	12.00	0.15	41–42	43–44
<i>S. durobrivensis</i> ⁶	74	45	0.61	24.0	0.32	5.4	0.07	8.8	0.12	18	0.24	30	31

Hua (1999), and as confirmed here with SMNS 91415, there are no significant differences in the rostrum proportions between *M. hugii* and the Pas-de-Calais specimen. Nevertheless, a comparative compilation of the skull measurements of different specimens of *Machimosaurus* does not reveal differences in the proportional width of the skulls either (Table 6). This is further reinforced by the absence of allometric change because all these specimens are of similar length (Table 6).

As observed by Hua (1999), ornamentation of the osteoderms differs between *M. hugii* and the specimen from Pas-de-Calais (referred to *M. mosae* by Hua 1999). Ornamentation of SMNS 91415 is identical to that of the specimen figured by Krebs (1968; and attributed by him to *M. hugii*) with large and spaced pits, whereas the Pas-de-Calais specimen displays a fine net of coalescing pits (Hua 1999). The specimen from Lot reported by Hantzpergue et al. (1982) has osteoderms recalling those of the specimen from Pas-de-Calais according to Hua (1999). But this is not compelling and the osteoderm figured by Hantzpergue et al. (1982) appears similar to the osteoderms figured in the present work. Therefore, the only observed difference between the specimen described by Hua (1999) as *M. mosae* and other specimens referred to *M. hugii* is alveolar counts on the dentary, osteoderm ornamentation remaining ambiguous. Whether these few differences are significantly different to warrant the recognition of a separate species must be evaluated by augmenting the sampling of specimens. If not discerning a separate species, they could as well be part of the morphological variability within a population or originate from another peculiar condition. In that sense, it is worth remembering that Hua (1999) observed numerous pathologies in the skeleton from Pas-de-Calais and among them recognised a case of exostosis. As speculative as it may be, a pathological condition could also affect the pattern of ornamentation, apparently unique to the specimen described by Hua (1999).

Sauvage & Liénard (1879) stated that the specimen they described from Issoncourt, Meuse, possesses teeth

that are not identical to *M. hugii* von Meyer, 1837 from Soleure. However, they never provided a reason justifying the differences in tooth morphology. More confusing, they provided a diagnosis for the genus *Machimosaurus*, including tooth characteristics stating: “dents rapprochées, peu nombreuses, mais très-fortes, obtuses, coniques, fortement striées, à coupe circulaire, ne portant pas de carènes sur la portion émaillée” (Sauvage & Liénard 1879, p. 20). Hua (1999, p. 167) states that *M. hugii* and *M. mosae* have an original and similar dental morphology, thus implicitly recognising the identical nature of the two alleged species of *Machimosaurus*. However, Hua (1999) states that not a single tooth crown is preserved in the specimen referred to *M. mosae* from Pas-de-Calais. The specimen described by Sauvage & Liénard (1879) is lost and the specimen from Pas-de-Calais does not preserve teeth, so it is impossible to provide a comparison of this important character. Therefore, on the basis of dental morphology, there is no evidence to discern a separate species of *Machimosaurus*.

Finally, the name *M. mosae* itself appears to be invalid. In their description of *Machimosaurus mosae*, Sauvage & Liénard (1879, p. 11) cite the work of “Liénard in Musée de Verdun” as the inventor of the taxon “*Machimosaurus mosae*, F. Liénard sp. (1)”. Félix Liénard coined *Teleosaurus mosae* in a hand-written document from 1876 and Sauvage & Liénard (1879) explicitly refer to this piece of work. Subsequent publications (e.g. Krebs 1967, 1968; Buffetaut 1982; Hua et al. 1993; Hua 1999) referred to Sauvage & Liénard (1879) as the original publication for the name *M. mosae*, but it is Liénard (1876) instead. However, according to ICZN (Article 8 and 9), a hand-written manuscript is not considered as a published work and the name *Teleosaurus mosae* associated with it is considered invalid. If further investigation (notably by examining the mandible from Verdun (Basse de Menorval 1961–62; Maubeuge 1963, 1968) proves the presence of a second species in Kimmeridgian strata, a species name different from *M. mosae* will have to be applied.

Comparison and affinities

Two teleosaurid synapomorphies were recognized according to the cladistic analysis of Young & Andrade (2009). In this regard, *Machimosaurus* shares with other teleosaurids a long ventral expansion of the basisphenoid and the position of the hypoglossal foramen for cranial nerve XII that opens in line with the foramen magnum. The genus *Machimosaurus* also shares with Teleosauridae a number of other characters such as a relatively long and straight rostrum with parallel edges and slightly expanded premaxillae, the circular orbits facing almost dorsally, the large rectangular and antero-posteriorly elongate supratemporal fenestrae and a deep splenial symphysis. *Machimosaurus* also shares with *Mycterosuchus nasutus* Andrews, 1913 and the genus *Steneosaurus* (see Andrews 1913) three alveoli per premaxilla, large and confluent third and fourth dentary alveoli, a pointed anterior palatine process, relatively small suborbital fenestrae and the square anterior process of the maxilla entering the premaxillae in ventral view.

Among Teleosauridae, *Machimosaurus* is unique in presenting the lowest alveolar count (22 maxillary and 19–22 dentary alveoli) in comparison to an average of 30 alveoli per maxilla or dentary for other teleosaurids. *Machimosaurus* can be further distinguished from *Peipehsuchus teleorhinus*, *Teleosaurus cadomensis* (Lamouroux, 1820) or the genus *Steneosaurus* because it has no antorbital fenestrae. However, it most resembles *Steneosaurus obtusidens* (on the basis of dentition and shape of the supratemporal fenestrae), although the shape of the supratemporal fenestrae of *Peipehsuchus* appears also similar but is less anteroposteriorly expanded in that latter one. Few complete specimens of *Machimosaurus* have been reported in the literature. *M. hugii* from Montmerle is indeed not perfectly preserved but Buffetaut (1982) could not discern an antorbital fenestra. The skull of *Machimosaurus hugii* reported by Krebs (1967, 1968) from Portugal is too fragmentary and does not preserve the area of interest. Hua (1999) did not report any antorbital fenestrae in *M. mosae* but the area under concern is broken and deformed. However, Hua (1999) stated that these fenestrae might have been of small size because the damaged area of concern is small as well. In SMNS 91415, no antorbital fenestra was detected. *Machimosaurus* is therefore best viewed as a large and robust version of *Steneosaurus*, as has been proposed by Buffetaut (1982). As noted by Krebs (1968), it is difficult to differentiate *Machimosaurus* from *Steneosaurus obtusidens*. Hua et al. (1994) even suggested evaluating whether *S. obtusidens* should be synonymous with the genus *Machimosaurus*. Andrews (1913) describes the dentition of *S. obtusidens* as possessing blunt crowns bearing a sculpture of fine ridges. This is indeed identical to what can be observed in *Machimosaurus*, but Andrews (1913) also remarks that the anterior and posterior faces of the teeth bear one more strongly marked

mesiodistal carinae. This would constitute a difference with the morphology of *Machimosaurus*, the mesiodistal carinae of which do not stand out from the rest of the vertical ridges ornamenting the enamel surface as described here and elsewhere. Indeed, the skull length of both taxa is comparable with 116 cm long for the specimen of *S. obtusidens* described by Andrews (1913) versus 93.5 cm long for *M. hugii* (SMNS 91415). However, according to the description of Andrews (1913), *Steneosaurus obtusidens* possesses a symphysis extending back to the level of the 24th alveolus, and possesses 28 teeth in the mandible as well as a slit-like antorbital foramen. In *Machimosaurus hugii*, the symphysis reaches the 20th alveolus, the dentary possesses 19–21 alveoli and so far no antorbital fenestra was detected in any skull of *Machimosaurus*. Also, in dorsal view, the supratemporal fenestrae are more elongate in *S. obtusidens* than they are in SMNS 91415. Indeed, that *Steneosaurus obtusidens* belongs to the genus *Steneosaurus* needs to be evaluated but this is out of the scope of the present study. Nevertheless, there is no reason to synonymize *S. obtusidens* with *M. hugii* (contra the proposition of Hua et al. 1994).

Sauvage & Liénard (1879) were the first to propose a diagnosis at the genus level. Krebs (1967) then proposed a diagnosis for *Machimosaurus hugii* but did not propose one for *Machimosaurus mosae* Sauvage & Liénard 1879 because he viewed it as a junior synonym of *M. hugii*. Hua (1999) considered *Machimosaurus mosae* as a valid species and proposed a diagnosis for it. Then, based on the work of Hua (1999), Pierce et al. (2009) updated the diagnosis for *Machimosaurus hugii* and *Machimosaurus mosae*. However, most of the content of these diagnoses reveal to be either diagnostic at the genus level or to characterize all Teleosauridae. As such the character list of Pierce et al. (2009, p. 1085) referring to the anteriorly positioned external narial opening, the very large, longitudinally expanded supratemporal fenestrae, the small and subcircular orbits, the frontal that terminates just anterior to the orbits, the irregular pits on the dorsal surfaces of the frontal and prefrontal, the longitudinal grooves of varying lengths on the rostrum are in fact characteristic of Teleosauridae to the exception of the shape of the supratemporal fenestrae, which are as long as wide in *Teleosaurus cadomensis* (Jouve 2009). Other characters from the diagnosis are problematic: for example, the marked posterior concavity of the palatine fenestra on the pterygoid is not preserved in *M. mosae* for comparison and is not visible in the complete skull of *M. hugii* described by Buffetaut (1982). In SMNS 91415, the palatine fenestra is comparable to that of any other teleosaurids. The contact between the ectopterygoid and the pterygoid is thought to differentiate the two taxa but might be related to ontogeny. Also, Pierce et al. (2009) indicate between 21–34 teeth on the maxilla and 24–31 teeth on the mandible of *Machimosaurus hugii*. This is clearly an overstatement as these authors synonymize *Steneosaurus durobrivensis* Andrews, 1913, *Steneosaurus ob-*

tusidens and *Steneosaurus hulkei* Andrews, 1913 with *Machimosaurus*, thus increasing the tooth count substantially. Presently however, there is no evidence for synonymizing the above-mentioned species of *Steneosaurus* with the genus *Machimosaurus*, let the tooth count itself be a sufficient difference to discard such an interpretation.

Phylogenetic analysis

A phylogenetic analysis was conducted in TNT (Goloboff et al. 2003) using the data matrix of Young et al. (2012). Codes for *Machimosaurus hugii* were updated from the matrix of Young et al. (2012), totaling 73 taxa and 240 characters with *Postosuchus kirkpatricki* as the outgroup taxon. Characters were treated as unordered. A heuristic search was conducted, which returned a strict consensus of 22 trees (best tree length = 655 steps). According to these results, *Machimosaurus hugii* is certainly to be included within Thalattosuchia, and more especially within Teleosauridae as has been previously recovered by Müller-Towe (2005). The topology recovered here is identical to that of Young et al. (2012) and for this reason, only the relevant part of the tree is detailed in Figure 10, presenting the relationships among Teleosauridae. The topology obtained places Teleosauridae as the sister group to Metriorhynchoidea. *Pelagosaurus typus* is not closely related to Teleosauridae and is here in a basal position relative to Metriorhynchoidea. *Machimosaurus hugii* sits in a more derived position than *Steneosaurus obtusidens*. From a general view, *Machimosaurus* sits in a terminal branch within a clade composed of five species of *Steneosaurus*. This topology highlights that *Machimosaurus* is more closely related to *Steneosaurus* than to *Teleosaurus cadomensis* or *Platysuchus multiscribicularatus*, which are in a sister position to the *Steneosaurus-Machimosaurus* clade. The earlier views of Buffetaut (1982) and Hua et al. (1999) that *Machimosaurus* derives from a common ancestor of *Steneosaurus* and particularly *Steneosaurus obtusidens* is sup-

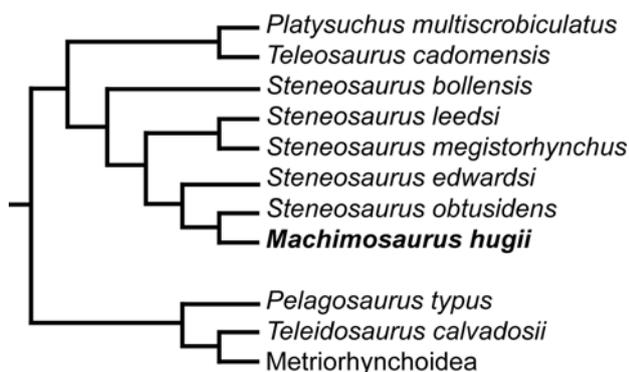


Figure 10. Simplified topology recovered in this study and depicting the phylogenetic affinities of *Machimosaurus hugii* von Meyer, 1837 within Thalattosuchia. *Machimosaurus hugii* sits in a derived position within Teleosauridae.

ported by the topology recovered under this phylogenetic hypothesis.

In conclusion, we view *Machimosaurus* as a monospecific genus with *M. hugii* appearing to be close in affinities with the species *S. obtusidens*, thus challenging the taxonomic stability of the genus *Steneosaurus*. Nevertheless, *S. obtusidens* and *Machimosaurus* are different from each other and do not belong to the same genus.

Acknowledgments

We warmly thank the curator R. Schoch (Staatliches Museum für Naturkunde, Stuttgart, Germany) for providing access to the collections of SMNS. This work would have been impossible without the colossal preparation efforts of Peter Riederle (SMNS) to whom we address our most sincere thanks. JEM is funded by a Marie Curie Fellowship, FP7 framework. PV acknowledges financial support from the A. v. Humboldt Foundation. D. Schwarz-Wings and two anonymous reviewers provided many valuable comments that significantly improved the content of this article. K. Janneau and P. Hantzpergue helped locating references.

References

- Andrews, C. W. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part II. British Museum (Natural History).
- Bardet, N. & Hua, S. 1996. *Stimolestes nowackianus* Huene, 1938 from the Upper Jurassic of Ethiopia is a teleosaurid crocodile, not a pliosaur. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1996: 65–71.
- Basse de Menorval, E. 1961–62. Un crocodylien fossile dans les carrières d’Haudainville. – Bulletin de la Société Naturelle et Archéologique du Nord de la Meuse 73, 74: 40–42.
- Buffetaut, E. 1982. Le crocodylien *Machimosaurus* von Meyer (Mesosuchia, Teleosauridae) dans le Kimméridgien de l’Ain. – Bulletin trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre 69: 17–27.
- Fraas, E. 1901. Die Meerkrokodile (Thalattosuchia n. g.), eine Sauriergruppe der Juraformation. – Jahreshefte des Vereins für vaterländische Naturkunde Württemberg 57: 409–418.
- Geoffroy Saint-Hilaire, E. 1831. Recherche sur de grands sauriens trouvés à l’état fossile aux confins maritimes de la Basse-Normandie, attribués d’abord aux crocodiles, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*. – Mémoires de l’Académie des Sciences 12: 1–138.
- Gmelin, J. F. 1789. Regnum animale. In Beer, G. E. (ed.). Caroli a Linné Systema Naturae per Regna tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Volume 1 (3). Leipzig: pp. 1033–1516.
- Goloboff, P. A., Farris, J. S. & Nixon, K. 2003. TNT: tree analysis using new technologies (Program and documentation available from the authors and at <http://www.zmuc.dk/public/phylogeny>).
- Hantzpergue, P., Lafaurie, G. & Lange-Badré, B. 1982. Un crocodylien du Jurassique supérieur marin des environs de Cahors. – Bulletin de la Société des Etudes du Lot 13: 375–385.
- Hua, S. 1999. Le Crocodylien *Machimosaurus mosae* (Thalattosuchia, Teleosauridae) du Kimméridgien du Boulonnais (Pas de Calais, France). – Palaeontographica A 252: 141–170.
- Hua, S., Vasse, D., Buffetaut, E., Martin, M., Mazin, J.-M. & Vadet, A. 1993. Un squelette de *Machimosaurus mosae* Sauvage et Liénard, 1879 (Crocodylia, Thalattosuchia) dans le Kimméridgien du

- Boulonnais. – Comptes Rendus de l'Académie des Sciences, Paris 317: 851–856.
- Hua, S., Vignaud, P., Pennetier, E. & Pennetier, G. 1994. Un squelette de *Steneosaurus obtusidens* Andrews 1909 dans le Callovien de Villers-sur-Mer (Calvados, France) et le problème de la définition des Teleosauridae à dents obtuses. – Comptes Rendus de l'Académie des Sciences 318: 1157–1562.
- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature, London.
- Iordansky, N. N. 1964. The jaw muscles of the crocodiles and some relating structures of the crocodylian skull. – Anatomischer Anzeiger 115: 256–280.
- Jouve, S. 2009. The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia) and phylogenetic analysis of Thalattosuchia. – Journal of Vertebrate Paleontology 29: 88–102.
- Karl, H.-V., Gröning, E., Brauckmann, C., Schwarz, D. & Knötschke, N. 2006. The Late Jurassic crocodiles of the Langenberg near Oker, Lower Saxony (Germany), and description of related materials. – Clausthaler Geowissenschaften 5: 59–77.
- Krebs, B. 1967. Der Jura-Krokodilier *Machimosaurus* H. v. Meyer. – Paläontologische Zeitschrift 41: 46–59.
- Krebs, B. 1968. Le crocodylien *Machimosaurus*. – Serviços Geológicos de Portugal, Memória 14: 1–53.
- Lamouroux, M. 1820. Sur le crocodile fossile trouvé dans les carrières du bourg d'Allemagne, à un quart de lieue de Caen. – Annales Générales des Sciences Physiques 3: 160–164.
- Liénard, F. 1876. Le *Teleosaurus Mosae*, fossile des marnes kimméridgiennes de la Meuse. – Unpublished work.
- Martin, J. E., Buffetaut, E., Liard, R., Lauprasert, K. & Suteethorn, V. 2011. A freshwater teleosaurid in the Late Jurassic of northeastern Thailand. In Forrest, R. (ed.). Abstracts of the 59th Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy, Lyme Regis, United Kingdom: p. 17
- Maubeuge, P. L. 1963. Découverte de restes importants de *Machimosaurus hugii* H. von Meyer dans l'Oxfordien de la Meuse. – Comptes Rendus de la Société Géologique de France 3: 104–105.
- Maubeuge, P. L. 1968. Quelques précisions sur le « monstre » des carrières d'Haudainville (Meuse). – Bulletin de Académie et Société Lorraines des Sciences 7: 203–209.
- Meyer, H. von 1837. Mittheilungen, an Professor Bronn gerichtet. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 557–562.
- Müller-Töwe, I. J. 2005. Phylogenetic relationships of the Thalattosuchia. – Zitteliana 45: 211–213.
- Pierce, S. E., Angielczyk, K. D. & Rayfield, E. J. 2009. Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation and temporal patterns. – Palaeontology 52: 1057–1097.
- Pol, D. & Gasparini, Z. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. – Journal of Systematic Palaeontology 7: 163–197.
- Sauvage, H. E. & Liénard, F. 1879. Mémoire sur le genre *Machimosaurus*. – Mémoire de la Société Géologique de France 4: 1–31.
- Simon, M. S., Korn, D. & Koenemann, S. 2011. Temporal patterns in disparity and diversity of the Jurassic ammonoids of southern Germany. – Fossil Record 14: 77–94.
- Young, C. C. 1948. Fossil crocodiles in China, with notes on dinosaurian remains associated with the Kansu crocodiles. – Bulletin of the Geological Society of China 28: 225–288.
- Young, M. T. & Andrade, M. B. 2009. What is *Geosaurus*? Redescription of *G. giganteus* (Thalattosuchia, Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. – Zoological Journal of the Linnean Society 157: 551–585.

Appendix

List of the coding for *Machimosaurus hugii* von Meyer, 1837, using data matrix of Young et al. (2012).

2000021?02	110?10000	?2?002????	?0?0000?00	0100000000	?000000100	
0000100001	0000102010	?100?00000	1000012001	02000000?0	0?101?0101	
?100002000	102?020110	1?010?010	02301?2000	1011000200	0?0031?1??	
011??01???	???101??1?	???????????	???????????	???????????	??1120???	0