ISSN: 0211-8327 Studia Palaeocheloniologica IV: pp. 11-24

REVISION OF *TROPIDEMYS SEEBACHI* PORTIS, 1878 (TESTUDINES: EUCRYPTODIRA) FROM THE KIMMERIDGIAN (LATE JURASSIC) OF HANOVER (NORTHWESTERN GERMANY)

[Revisión de* Tropidemys seebachi *Portis, 1878 (Testudines; Eucryptodira) del Jurásico Superior (Kimmeridgiense) de Hanover (NO de Alemania)]

Hans-Volker KARL[1,2], Elke GRÖNING[3] & Carsten BRAUCKMANN[3]

[1] Thüringisches Landesamt für Denkmalpflege und Archäologie. Humboldtstraße 11. D-99423 Weimar, Germany. Email: hvkarl@web.de
[2] Geoscience Centre of the University of Göttingen. Department of Geobiology. Goldschmidtstrasse 3. D-37077 Göttingen, Germany
[3] Institut für Geologie und Paläontologie. TU Clausthal. Leibnizstraße 10. D-38678 Clausthal-Zellerfeld, Germany. Email: carsten.brauckmann@tu-clausthal.de und elke.groening@tu-clausthal.de

(FECHA DE RECEPCIÓN: 2011-04-17)
BIBLID [0211-8327 (2012) Vol. espec. 9; 11-24]

ABSTRACT: The revision and new interpretation of the quite recently re-discovered type material of *Tropidemys seebachi* Portis, 1878 shows its taxonomic independence. The shell is covered by borings of presumed marine "worms" similar to the Recent *Osedax* for which the new ichnotaxon *Osedacoides jurassicus* n. ichnogen. n. ichnosp. is introduced.

Key words: Testudines, Eucryptodira, *Tropidemys seebachi* Portis, 1878, Late Jurassic, Kimmeridgian, Hanover, northwestern Germany, revision, *Osedacoides jurassicus* n. ichnogen. n. ichnosp.

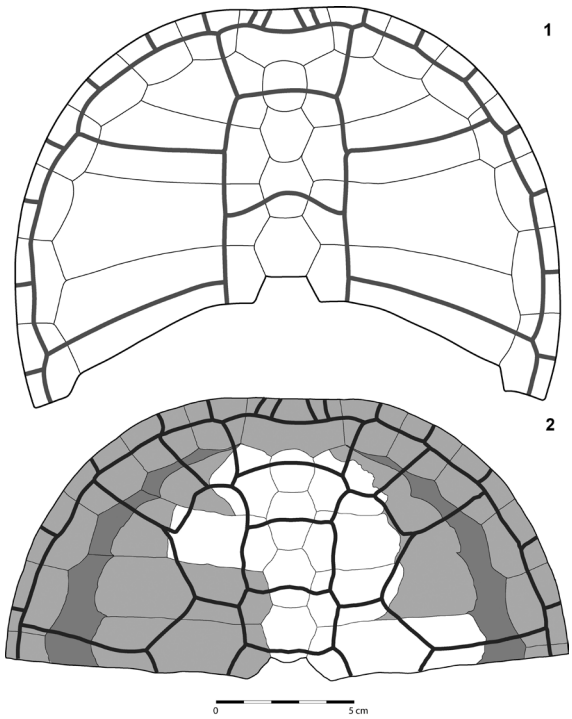
RESUMEN: Nuevo material, recientemente descubierto, de *Tropidemys seebachi* Portis, 1878, en el Jurásico Superior de Hannover, permite su revisión y nueva interpretación, que demuestran su validez taxonómica. El caparazón está cubierto

por perforaciones de probables "gusanos" marinos, similares a los de los actuales *Osedax*. Se han denominado *Osedacoides jurassicus* nov. ichnogen. nov. ichnosp.

Palabras clave: Testudines, Eucryptodira, *Tropidemys seebachi* Portis, 1878, Jurásico Superior, Kimmeridgiense, Hannover, Alemania noroccidental, revisión, *Osedacoides jurassicus* n. ichnogen. n. ichnosp.

INTRODUCTION

The here revised Late Jurassic (Kimmeridgian) specimens were originally described by MAACK (1869) under two species of his newly established genus *Stylemys*, e.g. *St. lindenensis* from the outcrop at the Lindener Berg and *St. hannoverana* from other sites in the Hanover region in northwestern Germany. MAACK did not select holotypes, but only regarded some of the figured specimens as particularly typical.



Figures 1-1. Tropidemys langii *Rütimeyer, 1873, reconstruction of the anterior part of carapace, after BRÄM (1965); Figure 1-2*. Tropidemys seebachi *Portis, 1878, new reconstruction of the anterior part of carapace*: *white = present, light grey = reconstructed plates, dark grey = fontanelles.*

The generic name *Stylemys* Maack, 1869 was preoccupied by *Stylemys* Leidy, 1851 (Oligocene-Miocene; North America, Asia, ?Europe) with *St. nebrascensis* Leidy, 1851 as type species.

PORTIS (1878a, b) assigned parts of the material to *Chelonides wittei* Maack, 1869 whereas he accepted at least "*Stylemys*" *hannoverana* Maack, 1869 which he allocated to *Plesiochelys* Rütimeyer, 1873. A third part of the Hanover material he placed under his new species *Tropidemys seebachi* Portis, 1878. As usual at that time, Portis did not select any holotypes except for specimen n.º GZG.V.24968 which he rendered prominent by expressing: "Das soeben besprochene, die drei Rippenpaare und die vier vorderen Neuralplatten zeigende Stück, welches ich hier als Hauptexemplar behandle…" ("I treat the specimen just mentioned as the main one, which shows three pairs of ribs and the anterior four neural plates"). Since this material was neither explicitly described nor figured by MAACK (1869), its status as a type is original.

Quite recently, when the material of *Tropidemys seebachi* was still believed to be lost, it was tentatively regarded as aberration of the type species *Tropidemys langii* Rütimeyer, 1873 (KARL *et al.*, 2007a,b). After its re-discovery in the collection of the Geoscience Centre, University of Göttingen, it can now be re-described in detail and interpreted anew as a separate species.

Parts of the bones of *Tropidemys seebachi* are covered by borings of presumed marine "worms" similar to the Recent *Osedax* for which the new ichnotaxon *Osedacoides jurassicus* n. ichnogen. n. ichnosp. is introduced (see "Appendix" below).

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758

Infraorder Cryptodira Cope, 1868

Carapaxorder Selmacryptodira Gaffney, Hutchinson, Jenkins & Meeker, 1987

Family Plesiochelyidae Baur, 1888

INCLUDED GENERA: *Plesiochelys* Rütimeyer, 1873 (type genus), *Craspedochelys* Rütimeyer, 1873, and *Tropidemys* Rütimeyer, 1873.

DIAGNOSIS: Diagnosis for skull characters: see GAFFNEY & MEYLAN (1988). Diagnosis for shell characters (according to KARL *et al.*, 2007b: 22): Mesoplastra absent and cocervicalia present; four submarginalia present.

REMARKS: The Plesiochelyidae are mainly characterized by the presence of cocervicalia and the absence of mesoplastra. Additionally, the inguinal columns are inserting into the pleuralia V/VI. Considering the enormous variability within the Plesiochelyidae, the presence of cocervicalia in

Plesiochelys solodurensis Rütimeyer, 1873, *P. etalloni* (Pictet & Humbert, 1857), *Craspedochelys picteti* Rütimeyer, 1873 and *Tropidemys langii* Rütimeyer, 1873 seems to be a character of the whole family (KARL *et al.,* 2007b).

A synopsis of the fossil turtles of Europe was given by DE LAPPARENT DE BROIN (2001). The Late Jurassic turtles of southern England were revised in detail by MILNER (2004).

Genus *Tropidemys* Rütimeyer, 1873

TYPE SPECIES: *Tropidemys langii* Rütimeyer, 1873.

DIAGNOSIS: Anterior three neuralia in 4/6B/6B; shape of carapace nearly round to elongated, cross-section distinctly roof-shaped, corresponding with the neuralia 6B; large sternal chambers present; Centralia considerably narrower than in *Plesiochelys etalloni*; furrows of caudalia only on pygale, not on the metaneuralia.

DISTRIBUTION: Late Middle Jurassic (Callovian) to Early Cretaceous (Valanginian: "*Chelone*" *valanginiensis* Pictet, 1858 in PICTET, CAMPICHE & TRIBOLET, 1858-1860) in Switzerland; Late Jurassic in England, France and North Germany.

REMARKS: The following names are synonyms of *Hylaeochelys* (according to KARL *et al*., 2007).

- 1858 *Chelone valanginiensis* Pictet in PICTET, CAMPICHE & TRIBOLET, p. 117.
- 1889 *Tropidemys valanginiensis* Pictet, LYDEKKER, p. 156.
- 1889 *Tropidemys valanginiensis* Pictet, ZITTEL, p. 117.

Tropidemys langii Rütimeyer, 1873

- 1873a *Tropidemys langii* RÜTIMEYER, pp. 28-43.
- 1873b *Tropidemys expansa* RÜTIMEYER, pp. 83, 90.
- 1873b *Tropidemys gibba* RÜTIMEYER, pp. 83, 90.
- 1889 *Tropidemys langi* Rütimeyer, LYDEKKER, p. 156.
- 1889 *Tropidemys expansa* Rütimeyer, LYDEKKER, p. 156.
- 1889 *Tropidemys gibba* Rütimeyer, LYDEKKER, p. 156.
- 1964 *Tropidemys langii* Rütimeyer, KUHN, p. 34.
- 1964 *Tropidemys gibba* Rütimeyer, KUHN, p. 34.
- 1964 *Tropidemys expansa* Rütimeyer, KUHN, p. 35.
- 1965 *Tropidemys langii* Rütimeyer, BRÄM, p. 176.

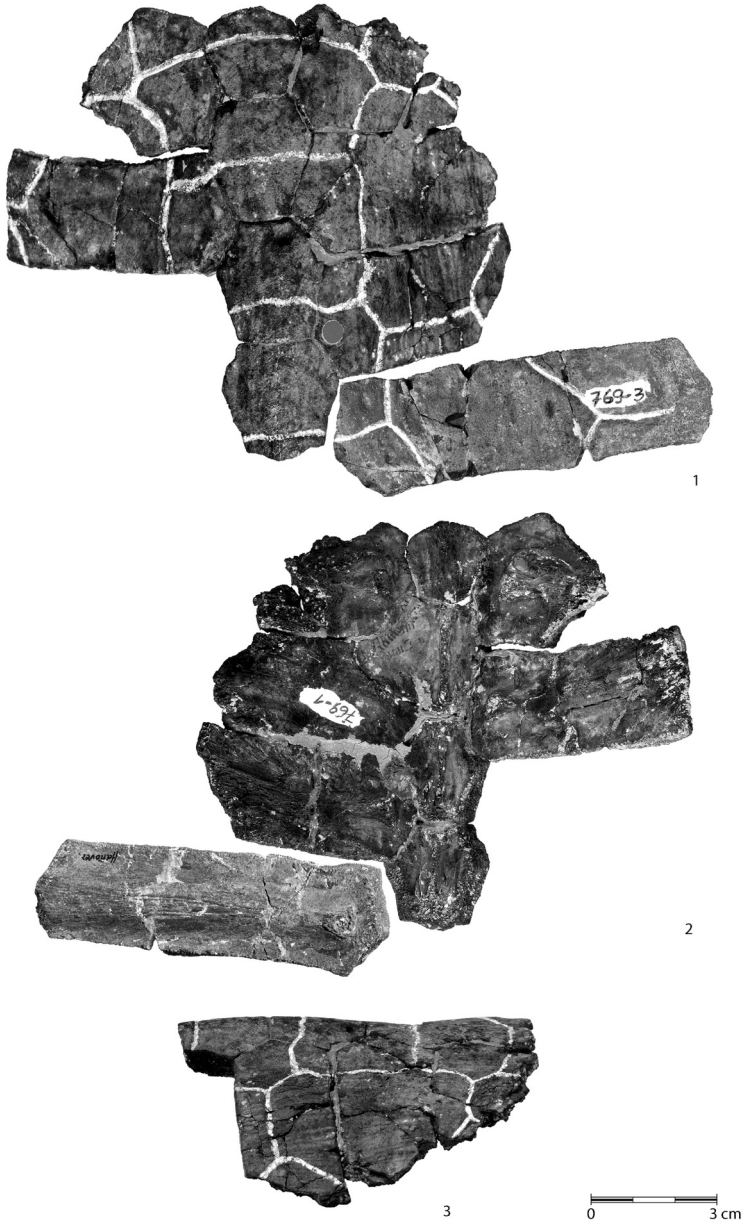


Plate 1. Tropidemys seebachi *Portis, 1878, lectotype, GZG.V.24968/ GZG.V.769-1*: *Anterior fragment of carapax with neuralia I-IV and remains of pleuralia I-III dex., I-II sin. 1 = dorsal view, 2 = visceral view, 3 = lateral view, right side.*

- 1965 *Tropidemys expansa* Rütimeyer, BRÄM, p. 176.
- 1965 *Tropidemys gibba* Rütimeyer, BRÄM, p. 176.
- 2001 *Tropidemys langii* Rütimeyer, DE LAPPARENT DE BROIN, p. 176.
- 2007b *Tropidemys langii* Rütimeyer, KARL *et al.*, p. 35 (pt.).
- 2007b *Tropidemys seebachi* Portis, KARL *et al.*, p. 36.

DIAGNOSIS: Number of centrals not enlarged, neurals not cut by a corresponding scutal furrow; no row of subcentralia on each side between rows of centralia and lateralia.

DISTRIBUTION: Late Middle Jurassic (Callovian) to Late Jurassic (Kimmeridgian) in Switzerland, England and North Germany (KARL, 1997).

***Tropidemys seebachi* Portis, 1878**

- 1869 *Stylemys Lindenensis* MAACK, p. 321 (in part.).
- 1878 *Tropidemys Seebachi* PORTIS, pp. 129-131.
- 1889 *Chelone*, *Tropidemys Seebachi* Portis, ZITTEL, p. 531.
- 1924 *Tropidemys seebachi* Portis, OERTEL, p. 47.
- 1930 *Tropidemys seebachi* Portis, WIMAN, p. 16.
- 1964 *Tropidemys seebachi* Portis, KUHN, p. 34.
- 2007b *Tropidemys seebachi* Portis = *Tropidemys langii* Rütimeyer, KARL *et al.*, p. 36.

LECTOTYPE: GZG.V.24968/ GZG.V.769-1: Anterior fragment of carapax with neuralia I-IV and remains of the pleuralia I-III dex., I-II sin. (plate 1).

PARALECTOTYPES: GZG.V.769-3: separate pleural IV dex. (plate 1); GZG.V.773-34: hyoplastron sin. (MAACK, 1869: pl. 35, fig. 35 = original of *Stylemys lindenensis*); GZG.V.773-20: hypoplastron sin. (MAACK, 1869: pl. 34, fig. 21 = original of *Stylemys lindenensis*) (plate 2).

TYPE LOCALITY: Lindener Berg, Hanover, Lower Saxony, Germany.

TYPE STRATUM: Late Jurassic: Middle Kimmeridgian.

DIAGNOSIS: Number of centrals considerably enlarged, presumably doubled, each neurale cut by a corresponding scutal furrow; a row of subcentralia inserted on each side between rows of centralia and lateralia.

REMARKS: In contrast to the type species *Tropidemys langii* Rütimeyer, 1873, *Tropidemys seebachi* Portis, 1878 shows a conspicuous symmetric structure of the carapace. In a previous contribution (KARL *et al.*, 2007b) this character was regarded as anomaly. But now the re-discovery of the original

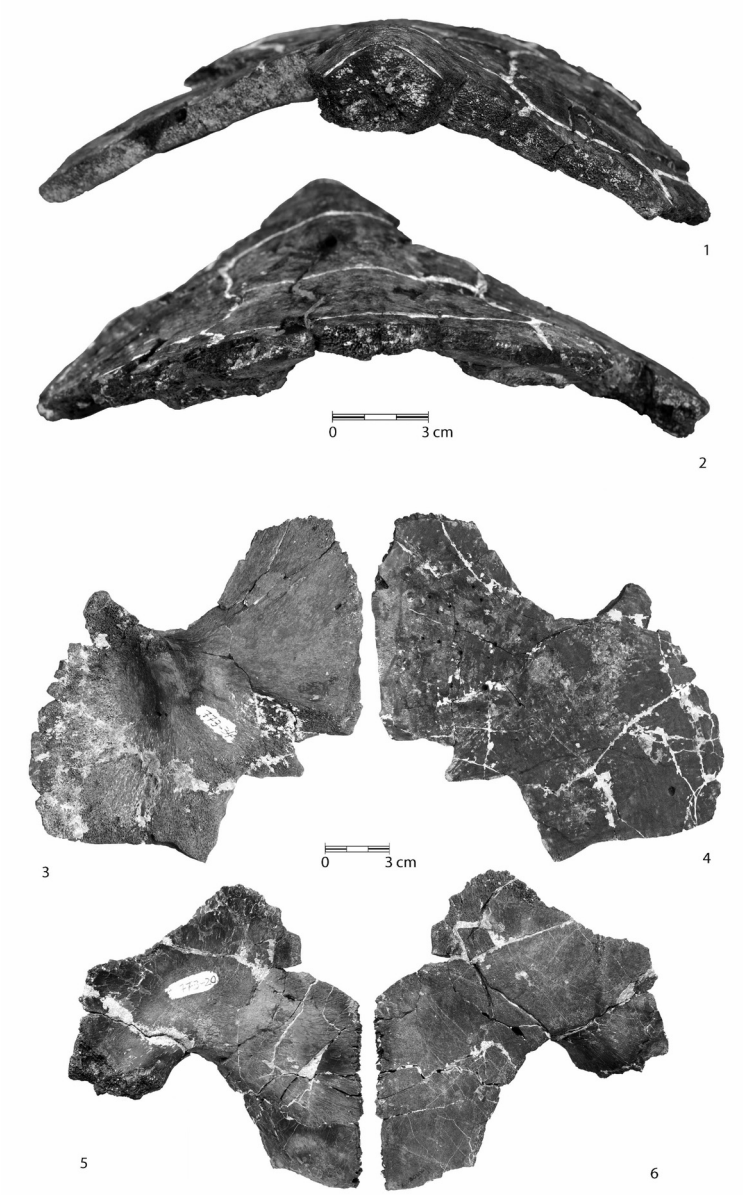


Plate 2. Tropidemys seebachi *Portis, 1878, 1 = lectotype, GZG.V.24968 in posterior view, 2 = lectotype, GZG.V.24968 in frontal view, 3 = paralectotype GZG.V.773-34: hyoplastron sin. (MAACK, 1869: pl. 35, fig. 35 = original of* Stylemys lindenensis*) in visceral view, 4 = in ventral view, 5 = paralectotype GZG.V.24968 GZG.V.773-20: hypoplastron sin. (MAACK, 1869: pl. 34, fig. 21 = original of* Stylemys lindenensis*) in visceral view, 6 = in ventral view. Borings of* Osedacoides jurassicus *n. ichnogen. n. ichnosp. are visible in figures 3-4.*

material of *T. langii* led to a new reconstruction which clearly displays the pronounced symmetry as well as the striking regular arrangement of the scutal plates. Therefore we regard *T. seebachi* now as separate species.

Additionally, the re-investigation shows that parts of the bones of *Tropidemys seebachi* are covered by borings of presumed marine "worms" similar to the Recent *Osedax* for which the new ichnotaxon *Osedacoides jurassicus* n. ichnogen. n. ichnosp. is introduced (see "Appendix" below).

TROPIDEMYS AND THE TURTLES OF THE JURASSIC/CRETACEOUS BOUNDARY IN THE REGION OF HANOVER

1. STRATIGRAPHIC DISTRIBUTION

During the Late Jurassic at least four turtle genera were present in Central Europe which were restricted to this epoch. Two of them were composed of two species, i.e. *Plesiochelys* and *Craspedochelys*. As far as known, the other two genera *Hylaeochelys* and *Tropidemys* are monospecific. All hitherto known genera of the European Early Cretaceous are monospecific, too. Four genera have a stratigraphical range from the Late Jurassic to the Early Cretaceous, i.e. *Tropidemys, Peltochelys*, *Hylaeochelys*, and the *Desmemys/Dinochelys* complex. The Early Cretaceous genera *Ctenochelys* and *Salasemys* at first appear in North Germany at all. Because of the Early Cretaceous (Valanginian) age of the type material of "*Chelone*" *valanginiensis* from Sainte-Croix, Switzerland, LYDEKKER (1889) already pointed out that in this case a genus crossed the boundary between Late Jurassic and the "Neocomian". As indicated by KARL *et al*. (2007b), both the other genera, *Plesiochelys* and *Craspedochelys*, of the Late Jurassic of Hanover did not survive this boundary.

With *Toxochelys gigantea* Oertel, 1914 from the Aptian sequence in the abandoned brickyard quarry of Kastendamm in Garbsen, NW Hanover, the most ancient species of true marine turtles (Chelonioidea) occurs. *Toxochelys* had an increasing radiation in the Late Cretaceous (Niobrara Formation) in North America. All the other Late Jurassic and Early Cretaceous groups of turtles (Pleurosternidae, Hylaeochelyidae) have no adaptations to marine life like flippers (paddle-like anterior extremities) (KARL, 2002). They became extinct at the end of the Early Cretaceous.

Peltochelys belongs to the basal group of the Trionychia (MEYLAN, 1988). This group had an increasing radiation not before the Late Cretaceous and became the dominating group of limnic to brackish turtles with an enormous distribution during the Tertiary.

Salasemys cannot be assigned to a particular group. It seems to occur episodically in the Early Cretaceous Wealden Facies (FUENTES VIDARTE *et al*., 2003).

Plate 3. Osedacoides jurassicus *n. ichnogen. n. ichnosp., holotype, in paralectotype GZG.V.773-34 (plate 2, figs. 3-4). Photograph by Brigitte Stefan, TLDA scale bars 1 mm.*

2. MODE OF LIFE

As generally supposed, the region of North Germany was largely covered by a shallow epicontinental sea with adjacent lagoons in a tropical to subtropical climate during the Late Jurassic. The climate became distinctly colder in the Early Cretaceous. Again, there were mainly littoral shallow water conditions, but strongly influenced by a fluviatile estuary. Thus the following mode of life can be concluded for the Late Jurassic and Early Cretaceous turtles in North Germany: They lived specialized as scavengers in near-shore areas of an epicontinental sea and large estuaries, respectively, with muddy bottom. Agglomerations of drift wood might have been used as refuge, since they were associated and in competition with crocodiles. Beyond turtles remains of crocodiles are common both in the Oker region (Harz Vorland; KARL *et al.*, 2006) and in Hanover. The Late Jurassic limestone succession which yielded remains of turtles was mainly deposited in a marine milieu, but already evidently influenced by fresh water from the close continental area. Even direct connections to river mouths can be supposed. Therefore it is strongly probable that the turtles lived similar to some of Recent fresh water genera, as for example the large *Batagur*, *Callagur* or *Orlitia* species of wide-spread brackish water estuaries and on shoals in southeastern Asia (MOLL & MOLL, 2004). With its strongly flattened carapace, in particular *Craspedochelys* is adapted to shallow water areas, maybe even the surf zone.

Tropidemys is characterized by a completely different morphology. In its extremely high and roof-like carapace it resembles the Recent *Kachuga* in southern Asia. The latter lives in the upper course of the large stream systems in India and adjacent areas which are supplied by cold melt water from the Himalayas. They are mainly herbivorous and need to warm up periodically outside the water by using the steep sides of the carapace as solar panels. The rarity of *Tropidemys* in Late Jurassic brackish-marine sediments in North Germany and the fragmentary condition of most of their remains maybe traced back to their original habitat in upper courses of river systems, too.

Most of the fossil turtles discussed in the present article are believed to be able to swim well, though not adapted to the open sea. *Plesiochelys* and *Craspedochelys* are also represented by vertebrae and parts of the extremities with still well-developed and non-reduced articulation, unlike in true marine turtles (Chelonioidea). Additionally their still completely developed claws indicate well movable hands and feet like they are generally present in typical fresh water turtles (KARL *et al.*, 2007a,b).

APPENDIX: THE HITHERTO MOST ANCIENT EVIDENCE OF OSEDAX-LIKE BORINGS

The Recent osteophagous marine "worm" morphogenus *Osedax* (Polychaeta: Palpata: Canalipalpata: Sabellida: Siboglinidae) was originally discovered in 2002 with two species on the ocean bottom in a depth of approximately (2800 m) in bones of whales where it produces borings. Up to now it was believed that it co-evolved with the whales, the source of its prefered diet (HIGGS, LITTLE & GLOVER, 2010). In the meantime it could be also experimentally cultivated in cattle bones. This fact as well as the reconstructed molecular clock back to at least the Cretaceous period led to the conclusion that *Osedax* originally might have infested fish or marine "reptiles" long before the marine Mammalia evolved. The first record in bones of birds (KIEL, KAHL & GOEDERT, 2010) proves that *Osedax* evidently feed upon penguin-like diving birds.

Our re-examination of the Late Jurassic turtle *Tropidemys seebachi* shows that *Osedax*-like marine animals lived even much earlier. This would be another strong reference to the fact that the specialization on whale bones evolved secondarily and a long time later. Additionally, the occurrence of *Osedax*-like animals in the Late Jurassic epicontinental sea in North Germany shows that such organisms were originally not restricted to the deep-sea. This is supported by the discovery of a third Recent species in 2005 which fed on

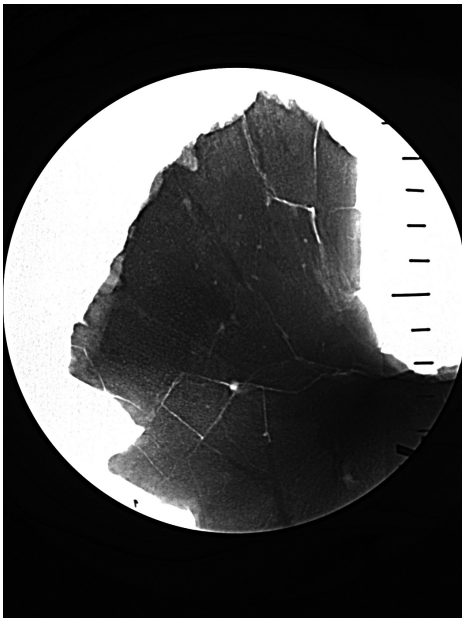


Plate 4: Osedacoides jurassicus *n. ichnogen. n. ichnosp., x-ray photograph of GZG.V.773-34 (plate 3). Photograph by Dipl.-Restaurator Norbert Eichelmann, TLDA scale bars 1 mm.*

whale bones in a depth of about 120 m. As osteophagous Polychaeta *Osedax* belongs to the decomposing animals among the carcass feeders. As a detritus feeder *Osedax* might not have been closely adapted to particular hosts like a true parasite.

In spite of the fact that the borings most probably were produced by an organism similar to *Osedax* there is no direct evidence that it was the genus *Osedax* itself. There are only ichnofossils known, but no body remains of the animal. A definite assignment of the borings to a particular body-based taxon (morphotaxon) is impossible. Therefore we prefer to establish a new ichnotaxon for these fossils.

Thereby we follow BROMLEY (1972) who proposed not to use the names of the animals but to establish ichnotaxa for borings in hard substrates, even if the producers (like for example Bivalvia or Bryozoa) can be largely ascertained by their typical morphology. BROMLEY (1972) used the ichnogenus *Trypanites* Mägdefrau, 1932 as an example which he defined as simple shaft- or pocket-like borings with a single opening whose producer is not incontestably known. Based upon his revised diagnosis, and calibrated by its type ichnospecies *Trypanites weisei* Mägdefrau, 1932 ("Simple, unbranched borings in hard substrate with a single opening to the surface") *Trypanites* can now be generally used in a wider sense for such borings.

***Osedacoides* n. ichnogen.**

TYPE ICHNOSPECIES: *Osedacoides jurassicus* n. ichnosp.

ETYMOLOGY: *Osedacoides* = *Osedax*-like.

DIAGNOSIS: Simple, basally branched borings in marine vertebrate bones with a single opening to the surface.

***Osedacoides jurassicus* n. ichnosp.**

HOLOTYPE: GZG.V.773-34: Borings in hyoplastron sin. (MAACK, 1869: plate 35, fig. 35 = original of *Stylemys lindenensis*, now: *Tropidemys seebachi*, pl. 2, figs. 3-4, pls. 3-4).

ETYMOLOGY: Jurassicus = Jurassic, the type stratum.

TYPE LOCALITY: Lindener Berg, Hanover, Lower Saxony.

TYPE STRATUM: Late Jurassic: Middle Kimmeridgian.

DIAGNOSIS: Average diameter of openings = 1-3,5 mm.

REMARKS: In agreement with BROMLEY (1972; see above) the name of the Recent morphospecies *Osedax* should no more used for fossil borings in vertebrate bones.

ACKNOWLEDGEMENTS

We are grateful to the following persons: Dr. Mike Reich (Göttingen) who made the specimens available to us, as well as Brigitte Stefan and Dipl.-Restaurator Norbert Eichelmann (TLDA, Weimar) who prepared the photographs for plate 3 and plate 4, respectively.

BIBLIOGRAPHY

BRÄM, H. (1965): Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweiz. Paläont. Abh.*, **83**: 3-190.

BROMLEY, R. G. (1972): On some ichnotaxa in hard substrates, with a redefinition of *Trypanites* MÄGDEFRAU. *Paläont. Z.*, **46 (1/2)**: 93-98.

DEUTSCHE STRATIGRAPHISCHE KOMMISSION (DSK) (ed.; co-ordination and layout: M. MENNING & A. HENDRICH) (2002): Stratigraphische Tabelle von Deutschland 2002. Plate 96 x 130 cm and folding plate A4, Potsdam (GeoForschungsZentrum). Frankfurt a. M. (Forsch. Inst. Senckenberg).

FUENTES VIDARTE, C.; MEIJIDE CALVO, M. & MEIJIDE FUENTES, F. (2003): Nueva tortuga para el Cretácico Inferior de Salas de los Infantes (Burgos, España): *Salasemys pulcherrima* nov. gen. nov. sp. [A new turtle for the Lower Cretaceous of Salas de los Infantes (Burgos, Spain): *Salasemys pulcherrima* nov. gen. nov. sp.]. *Stud. Geol. Salmant.*, **39**: 109-123.

GAFFNEY, E. S. & MEYLAN, P. A. (1988): A phylogeny of turtles. 103-156. *In*: BENTON, M. J. (Ed.): *The phylogeny and classification of tetrapods*. Volume 1. *Amphibians, Reptiles, Birds. Systematics Association*, Special Volume 35A. Oxford University Press, Oxford, 377 pp.

HIGGS, N. D.; LITTLE, C. T. S. & GLOVER, A. G. (2010): Bones as biofuel: a review of whale bone composition with implications for deep-sea biology and palaeoanthropology. *Proc. Roy. Soc. B*, published online 2010-08-11: <http://rspb.royalsocietypublishing.org/content/early/2010/08/05/rspb.2010.1267.full.html#ref-list-1>.

KARL, H.-V. (1997): Schildkröten aus dem Kimmeridge von Nettelstedt und Wallücke/Deutschland (Reptilia, Testudines). *Mauritiana (Altenburg)*, **16** (2): 289-298.

KARL, H.-V. (2002): Übersicht über die fossilen marinen Schildkrötenfamilien Zentraleuropas (Reptilia, Testudines). *Mauritiana (Altenburg)*, **18 (2)**: 171-202.

KARL, H.-V.; GEHLER, A.; RODEN, V. J. & REICH, M. (2007a): Die Schildkröten des nordwestdeutschen "Wealden" (Unter-Kreide: Berriasium) und ihre Paläoökologie.- *In*: ELICKI, O. & SCHNEIDER, J. (Eds.): Fossile Ökosysteme. 77. Jahrestagung Paläont. Ges., Wiss. Mitt. Inst. Geol. TU Bergakad. Freiberg, **36**: 64-65 [poster presentation, 77th Annual Meeting, Paläontlogische Gesellschaft, Freiberg].

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 (with remarks on the history of quarrying the "Langenberg Limestone" and "Obernkirchen Sandstone"). *Clausthaler Geowiss.*, **5**: 59-77.

KARL, H.-V.; STAESCHE, U.; TICHY, G.; LEHMANN, J. & PEITZ, S. (2007b): Systematik der Schildkröten (Anapsida: Chelonii) aus Oberjura und Unterkreide von Nordwestdeutschland. *Geol. Jb.*, B **98**: 5-89.

KIEL, S.; GOEDERT, J. L.; KAHL, W.-A. & ROUSE, G. W. (2010): Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones. *Proc. Nat. Acad. Sci. USA*, **107 (19)**: 8656-8659.

KIEL, S.; KAHL, W.-A. & GOEDERT, J. L. (2010): *Osedax* borings in fossil marine bird bones. *Naturwissenschaften. The Science of Nature*, published online: 2010-11-20: doi: 10.1007/s00114-010-0740-5: <http://www.springerlink.com/content/6vpv015338513652/>.

KUHN, O. (1964): Testudines. *In*: WESTPHAL, F. (Ed.): *Fossilium Catalogus, I: Animalia*, **107**: 5-299.

LAPPARENT DE BROIN, F. de (2001): The European turtle fauna from the Triassic to the Present. *Dumerilia*, **4 (3)**: 155-217.

LYDEKKER, R. (1889): *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Nat. Hist.)*. Part. III. *The Order Chelonia*. London (Longmans), 239 pp.

MAACK, G. A. (1869): Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. *Palaeontographica*, **18**: 193-336.

MÄGDEFRAU, K. (1932): Über einige Bohrgänge aus dem unteren Muschelkalk von Jena. *Paläont. Z.*, **14**: 150-160.

MEYLAN, P. A. (1988): *Peltochelys* Dollo and the relationships among the genera of the Carettochelyidae. *Herpetologica*, **44 (4)**: 440-450.

MILNER, A. R. (2004): The Turtles of the Purbeck Limestone Group of Dorset, Southern England. *Palaeontology*, **47 (6)**: 1441-1467.

MOLL, D. & MOLL, E. O. (2004): *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford University Press, 393 pp.

OERTEL, W. (1924): Die Schildkrötenfauna des nordwestdeutschen oberen Jura. *Paläont. Z.*, **6**: 43-79.

PICTET, F.-J.; CAMPICHE, G. & TRIBOLET, G. de (1858-1860): Descriptions des fossiles du terrain Crétacé des environs de Sainte-Croix. Première Partie. *Matériaux pour la Paléontologie Suisse*, **2 (1)**: 380 pp. Genève.

PORTIS, A. (1878a): *Ueber fossile Schildkröten aus dem Kimmeridge von Hannover*. Von der phil. Fac. der Univ. Göttingen gekrönte Preisschrift, 1-18, Taf I-IV, Cassel (Theodor Fischer).

PORTIS, A. (1878b): Ueber fossile Schildkröten aus dem Kimmeridge von Hannover. *Palaeontographica*, **25 (1)**: 125-140.

RÜTIMEYER, L. (1873a): Die fossilen Schildkröten von Solothurn. *N. Denkschr. allg. schweiz. naturforsch. Ges.*, **25 (2)**: 1-185.

RÜTIMEYER, L. (1873b): Über den Bau von Schale und Schädel bei lebenden und fossilen Schildkröten, als Beitrag zu einer paläontologischen Geschichte dieser Thiergruppe. *Verhandl. schweiz. naturforsch. Ges.*, **6**: 1-137.

WIMAN, C. (1930): Fossile Schildkröten aus China. *Palaeontol. Sinica* (C), **6**: 1-56.

ZITTEL, K. A. (1889): *Handbuch der Paläontologie, Reptilien*: 3. *Ordnung Testudinata*: 500-553, figs. 478-504. München.

