

Mainzer naturwiss. Archiv	57	S. 93–100	6 Fig., 1 Plate	Mainz 2020
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**On the humerus of the most ancient sea turtle,
Oertelia gigantea (OERTEL, 1914), from the Berriasian of
Northern Germany**

HANS-VOLKER KARL, ELKE GRÖNING & CARSTEN BRAUCKMANN

Kurzfassung

**Der Humerus der ältesten Meeresschildkröte, *Oertelia gigantea* (OERTEL, 1914),
aus dem Berriasium von Norddeutschland**

Der bislang unpublizierte Humerus einer Meeresschildkröte aus dem Oberen Berriasium (Unterkreide) von Gronau in Nordrhein-Westfalen (Norddeutschland) wird beschrieben und *Oertelia gigantea* (OERTEL, 1914) zugeordnet. Dieser Humerus aus dem Berriasium ist etwa 20 Millionen Jahre älter als das aus dem Aptium stammende Typusmaterial der Art und repräsentiert den weltweit ältesten Nachweis einer echten Meeresschildkröte.

Abstract

A yet unpublished right humerus of a sea turtle of Upper Berriasian (Early Cretaceous) age from Gronau in North Rhine-Westphalia, Northern Germany, is described and assigned to *Oertelia gigantea* (OERTEL, 1914). With a Berriasian age the humerus is significantly older than the Aptian type material of *Oertelia gigantea* and thus now the most ancient record of true sea turtles, dating back their first appearance approximately 20 million years.

Key words

Testudines, *Oertelia gigantea* (OERTEL, 1914), Early Cretaceous, Upper Berriasian, Northern Germany, humerus

1. Introduction

The specimen described in this article originates from the abandoned and now flooded clay pit “Ziegleitongrube Gerdemann & Co.” (former pit of Gerdemann & Co. brickworks - today Schieferkuhle) (Fig. 1) in Gronau, North Rhine-Westphalia, Northern Germany (7°00'20.69"E, 52°13'15.72"N). Palaeogeographically the locality is situated in the western limnic to brackish marginal facies of the Lower Saxonian Wealden Basin. The exposure comprises a succession from the brackish Upper Berriasian (Osterwald Member of the uppermost Bückeberg Formation) to the marine ammonite-bearing Lower Valanginian (Fig. 2). The Osterwald Member consists of interbedded strata of mudstones and thin lumachelles. Detailed sections and further information on the geology and palaeontology of the locality are given in BES-



Fig. 1: Compiled distribution map of the locations of Toxochelyidae and *Desmemys* in Germany, based upon KARL (2002), KARL & NYHUIS (2012) and KARL et al. (2012a, b): circle – *Oertelia*, square – *Ctenochelys*, asterisk – *Desmemys*. 1 – Former brickyard of Windmeyer & Schünhoff, Kastendamm, Garbsen-Berenbostel NW Hanover, Lower Saxony, type locality of *Toxochelys gigantea*; 2 – Former clay pit of Gerdemann & Co., Gronau, North Rhine-Westphalia, type locality of *Desmemys bertelsmanni*; 3 – Alsen quarry, Lägerdorf near Itzehoe, Schleswig-Holstein; 4 – Langenberg near Oker, Lower Saxony. With use of an icon by Triebold Paleontology Inc.: <http://www.trieboldpaleontology.com/toxochelys.html>

SIN (1928), HOSIUS (1893), KEMPER (1961a, b, 1963, 1970, 1971, 1976, 1992), WEGNER (1926), and HAMPE (2013). It was one of the most important outcrops yielding fossils of the Wealden facies (Bückeberg Formation, Berriasian, lowermost Cretaceous) in Germany during the first part of the 20th Century. It is well known for a number of vertebrate fossils, e. g. a skeleton of the elasmosaurid *Brancaasaurus brancai* (WEGNER, 1914), the leptocleidid plesiosaur *Gronausaurus wegneri* HAMPE, 2013, an armoured dinosaur (SACHS 1997, SACHS et al. 2016) [Ankylosauria, gen. et sp. indet./ ichnospecies *Metatetrapous valdensis* NOPCSA, 1923] and the pleurosternid turtle *Desmemys bertelsmanni* WEGNER, 1911 (KARL et al. 2012b).

The owners of the clay pit, Mr. GERDEMANN and Mr. BERTELSMANN, donated the turtle remains to the Mineralogical and Geological Museum of the University of Muenster. Some parts of it have been described by Th. WEGNER (1911) who established the name *Desmemys bertelsmanni* for them. These remains were completely destroyed during World War II. Fortunately Dr. Lennart SCHLEICHER integrated a single hypoplastron from the original material into the exhibition of the Driland-Museum in Gronau (Westphalia) after the war. This specimen was described by KARL et al. (2012b). Only the storage boxes with several bone fragments and their labels withstood until today.

In 2013, Dr Markus BERTLING, Geomuseum of Westfälische Wilhelms Universität, Muenster (GMM), discovered a turtle bone in an adjacent drawer which is very similar in preservation and mineralization to the original samples as well as to new collections by one of us (HVK 2010) at the type locality. Therefore it can be assumed to belong to WEGNER's specimens, too.

The bone is a humerus of the skeleton of the Toxochelyidae and is extremely similar to the hitherto most ancient (Aptian, Early Cretaceous) sea turtle *Oertelia gigantea* (OERTEL, 1914) to which it is assigned here. The type material of *Oertelia gigantea* was collected in the former Kastendamm brickyard of WINDMEYER & SCHÜNHOF (now transformed

into the so-called Berenbostel Lake) in Garbsen-Berenbostel NW Hanover (Lower Saxony, Northern Germany) where exploitation was active from 1890 until 1922. The horizon with *Oertelia gigantea* in the Kastendamm section belongs to the biozone of *Deshayesites deshayesi* and thus to the middle part of the Lower Aptian (BIERMANN 2010, KARL et al. 2012b).

For general remarks concerning Cretaceous Toxochelyidae in North America see EVERHART (2005), HAY (1908), and ZANGERL (1953). The detailed anatomy of the humerus of sea turtles is dealt with in WYNEKEN (2001). KARL (2002) presented palaeogeographic maps for toxochelyid turtles in Central Europe. The ultrastructure of the humerus of turtles is shown in NAKAJIMA et al. (2014).

With a Berriasian age the humerus described here is significantly older than the Aptian type material of *Oertelia gigantea* and thus now the most ancient record of true sea turtles, dating back their first appearance approximately 20 m. y.

2. Systematic Palaeontology

Order Testudines LINNAEUS, 1758

Infraorder Cryptodira COPE, 1868

Superfamily Chelonioidea BAUR, 1893

Family Toxochelyidae BAUR, 1895

Genus *Oertelia* KARL, BIERMANN & TICHY, 2012

Oertelia gigantea (OERTEL, 1914)

Locality: Ziegeleitongrube GERDEMANN (former pit of GERDEMANN & Co. brickworks) in Gronau, North Rhine-Westphalia: Westphalia, Northern Germany (Fig. 1).

Horizon: Osterwald Member; Berriasian, lowermost Early Cretaceous, Wealden facies, western part of the Lower Saxonian Cretaceous Basin) (Fig. 2).

Description of the new material: The comparison of the humerus of a sea turtle with that one of a terrapin is shown in Fig. 3. The dimensions of the new humerus are compared with several other humeri previously described by KARL et al. (2012a) in plate 1. Incomplete measurements are in parentheses.

Abbreviations: GMM: Geomuseum, Westfälische Wilhelms-Universität Münster; GZG: Geoscience Centre, University of Göttingen.

Number	Length	Proximal width	Distal width	Thickness
GMM	195	98.5	78.5	25.25 × 26.05
GZG.V.5005	(65.95)	(54.88 × 49.70)	-	20.14
GZG.V.5032	-	Corpus (7.09) Caput 11.76 × 9.68	-	-
GZG.V.5006	-	-	73.68 × 32.36	48.40 × 22.70
GZG.V.5033	(15.18)	-	16.75 × 6.53	(9.44 × 3.75)
GZG.V.5034	(11.86)	-	18.45 × 6.22	(11.70 × 2.56)

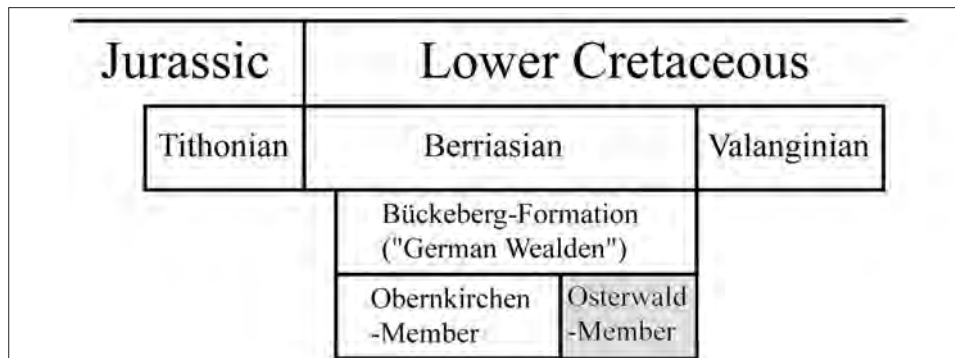


Fig. 2: Lithostratigraphy of the Berriasian in Northwestern Germany, modified from KEMPER (1992), from KARL et al. (2012), Osterwald Member marked in gray.

The present humerus is mainly characterized by the following features:

- (i) relatively greater extent than the hitherto known bone of *Desmemys*;
- (ii) very broadened proximal and distal humerus ends like in *Toxochelys*;
- (iii) round to oval cross-section of the humerus shaft, contrary to *Toxochelys* where it is significantly flatter.

Remarks: The main question is to distinguish the humeri of both, *Desmemys bertelsmanni* and *Oertelia gigantea* of the same locality and age.

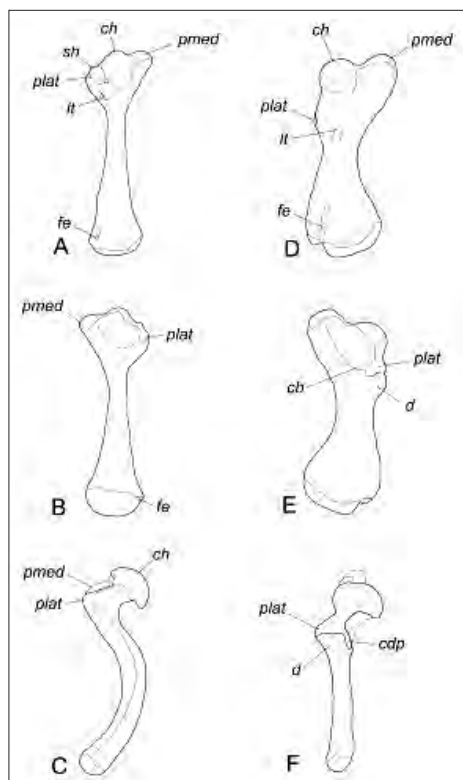


Fig. 3: Comparison of the humeri of the geoemydid Japanese pond turtle (*Mauremys japonica*; A-C) and of the loggerhead turtle (*Caretta caretta*; D-F). Dorsal (A, D), ventral (B, E) and frontal view (C, F). Abbreviations: cb – muscle attachment scar for the musculus coracobrachialis brevis; cdp – crista deltopectoralis; ch – caput humeri; d – muscle attachment scar for the m. latissimus dorsi and m. teres major; plat – processus lateralis; pmed – processus medialis; sh – shoulder of the caput humeri; redrawn after HIRAYAMA (1992).

According to WEGNER (1911), the lost humerus of *Desmemys bertelsmanni* was flat and sigmoidal (Fig. 4) (for the pelvic girdle see KARL & SAFI 2019). The processus medialis was exactly half as long as the flattened proximal part (“proximal” and “distal” exchanged by mistake in the original description). The joining caput was only slightly longer and passed into the likewise stretched processus lateralis without contraction. This flattening passed into the cylindrical corpus and widened again towards the narrower distal end. From the centre a furrow of about 1 mm depth ran along the anterior margin of the humerus. This furrow as well as the flattened areas might have been caused by tectonic deformation. A phalanx of the right hand was mentioned as short, robust and emyd-like. These characters are typical for the Pleurosternidae and thus for a freshwater turtle. They are clearly different from those of *Oertelia* as in particular shown in Fig. 5. The latter represents a true marine turtle.

The distinct differences in the dimensions between *Desmemys* and *Oertelia* are also very important to distinguish both genera. Though *Desmemys* is hitherto only known by remains of juvenile and subadult animals, a maximal CL of about 0.75 m can be estimated by comparison with other genera of the Pleurosternidae. Measurements on a cast of a complete juvenile animal of *Toxochelys latiremys* show a humerus / CL relation of 4.9. Therefore the total length of 195 mm of the present humerus of *Oertelia* leads to a total CL of 96 cm. Considering the still juvenile characters of the distal parts of the articulation areas, the CL of the adult animals must have been distinctly longer than 1 m. Even the lost skull of the type specimen had an estimated condylobasilar length of 34.38 cm which caused OERTEL (1914) to establish the specific name “*gigantea*”.

The strong differences between the shapes of the humeri of *Desmemys* and *Oertelia* as well as the similar morphology of the latter with *Toxochelys* are evident as also shown in Fig. 5. The dendrogram of the character analysis of the humeri of some selected comparable taxa leads to two distinct main groups (Fig. 6). *Desmemys*



Plate 1: *Oertelia gigantea* (OERTEL, 1914), GMM, without number, right humerus, Berriasian, Early Cretaceous, Gronau, North Rhine-Westphalia, Germany: a) dorsal view, b) ventral view, c) frontal view, d) posterior view (Photo: Hauke ARNOLD).

and *Mauremys* are terrestrial freshwater turtles which can also live in brackish habitats. On the other hand, *Toxochelys* and *Caretta* are pelagic genera and shelf-dwellers. Their descendant *Psephophorus* is a highly pelagic sea turtle. *Oertelia* is certainly a sister taxon of the latter, but it is still allocated to the centre between the two main groups. This again confirms the assignment of the present humerus to a true sea turtle.

3. Discussion

As pointed out by KARL et al. (2012a), *Oertelia gigantea* is the most ancient true sea turtle, with a stratigraphical age of about 120 million years and thus even older than *Santanachelys gaffneyi* HIRAYAMA, 1998. The latter is nearly ten million years younger. *Santanachelys gaffneyi* comes from the Romualdo Unit of the Santana Formation in Brazil. It was discov-

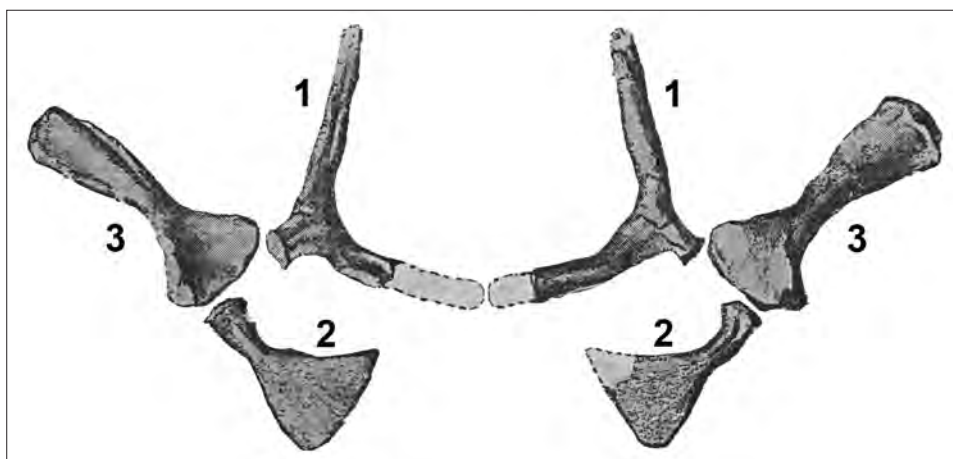


Fig. 4: Historical reconstruction of the shoulder girdle of *Desmemys bertelsmanni*, from the original description (WEGENER 1911). 1 – Scapula, 2 – coracoid, 3 – humerus, see KARL & SAFI (2012).

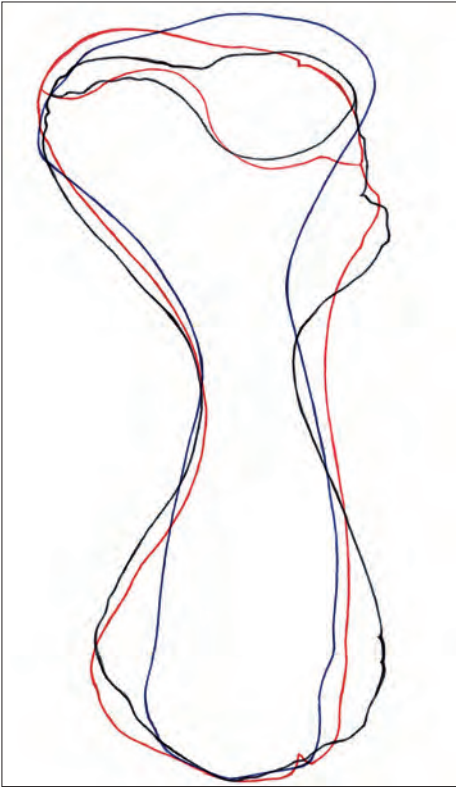


Fig. 5: Differences between the outlines of the right humeri of *Desmemys* (blue), *Oertelia* (black), and *Toxochelys* (red), drawn to the same size.

ered in the vicinity of Santana do Cariri (GPS data: -7.185, -39.737) in the state of Ceará. The Romualdo Unit is allocated to the Upper Aptian or Lower Albian. Both, *Santanachelys* as well as *Oertelia* developed elongated and flattened phalanges as a typical adaption for a paddle or flipper. Due to the morphology of the extremities HIRAYAMA (1997) assumes that the Protostegidae mainly lived at the top of the water column and their diving capabilities were not yet well developed. Compared with modern sea turtles, the morphology of the paddle of the Protostegidae was even more derived. This is the reason why for this family a diet of planktonic organisms is assumed (HIRAYAMA 1997). It is possible that the limb with immovable metacarpals and elongated fingers within the Protostegidae and the remaining Chelonioidae (Cheloniidae and Dermochelyidae) could have developed by convergence (HIRAYAMA 1998), relating to the development of the paddle. As shown by HIRAYAMA (1998), Ctenochelyidae are rather ground dwellers as good swimmers which lived in very shallow sea areas, and subsisted by benthos, which also is true in modern Chelydridae (snapping turtles) and Trionychidae (trionychine turtles). Other features for the primitive state of development of *Toxochelys* are (i) the small plastron with a narrow bridge area and (ii) the weak development of the shoulder girdle and pelvic girdle (HIRAYAMA 1997). The

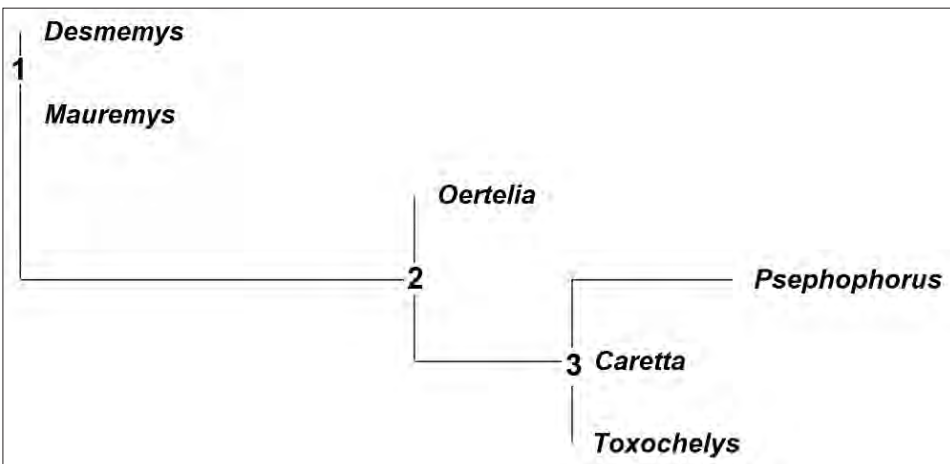


Fig. 6: Most parsimonious tree of the compared genera found by PARS, Discrete character parsimony algorithm, version 3.6a3© Joseph FELSENSTEIN (1986), prepared by using TreeView©Roderic Page (see Fig. 5).

rather primitive transformation of running feet to paddling (mobile device displacements between the 1st and 2nd finger) and the dorsal direction of orbitae should be an evidence for his theory (HIRAYAMA 1997). In this case, extended migrations to the nesting sites would not be needed, since habitat and nestling sites would be only in short distance from each other. This assumption would limit the life of *Oertelia gigantea* mainly to the coastal areas of an adjacent sea, however, the strongly flattened and wide extended articulation ends of the present humerus suggest a more pelagic mode of life.

4. Acknowledgements

We are grateful to the following persons: Dr Markus BERTLING (Geomuseum, Westfälische Wilhelms Universität, Muenster, Germany = GMM), who made the specimen available to us, Dr Mike EVERHART (Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA) for helpful comments on specimens under his care, and to Prof Dr Hans-Jürgen GURSKY (Clausthal University of Technology, Germany) for linguistic corrections.

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APPENDIX 1:

Character description and analysis:

- 1 – Originally in terrestrial turtles the humerus shaft is round to oval in cross-section (0); in marine turtles it is much flattened (1).
- 2 – In terrestrial turtles the proximal and distal ends of humeri are slender or only moderately widened (0); in marine turtles they are strongly broadened (1).
- 3 – In terrestrial turtles the processus medialis (pmed) does not protrude the caput humeri (ch) (at least not essentially); in marine turtles it is significantly longer (1).
- 4 – In terrestrial turtles the lateral processus (plat) is close to the caput humeri (but not fused) but separated from it (0); in marine turtles it is fused with the caput humeri and shifted towards the corpus (1).
- 5 – Crista deltopectoralis (cdp) originating in lateral processus (plat) is absent (0); present (1).
- 6 – In terrestrial turtles the attachment of musculus latissimus dorsi and m. teres major (lt) is always close to the plat and thus close to the caput humeri (0); in marine turtles it is shifted on the humerus shaft (1).
- 7 – In terrestrial turtles the foramen ectepicondylare is absent or hole-like and lies in the distal region of the humerus shaft (0); in marine turtles it is groove-shaped and lies in the distal region of the humerus shaft from where it extends through the joint area (1).
- 8 – Processus radialis (the transformed lateral processus) is absent (0); present (1).

Data Matrix: *Mauremys* 00000000, *Desmemyx* 000000?0, *Oertelia* 011111100, *Toxochelys* 111111110, *Caretta* 111111110, *Psephophorus* 11110111.

PARS – Discrete character parsimony algorithm, version 3.695: One most parsimonious tree found: ((*Psephophorus*:2.00,*Caretta*:0.00,*Toxochelys*:0.00):2.00,*Oertelia*:0.00): 5.00,*Desmemyx*:0.00,*Mauremys*:0.00) requires a total of 9.00 steps

between	and	Length
1	2	5.00
2	3	2.00
3	<i>Psephophorus</i>	2.00
3	<i>Caretta</i>	0.00
3	<i>Toxochelys</i>	0.00
2	<i>Oertelia</i>	0.00
1	<i>Desmemyx</i>	0.00
1	<i>Mauremys</i>	0.00

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Autor(en)/Author(s): Karl Hans-Volker, Gröning Elke, Brauckmann Carsten

Artikel/Article: [On the humerus of the most ancient sea turtle, *Oertelia gigantea* \(Oertel, 1914\), from the Berriasian of Northern Germany 93-100](#)