Turtle remains (Testudines, Chelonioida) from the Middle Turonian of northwest Germany

C. Diedrich & R. Hirayama

1 Nansenstr. 8, D-33790 Halle/Westphalia, e-mail: cdiedri@gmx.net
2 Faculty of Information Teikyo Heisei University Uruido, 2289-23 Ichihara, Chiba 290-0193, Japan; e-mail: renhrym@ab.mbn.or.jp

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Abstract

Turtle remains ascribed to the family Cheloniidae (Testudines, Cryptodira, Chelonioida), collected from the lamarcki zone (Middle Turonian) at Wullen (NW Germany) are described. The material consists of a right humerus, a scapula, a complete costalia, and costalia fragments of a single individual with the humerus indicating a primitive cheloniid of the ‘toxochelyid grade’. The present material, as well as previously recorded chelonioid humeri from the Cenomanian and Turonian of Germany illustrate a progressive diversification of chelonioids during the early Late Cretaceous.

Keywords: Humeri, Turtles, Cheloniidae, Upper Cretaceous, Europe

Introduction

The turtle remains described in the present paper were collected in the 1970s by Mr. A. Duckstein (Münster), from the Middle Turonian as formerly exposed at the Hollekamp quarry (topographical map, 1:25 000 sheet 3907 Ottenstein, co-ordinates R 256755 and H 577120, Fig. 1), which is now flooded and actually a freshwater lake. This important fossil site is very well known in North Germany especially for its rich echinid faunas (Ernst et al. 1998).

Turtle remains are quite rare in the Cenomanian/Turonian of Europe and of special interest. Specimens described here are compared with previously recovered material, in particular humeri. Described have been squamate remains of Coniosaurus crassidens Owen 1850 (Diedrich, 1997, 2001), Dolichosaurus longicollis Owen 1850 (Diedrich, 1999a, 2001) and a cheloniid remain (Diedrich, 1999b).

The material described here is housed in the Geologisch-Paläontologische Institut und Museum der Westfälischen Wilhelms-Universität Münster.
Geological setting

Cretaceous deposits are widely distributed in North Germany. The Late Cretaceous Turonian sediments occur at the margin of the Münster Basin and consist at the Wüllen quarry of slightly cemented white chalks.

The section formerly exposed at the Hollekamp quarry at Wüllen (Fig. 2) ranged from the uppermost Upper Cenomanian, dated by a rare huge *Puzosia dibleyi* Spath var. *spinosus* in the *M. geslinianum* ammonite zone, to the Lower Coniacian is developed as Rotpläner Member swell facies (compare Diedrich, 2001, Ernst et al. 1998). The section published by Ernst (1978) is here extended (Fig. 2). The turtle remains were collected from the Middle Turonian *lamarcki* inoceramid zone. This zone is highly fossiliferous, having yielded echinoids, ammonites and other macroinvertebrates (Ernst, 1967, 1978; Löschner, 1910, Ernst et al., 1998).

The environment of the cheloniid finding must have been the slope facies in the Münster Cretaceous
Basin (compare Ernst, 1967). Löscher (1910) and Ernst (e.g. 1978) published many macroinvertebrates. The echinid genera Conulus, Discoides, Echinogallerus, Echinocorys, Sternotaxis, Infultaster, Micraster and Hemaster are often accumulated in scour troughs or the body chambers of the huge ammonites Lewesiceras peramplum or Puzosia sp. The most abundant irregular echinid is Conulus.

Systematic palaeontology

Order Testudines Linné 1758
Superfamily Chelonioidae Agassiz 1857
Family Cheloniidae Gray 1825
Genus and species indeterminate
Fig. 3.1-3.3

Material

A right humerus, one costalia, a fragmentary scapula, and eleven costal fragments, all assumed to have belonged to a single individual, Geologisch-Paläontologisches Institut und Museum der Westfälischen Wilhelms-Universität Münster, No. A.3A-32.

Description

As preserved the right humerus (Fig. 3.1) is 83 mm long, the maximum width proximally being 39 mm, the maximal distal brightness 21 mm, and the smallest width medially of the corpus femura 12 mm maximum width distally. Slightly flattened and only 7-10 mm thick, although the caput humeri and distal portion appear slightly worn. The medial process is poorly developed, and along the proximal edge not distinctly separated from the humerus. The medial process appears slightly worn. The correct form is nearly 90°. The scar for the M. latissimus dorsi & M. teres major is of 50 mm length and 106 mm in width, and shows well-defined scute sulci of vertebral and costal scutes. This suggests a relatively wide vertebral scute, equalling the costal in width. The size of this costal indicates the carapace to have been of about 500 mm in total length.

Discussion

An overview of the Testudines was given by Mlynarski (1976). Important monographies and papers of Upper Cretaceous Chelonioids of North and South America were published by Case (1897), Hay (1908), Zangerl (1953a, b) and Zangerl & Sloan (1960). Recently Hirayama (1992, 1995, 1997, 1998), Hirayama & Chitoku (1996), and Hirayama & Hikida (1998) compared Cretaceous sea turtles worldwide.

Cenomanian/Turonian marine sea turtles of Europe are rare and were first figured for the first time from Southeast England by Mantell (1841) as Emys benstedii. New finds from England were described by Owen (1842), who established a new genus Cimochelys benstedii. After some years Geinitz (1849) mentioned one humerus of a chelonioid in central Germany, described later together with a second humerus, both as Chelone carusiana Geinitz 1875 (Geinitz, 1872-75) (now Protostegidae gen. and sp. indet.). Owen (1850, 1851) worked on English Cretaceous cheloniods and described a skull of Chelone pulchriceps (=Rhinochelys pulchriceps). Meyer (1856) collected a carapace with articulated femur of a new turtle from the Greensand (Cenomanian/Turonian) of Kelheim (South Germany) first believed to be an chelonioid and named Helochelis Danubiana Meyer (= Helochelys danubianus Von Meyer 1855, see Mlynarski 1976), but Helochelis is one of the few terrestrial pleurodiran cretaceous turtles of Europe, closely related to the genus Testosteron (cf. Hirayama et al. 2000). Seeley (1869) created the new genus Rhinochelys for a skull of the Cambridge Greensand (Upper Albion to Lower Cenomanian), and referred Owen's material (1850, 1851) to this genus. A carapace fragment of the cheloniid Cimochelys benstedii (Owen 1850) was first figured by Fritsch (1878). The fragment was stored in the Weissenberg Member (Turonian) of Bohemia. Lydekker (1889a, b) described isolated skulls of Rhinochelys as R. cantabricensis Lydekker, R. macrorhina Lydekker 1889, R. elegans Lydekker 1889, R. brachyrhina Lydekker 1889, R. jessoni Lydekker 1889, and R. pulchriceps (Owen 1850) from the Cambridge Greensand (Upper Albion to Lower Cenomanian) of England. In the same year Woodward (1889) mentioned carapace fragments of Cimochelys. In France Moret (1935) collected skulls of R. amaberti Moret 1935 from the Vra-
conien' (Albian). Collaborations (1970) revised this genus *Rhinochelys*, only *R. pulchriceps, R. elegans* and *R. cantabrigiensis* of the Cambridge Greensand (Upper-Albian to Upper-Cenomanian) being valid species. Hirayama (1997) considered the latter two, as well as *R. amaberti* and *Cimochelys benstedi* as synonyms of *R. pulchriceps*. Milner (1987) Fig.e a *Rhinochelys*-skull from Southeast England (Middle to Upper Cenomanian). The described *Cimochelys benstedi* shell remains of the Middle Cenomanian to Turonian represent juvenile protostegids and may belong to the skulls of *Rhinochelys* (Collins, 1970; Milner, 1987).

Humeri of representatives of the superfamily Che- lonioidea are quite diverse, reflecting their specialised locomotion in marine environments (Walker, 1971; Hirayama, 1992). Their morphology was summarised by Hirayama (1992) there we follow his terminology (also Fig.d by Diedrich 1999b) and systematics. For recent reviews of chelonioid systematics based on cladistics, especially of Cretaceous taxa, reference is made to Hirayama (1995, 1997, 1998), Hirayama & Chitoku (1996), and Hooks (1998).

The caput humeri of the described new humerus from Wülten (Fig. 3.1) appears to lack the shoulder developed in most chelonioids except *Toxochelys* and *Osteopygis* (Hirayama, 1992), and is proportionally much smaller than in most chelonioids, including *Cienochelys* (= *Lophochelys* of Hirayama, 1992), *Allopleuron*, Cenozoic cheloniids, most protostegids, as well as dermochelyids (Hirayama, 1992). The angle between the axis of the caput humeri and the humeral shaft is about 135° such as in *Rhinochelys*, but neither

Fig. 3. Chelonioid from the Middle Turonian (*lamarcki* zone) of Wülten. 1. Right humerus, a-b. dorsal, c-d. cranial, e-f. ventral, g-h. caudal; 2a-b. Costalia, dorsal with costal scutes, 3. Right scapula, ventral. Geologisch-Palaontologisches Museum der Westfalischen Wilhelms-Universität Münster, collection No. A.3A-32.
right angle as in *Osteopygis*, nor nearly straight as in *Dermochelys*. The lateral process is small and located very proximally, directly connected to the caput humeri by a bony ridge as in primitive cheloniids such as *Toxochelys* and *Osteopygis*. The scar for the M. latissimus dorsi & M. teres major is small and located anteriorly of the humeral axis as in primitive cheloniids e.g. *Osteopygis* and protostegids e.g. *Rhinochelys*. The present specimen represents a chelonioid of advanced humeral features such as the distal position of the lateral process and the absence of a caput humeri shoulder not seen in freshwater or terrestrial turtles. The shoulder is definitely present in *Toxochelys* and *Osteopygis*, suggesting important differences in phylogenetic and functional meanings in chelonoid evolution. However, other features, such as the poor development of a medial process and the very distal position of the scar for M. latissimus dorsi & M. teres major, suggest it to be a rather primitive cheloniid of the ‘toxochelyid grade’ of Hirayama (1992), which includes *Toxochelys*, *Ctenochelys* and *Osteopygis*. Isolated humeri from the Gault and Cambridge Greensand (Middle-Late Albian) of England, referred to an unnamed cheloniid, are most similar to our specimen in having a relatively small caput humeri and in lacking of the shoulder (Hirayama, 1992; Figs 4A-C). The ratio between the humerus length and the carapace length estimated to have been about 500 mm long (is about 1:5 to 1:6), suggest that its paddles must have been very small, as in primitive chelonioids such as *Toxochelys* and *San- tanachelys gaffneyi* Hirayama 1998 (Hirayama, 1995, 1997, 1998).

Previous records of Cretaceous chelonioid humeri from Germany include specimen described as *Rhinochelys (?) carusiana* from the Turonian of central Germany (Fig. 4.1, 4.3). These specimens illustrated by Geinitz (1872-75) and the one from the Middle Cenomanian recorded by Diedrich (1999b, Fig. 4.2) appear to represent primitive protostegids in view of the development of the lateral process being limited to the anterior region of the humeral shaft. The medial process of those humeri is developed more proximally than in primitive cheloniids of the ‘toxochelyid grade’. However, placement in *Rhinochelys* is doubtful, because humeri from England referred to *Rhinochelys* (e.g. Fig. 4.4), are more slender and have much smaller caput humeri than the humerus of Halle/Westph. (Hirayama, 1992, Fig. 6G-I). *Rhinochelys* humeri show the protostegid derived features such as the anterior faced lateral process and a median concavity of the lateral process, which are absent in the new humerus of Wüllen (Fig. 4.5). The proportions of a humerus figured by Geinitz (1872-75; pl. 46, Fig. 1) are more close to those of *Desmatochelys* from the Cenomanian-Turonian of North America and Japan (Hirayama, 1992, 1995, 1997; Elliott et al., 1997).

![Fig. 4. Comparison of various European chelonioid humeri. 1: Protostegidae, left humerus, Turonian of Bohemia (after Geinitz, 1872-75), Museum Dresden, without No., 2: Protostegidae, left humerus, Middle Cenomanian of Halle/Westphalia (after Diedrich, 1999b), ErdZeit- Center Borgholzhausen, collection No. Ascheloh-mc-1, 3: Protostegidae, right humerus, Upper Albian/Lower Cenomanian of Cambridge (Rhinochelys cantabrigiensis) (Lydekker) after Lydekker, 1889a, b), British Museum of Natural History, collection No. 35175, 4: Protostegidae, right humerus, Turonian of Bohemia (after Geinitz, 1872-75), Paläontologisches Museum der Universität Freiberg, without No., 5: Protostegidae, right humerus, Middle Turonian of Wüllen, Geologisch-Palaontologisches Museum der Westfalischen Wilhelms-Universität Münster, collection No. A.3A-32.](https://www.cambridge.org/core/terms).
The humeri described by Geinitz (1872-75) are best considered a Protostegidae gen. and sp. indet. The isolated left humerus from the Cenomanian of Halle/Westph. was originally referred to *Rhinochelys* (? cf. *carusiana* by Diedrich (1999b). Upon re-examination it appears more likely that this belongs to more advanced protostegids such as *Chelosphargis*, rather than to *Rhinochelys*, since the specimen shows a definite protostegid feature, e.g. the anteriorly faced lateral process with a median concavity absent in *San- tanachelys*, the most primitive protostegid from the Albian of Brazil (Hirayama, 1998). The lateral process is well developed, the distal portion of which is positioned anteriorly of the centre of the humerus as in fairly advanced protostegids such as *Chelosphargis, Protostega*, and *Archelon* (Hirayama, 1992, fig. 6M-U).

The scar for the M. latissimus dorsi & M. teres major is positioned anteriorly of the axis of the humeral shaft unlike in the above-mentioned protostegids where the scar is located at the centre of the shaft. In this feature, it more closely resembles *'Protostega' anglica* Lydekker 1889, a poorly known protostegid, based on isolated humeri from the Albian-Cenomanian of England (compare Hirayama, 1992, fig. 6J-L).

However, in the Halle/Westph. specimen the lateral process is more massive than in *'Protostega' anglica*, and the humeral shaft is wider and more flattened in the latter. Thus, the humerus from Halle/Westph. is best considered a Protostegidae gen. and sp. indet.

The angle between the scapular prong and the acromion of the Wiillen material is nearly 90° in some chelonioids such as extinct *Toxochelys*, *Osteochelys*, *Tasbaka*, *Puppigerus*, extant *Caretta* and *Lepidochelys* (Zangerl, 1953; Moody, 1974; Nessov, 1987; Zangerl et al., 1988). The costalia (Fig. 3.2) and costal fragments of the Wiillen specimen do not contribute anything to the assignment among chelonioids because of lacking well comparable material. The presence of acute sulci of the costal plate just indicates a generalized primitive pattern of the chelonioids and corresponds to the humeral identification. Only humeral morphology can be used for taxonomic analysis in this case.

Cenomanian and Turonian chelonioids are still poorly known worldwide and comparable by their humeri (Fig. 4). Thus, the protostegid humerus from the mid-Cenomanian described by Diedrich (1999b) and protostegid reported material of the mid-Turonian of the open marine facies here seem making a first contribution to our knowledge of morphological diversifications in Cenomanian-Turonian chelonioids. These finds strongly suggest that chelonioid sea turtles of the early Late Cretaceous had possibly reached a diversity comparable to Latest Cretaceous ones. However, some protostegid chelonioids from the Cenomanian/Turonian of Europe have been described, and here a new primitive cheloniid can be added. The diversification of the Chelonioida had begun during the early Late Cretaceous. In post-Turonian, marine turtles were recorded from the Coniacian to Campanian of North America, the Maastrichtian of the Netherlands, and Belgium, the middle to upper Yezo Supergroup (Turonian to Maastrichtian) of northern Japan (Zangerl, 1953a, b, 1960; Nicholls & Russell, 1990; Hirayama, 1995, 1997; Hirayama & Chitoku, 1996; Hirayama & Hikida, 1998; Mulder et al., 1998), and the Maastrichtian of France (Tong, et al., 1998) with much more complete skeletons.

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**References**


