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Amazing graze – Grazing traces of sea urchins on turtles – An example from the Late Jurassic of Switzerland

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(With 7 figures)

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Abstract

Carapaces of marine turtles from the Late Jurassic Solothurn Turtle Limestone (Reuchenette Formation, Late Kimmeridgian) commonly yield rounded pits that may have resulted from epibionts or ectoparasites, although a conclusive interpretation has not yet been presented. Out of a large collection, only very few specimens of carapaces display areas that are more or less densely covered by stellate v-shaped grooves. These are attributed to the ichnotaxon *Gnathichnus pentax* BROMLEY and are interpreted as gnawing and rasping traces of the teeth of hemicidaroid sea urchins. The size of the traces suggests that *Hemicidaris mitra* (AGASSIZ) which is a very frequent and autochthonous part of the fauna was the producer of these stellate grooves. The grazing traces suggest the presence of a post-mortem dense algal cover and indicate an extended exposure time of the carapaces at the sediment-water interface.

Keywords: echinoid grazing traces, ichnofossils, marine turtles, Jurassic, Switzerland.

Zusammenfassung

Rückenpanzer mariner Schildkröten aus den spätjurassischen Solothurner Schildkrötenkalken (Reuchenette Formation, Spätes Kimmeridgium) weisen häufig gerundete Vertiefungen auf. Möglicherweise stammen sie von Epibionten oder Ektoparasiten, eine überzeugende Interpretation fehlt aber bis heute. In zwei grossen Museumssammlungen konnten nun Panzer beobachtet werden, die Bereiche aufweisen, die dicht mit sternförmigen Kratzern überzogen sind. Diese werden dem Ichnotaxon *Gnathichnus pentax* BROMLEY zugewiesen und als Nage- und Weidespuren der Zähne von hemicidariden Seeigeln interpretiert. Die Grösse der Spuren deutet daraufhin, dass *Hemicidaris mitra* (AGASSIZ) – ein sehr häufiger und autochthoner Teil der Fauna – diese sternförmigen Marken erzeugte. Diese Weidespuren deuten auf einen dichten *Post-mortem* Algenbewuchs der

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Panzer und auf eine verlängerten Aufenthaltszeit der Panzer an der Sediment-Wasser Grenzfläche vor ihrer Einbettung.

Schlüsselwörter: Seeigel-Weidespuren, Ichnofossilien, marine Schildkröten, Jura, Schweitz.

Introduction

The first publication on the fossil turtles and the invertebrates from the Solothurn Turtle Limestone was a monograph published in 1863 by Rütimeyer, in which the local stratigraphy and the main fossil producing quarries are described. At that time these limestone where thought to be of Tithonian age. In the 20th century, most of the fossil producing quarries (13 in number) had to be closed down due to economic reasons. Nevertheless, scientific work continued with specimens of museum collections (cf. Bräm 1965; Gaffney 1975, 1976; Fig. 6). In 1986 one of these abandoned quarries (Zetter Quarry; St. Niklaus) was reactivated for a short period of time allowing for systematic excavations to be conducted (Meyer 1994). The Solothurn Turtle Limestone is the uppermost member of the Reuchenette Formation (Thalmann 1966; Meyer & Pittman 1994) and is Late Kimmeridgian in age (*autissiodorensis* Zone). It consists of a series of very fossiliferous biomicrites deposited in a shallow water marine setting (Meyer 1989, 1994; Meyer & Jordan 2000). These and the nerineid packstones were widely used as building stones. The proximity of dried-up tidal flats can be demonstrated by the presence of numerous sauropod dinosaur trackways at the base of the member (Meyer 1993) as well as by the presence of terrestrial plants and vertebrates (Meyer & Thüring 2003). Most of the old localities lie within the Verena Anticline, a small tectonic structure close to the city of Solothurn.

Nine different turtle taxa have been described from all the quarries in the Verena anticline (*Plesiochelys santcaeverenae* Rütimeyer, *Craspedochelys picteti* Rütimeyer, *Thalassemys hugii* Rütimeyer, *Thalassemys moseri* Bräm, *Eurysternum ignoratum* Bräm, *Tropidemys langi* Rütimeyer, *Plesiochelys solodurensis* Rütimeyer, *Plesiochelys etalloni* Pictet & Humbert, *Solnhofia parsonsi* Gaffney, *Platychelys oberndorferi* Wagner). The validity and phylogenetic position of these taxa are still under debate (e.g. Joyce 2000).

The turtles of Solothurn belong to the historically earliest discoveries of marine turtles. Today, they are considered to be the worldwide most significant occurrence of Late Jurassic turtles and still form part of major research topics (see Scheyer 2009).

This paper sets out to describe and interpret special trace fossils that are quite known in the ichnological literature, however, they have never been observed in the palaeoecological context presented here. The first observation of these peculiar traces on turtle carapaces were made by the author in 1990, since then, one additional specimen could be detected in the collection of the Naturmuseum Solothurn.

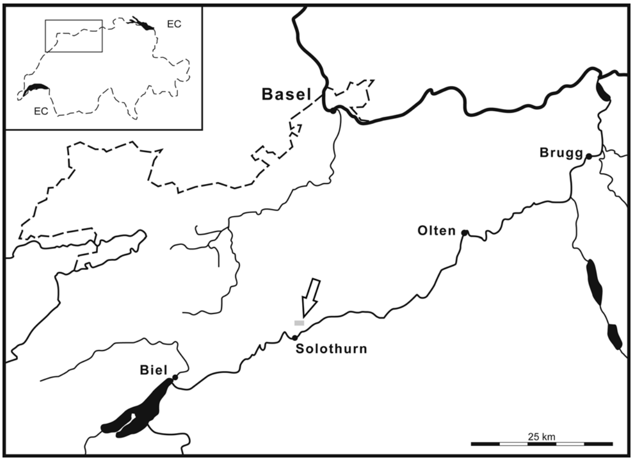

Fig. 1: Map of North-western Switzerland showing the area of Solothurn (Canton Solothurn) where the specimens were found (indicated by an arrow).

Material and Methods

Among the many hundreds of isolated turtle bones and complete specimens of two large collections (Naturmuseum Solothurn (NMS); Naturhistorisches Museum Basel) only two specimens with these distinct trace fossils have been found. Out of 1812 registered turtle remains, 203 specimens consist of either complete carapaces and plastra or half of a complete specimen; the remaining specimens are fragments of different sizes. The Basel collection contains 31 registered turtle remains from the Solothurn area, however, none of the three taxa present (*Plesiochelys*, *Platychelys*, *Thalassemys*) showed any signs of stellate traces.

Very common are rounded holes or pits that seem to be the result of either diagenetic dissolution of pyrite or traces of unknown epibionts such as lepadid cirriped arthropods or ectoparasites such as leeches (e.g. SIDDALL & GAFFNEY 2004).

Results

Description of the traces

V-shaped traces, sometimes arranged in stellate groupings depending on the overall density of traces. They occur as overlapping stars. These grooves have similar extensions and intersect at an angle of around 70°. The size (i.e. length) of the V-shaped markings is around 2 mm.

The marks are not evenly distributed over the whole shell fragments. They occur in dense patches criss-crossing each other and as compound stellate structures and rarely occur

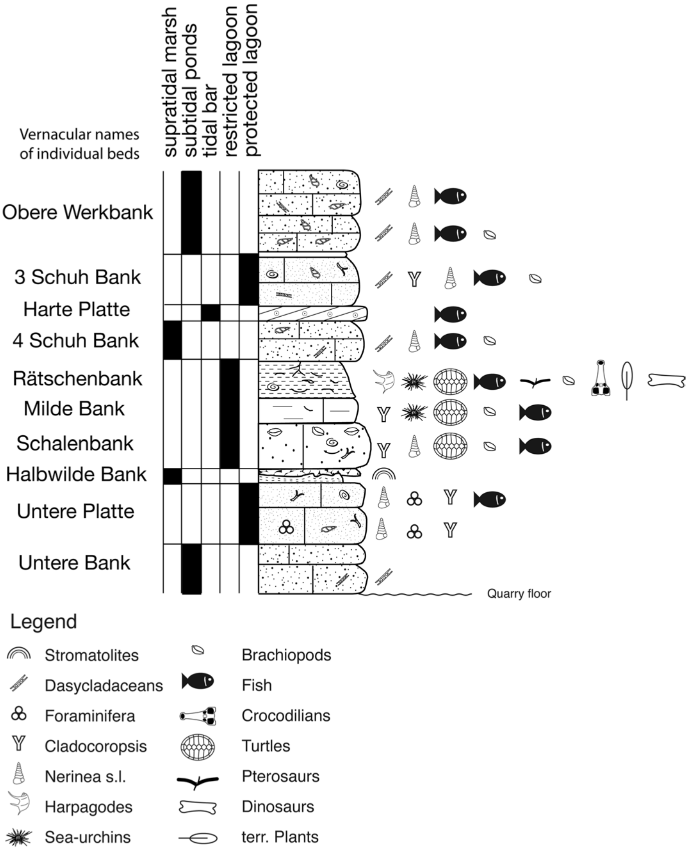

Fig. 2: Geological section of the Solothurn Turtle Limestone Member (Reuchenette Formation, Late Jurassic, Kimmeridgian) with the occurrence of vertebrate and invertebrate fossils. (Zetter Quarry, St. Niklaus; from Meyer & Thüring 2009).

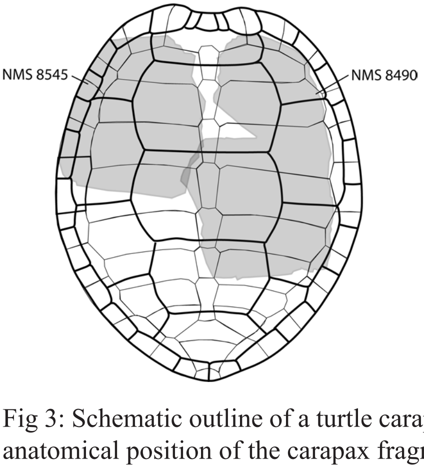

Fig 3: Schematic outline of a turtle carapace (*Plesiochelys etalloni*). Gray shade areas indicate the anatomical position of the carapace fragments.

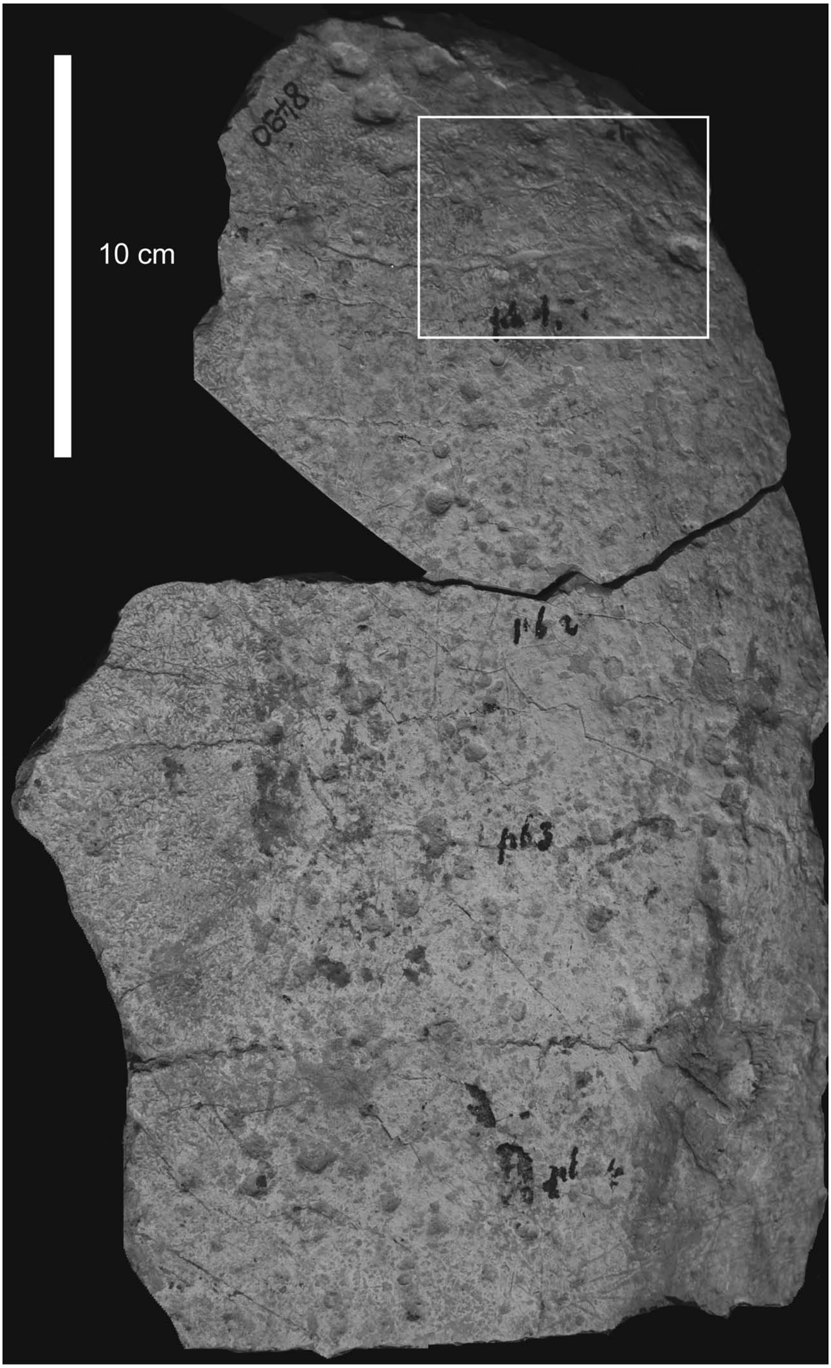

Fig. 4: Right anterior part of a carapax of *Plesiochelys* (NMS 8490) with location of Figure 5, rounded pits are present (see text for interpretation).

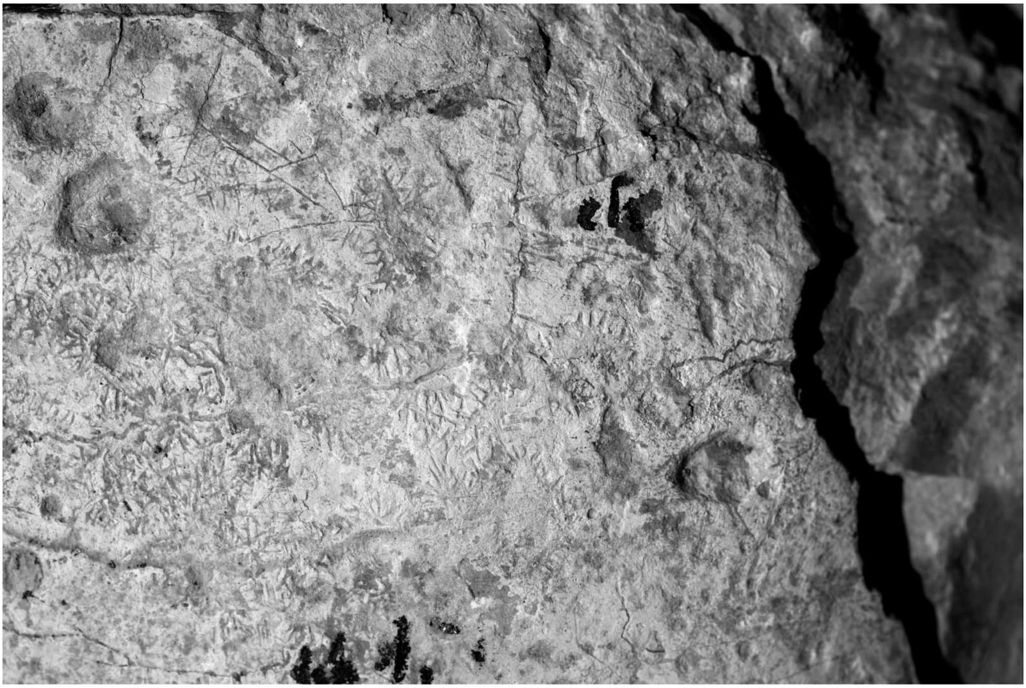

Fig. 5: Details of *Gnathichnus pentax* Bromley on NMS 8490.

as a single pentaradiate stellate module. The traces penetrate the surface of the compacta of the bone. They occur as negative epichnia on the dorsal surface of carapaces of the marine turtle *Plesiochelys etalloni* Pictet & Humbert. Two turtle specimens with these traces have been observed:

1) Specimen NMS 8490 (alte Nummer 404) consists of a right anterior part of the carapax of *Plesiochelys etalloni* turtle (Figs 3, 4, 5) with a length of 23 cm and a width of 15 cm. It was embedded in disarticulated state. About half of the visible surface is affected by these traces.

2) Specimen NMS 8545 (a.N. 83) is a left anterior to mid part of the carapax of a *Plesiochelys etalloni* with a length of 20 cm and a width of 30 cm. Like NMS 8490, it was embedded in disarticulated state (Figs 3, 6, 7). The microfacies of the adhering matrix allows an attribution to a specific horizon within the STL unit, the so-called Rätschenbank (Fig. 2)

Interpretation

The regular stellate v-shaped grooves are highly distinctive and are interpreted to have been produced by regular echinoids. The grooves represent the browsing, grazing or foraging traces made by the dental erosion of their lantern. These traces have been attrib-

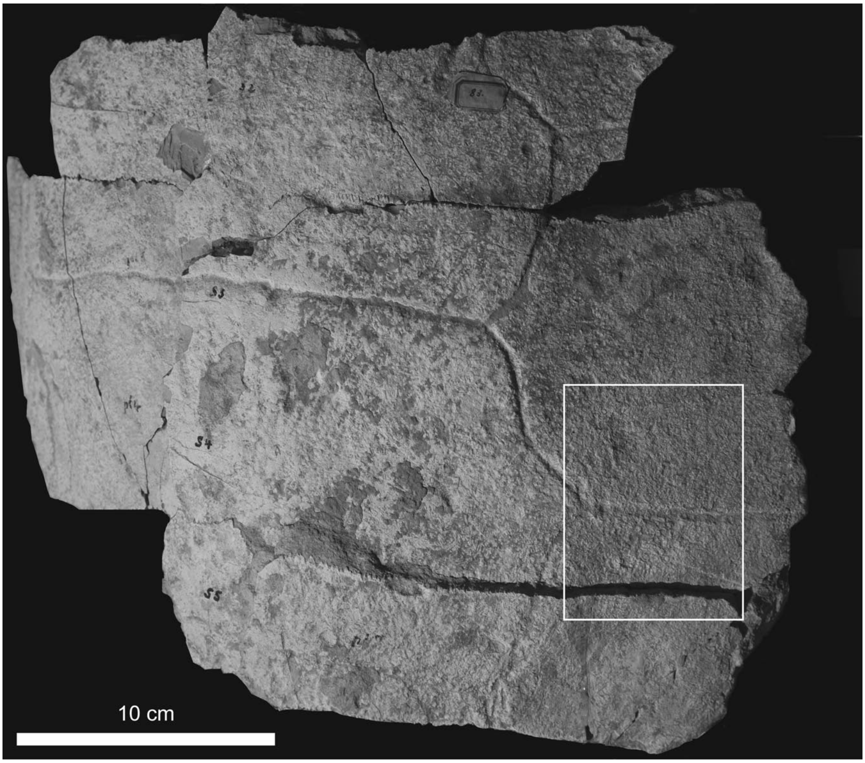

Fig. 6: Left anterior part of a carapax of *Plesiochelys* (NMS 8545) with location of Figure 7.

uted to the ichnospecies *Gnathichnus pentax* by BROMLEY (1975) and there seems to be a wide understanding that *Gnathichnus* is a pascichnion, being the product of the grazing activity of vagile herbivorous echinoids. Another ichnospecies *Gnathichnus stellarum* BRETON et al. (1992) has been described from the Campanian of France. The traces described above, however, are attributed to the ichnospecies *Gnathichnus pentax* because of their overall similarity.

Discussion

The ichnotaxon *Gnathichnus* has been found on a wide variety of hard substrates from the Triassic onwards (FÜRSICH & WENDT 1977; BROMLEY1975). Among these substrates are Early Jurassic belemnites, Middle Jurassic oysters, Late Cretaceous inoceramids, gastropods as well as extant algal covered limestones (BROMLEY 1975; BRETON et al. 1992; MACHALSKY 1998; RADLEY 2006). Other examples are found on Cretaceous sea star ossicles (NEUMANN 2000), Miocene Echinoid coronas (KROH 2005) and from Pliocene shell beds where the hard substrates include oysters and pectinid bivalves (MARTINELL 1982; GIBERT el al. 2007). Similar traces, although somewhat smaller in size, have been

Fig. 7: Details of *Gnathichnus pentax* Bromley on NMS 8545. Length of inset 11 cm.

observed on disarticulated remains of the extant marine turtle *Eretmochelys imbricta* from shallow water back reef sediments of the Seychelles Island La Digue (Indian Ocean). Here a thin greenish cover indicates that the sea urchins were feeding on an algal cover that developed after the decay of the individuals (pers. observation 1989). Extant regular shallow water echinoids feed on a variety of hard substrates. They are known to graze on algal films growing on hard substrates as well as on epizoans such as bryozoans (Jensen 1969), serpulid tubes or on the periostracum of living bivalves (Milligan 1916).

In the case of the Solothurn Turtle Limestone, many hard parts of potential shells were available for grazing at the time, such as frequent bivalves or rare serpulids. The main turtle producing bed, the Rätschenbank, was a soft sediment assemblage dominated by semi-infaunal strombid gastropods (*Harpagodes*) and regular echinoids (*Hemicidaris*). No other shelly remains or bones other than the mentioned specimens, however, have been found that were affected by the grazers. Some of the turtle fragments as well as also complete but disarticulated plastra show incrustation by small oysters (*Nanogyra*) which range from 4 mm up to 3 cm. The pacific oyster *Crassostrea gigas* reaches sizes up to 4 – 6 cm in their first year and adds another 3 cm in next six months (Diederich 2000). However, growth rates in extant and Pleistocene oysters (*C. titan, C. virginica*) are etremely variable (Kirby 2001). Average life spans range from one to twentythree years and thickness increase lies between 0.9. to 8 mm per annum (Kirby 2000). The annual ligament increments as seen in living and Pleistocene oysters are correlated with isotopic seasonality. Even though these observations are not directly comparable to the unknown growth rate of the fossil taxon *Nanogyra*, the epibiontic growth on the turtles restricts the resident time of the bones at the sediment water interface to probably less than 5 years before final burial. It is thus suggested that *Gnathichnus pentax* BROMLEY was left by the hemicidarid sea urchin *Hemicidaris mitra* (AGASSIZ). This very frequent epibenthic form can be found with its primary and secondary spines still attached to the corona, demonstrating that they were deposited *in situ*. These echinoids most probably grazed on the algal covers that grew on shell turtle fragments lying on the floor of the lagoon.

The specimens were probably recovered from the "Rätschenbank" as indicated by the sediment remains in the carapax. The bed has the highest faunal diversity and at the same time the highest content of C_{org} of the sediments within the Solothurn Turtle Limestone member (MEYER 1994). The facies and palaeoecology indicate subtidal deposition in a shallow marine lagoon. Sedimentological observations suggest a small embayment adjacent to large tidal flats in the north and a connection to the open sea in the southeast. Optimal conditions led to a continuous development of a stable ecosystem with an individual- and species rich benthic community that formed the base for a diverse neritic vertebrate community. A complete account of the fauna has been given by MEYER & THÜRING (2009).

An explanation must be found for the unusually dense accumulation of fossil turtles including both more necto-benthic forms (*Platychelys*) and those well adapted for open waters (*Plesiochelys*). The main marine turtle yielding layer, the so-called "Rätschenbank" is slightly marly at its base and can be classified as an echinoderm biomicrite. Within this 90 cm thick bed, 8 horizons with turtles in different preservation stages are present. They occur in a wide range of decay ranging from single abraded bone fragments to almost completely articulated turtles including skulls. Isolated fragments of carapaces of the same individual are often dispersed over several square meters (MEYER 1989). Some carapax remains show signs of crushing and circular holes that can be interpreted as bite marks of mesosuchian crocodiles (*Machimosaurus*).

One of the reasons for high occurrences of turtles may have been the primary food sources within the lagoon or the presence of nearby "nesting sites" as already suggested by RÜTIMEYER (1863). The remains of a crumpled mineralized coat-like fossil found in 1988 has been radially thin sectioned. It reveals a structure that is reminiscent of a turtle eggshell. Minute holes probably of endolithic algae and diagenetic alternation obscure the definite determination of this fossil (Karl HIRSCH pers. comm. 1994). Finally, the occurrence of lethal bite marks and also healed injuries on turtle carapaces indicate that these finds represent a secondary "biological" accumulation of dead animals by marine crocodilians (MEYER 1991).

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