WALTER G. JOYCE & DARLA K. ZELENITSKY

Turtle egg pseudomorphs from the Late Jurassic of Schamhaupten, Germany

Schildkröteneier-Pseudomorphe aus dem Oberjura von Schamhaupten (Deutschland)

Abstract
The shell of a turtle, tentatively identified as a eurysternid, was recovered from a Late Jurassic limestone concretion found near the village of Schamhaupten, Germany. Transverse sections through the body cavity revealed four spherical crystalline objects that are embedded in a micritic matrix and surrounded by a thin calcareous crust that superficially resembles inside-out turtle eggshell. Although various hypotheses can be put forward regarding their origin, we interpret these structures as the heavily altered eggs of a gravid female turtle. This is the first report of fossil eggs from within the body cavity of a fossil taxon and allows limited inferences regarding the reproductive biology of eurysternid turtles.

Zusammenfassung
Eine fossile Schildkröte, die bei einer Grabung des Jura-Museums in der Nähe von Schamhaupten in einer Konkretion gefunden wurde, bietet neue Einblicke in die Paläobiologie eurysternider Schildkröten. Da während der anfänglichen Präparation keine Knochen in der Konkretion gefunden werden konnten, wurde die Konkretion mehrfach aufgesägt und dabei das darin enthaltene Fossil im Querschnitt freigelegt. Auf den Schnittflächen sind ein Bauch- und Rückenpanzer mitsamt der Wirbelsäule zu erkennen, was eine eindeutige Identifizierung des Fundes als Schildkröte erlaubt. Obwohl die meisten diagnostischen Merkmale oberjurassischer Schildkrötenarten nicht erkennbar sind, kann der Fund aufgrund des dünnwandigen und unskulpturierten Panzers dennoch als eurysternide Schildkröte angesprochen werden. Bemerkenswert sind paarweise angeordnete, rundliche Strukturen, die in der Leibeshöhle der Schildkröte zu erkennen sind und höchstwahrscheinlich die fossilen Eier einer graviden Schildkröte darstellen (Abb. 1). Eine Analyse dieser Strukturen ergab, dass sie in der Tat kugelförmige Körper darstellen, die mit einer dünnen, kalzitischen Kruste umgeben und innen teilweise mit grobkörnigem Sparit verfüllt bzw. hohl sind. Obwohl nur wenige Schnitte an der Schildkröte vorgenommen wurden, konnten wenigstens vier dieser Körper identifiziert werden. Im Dünnschliff lassen sich die Krusten in zwei Lagen gliedern: Die äußere Lage ist ca. 60 bis 80 µm dünn und besteht aus Mikrit. Die innere Lage ist mit ca. 220 bis 260 µm etwas dicker und besteht aus dichten, säulenartigen Kristallbündeln, die von der äußeren Lage ausgehend in das Innere der Körper strahlen (Abb. 2). Sowohl die Größe der Kugeln, als auch die Dicke und Mikrostruktur der Krusten, erlauben einen Vergleich mit den Eiern heute lebender Schildkröten. Dennoch sind gravierende Unterschiede zu den modernen Schildkröteneiern vor allem in den Krusten erkennbar. So ist die Mikrostruktur der fossilen »Eierschale« kalzitisch und nicht aragonitisch. Zudem sind die fossilen Lagen genau entgegengesetzt der Abfolge bei modernen Schildkröteneiern angeordnet.
Diese Fakten können mithilfe verschiedener Hypothesen erklärt werden. Zum einen können die kugeligen Strukturen das Resultat anorganischer Prozesse darstellen, die zufällig in der Leibeshöhle einer fossilen Schildkröte stattfanden. Zum anderen kann es sich in der Tat um Eier handeln, die entweder in ihrem natürlichen Aufbau vorliegen oder aber diagenetisch stark verändert wurden. Wir

halten letztere Interpretationen für wahrscheinlicher, da die vorhandenen Strukturen generell mit fossilen Schildkröteneiern übereinstimmen. Uns erscheint es auch glaubhafter, dass eine eiertragende Schildkröte im Schamhaupten-Becken zur Ablagerung kam, als dass verschiedene, uns unbekannte diagenetische Prozesse zufällig in der Leibeshöhle der Schildkröte diese Ei-ähnlichen Strukturen erzeugten. Da sich die Mineralogie und Mikrostruktur der »Eierschalen« grundlegend von denen lebender Schildkröten unterscheiden, kann darüber hinaus ausgeschlossen werden, dass die Eier in ihrer ursprünglichen Form vorliegen. Daher gehen wir davon aus, dass die gefundenen Strukturen die fossilen Eier einer graviden Schildkröte darstellen, und dass die ursprüngliche Eierschale während der Diagenese vollkommen umkristallisiert ist. Da nur etwa ein Drittel bis ein Viertel der Schildkröte aufgeschnitten wurde, kann man davon ausgehen, dass die Schildkröte 10 bis 15 Eier enthielt, was eine erste Schätzung der Gelegegröße einer fossilen Schildkrötengruppe zulässt.

1. Introduction

The limestone quarries of the Solnhofen region, Germany, have yielded numerous remains of Late Jurassic turtles. Classic localities include the lithographic limestone quarries of Eichstätt (MEYER 1864), Kelheim (MEYER 1839a, 1843, 1860), and Solnhofen (MEYER 1839b; WAGNER 1859). Recent excavations by a field crew from the Jura-Museum Eichstätt near the village of Schamhaupten, Germany, resulted in a surprising number of additional specimens (see RENESTO & VIOHL 1997 and JOYCE 2000 for locality description). While the large majority of turtles from the lithographic limestone consist of rather complete and uncrushed individuals embedded on the underside of a limestone slab (WELLNHOFER 1967), the new turtles from Schamhaupten exhibit a surprising variety of preservational conditions, especially considering that they were found in close proximity to one another.

Soon after the discovery of a beautifully preserved specimen of *Solnhofia parsonsi* that was found in a silicic concretion (JOYCE 2000), another such concretion was found that also showed promise of containing a fossil turtle. Because no bone was discovered during the initial preparation, it became questionable whether the concretion was fossiliferous. The concretion was then cut through the center three times, producing two large end pieces and two central slices (pers. comm. G. VIOHL 1999). The cut surfaces reveal faint, bony outlines that can confidently be interpreted as the carapace and plastron of a turtle (Fig. 1). Though most characters used to diagnose Late Jurassic turtles are not exposed, we tentatively refer the specimen to Eurysternidae (*sensu* LAPPARENT DE BROIN et al. 1996), based on the thin, smooth nature of the shell and the modest carapace length of ca. 20 to 25 cm. The most interesting aspect of this turtle specimen is the presence of circular objects that are symmetrically placed inside the body cavity and which appear to be the fossilized eggs of a gravid female. The detailed description and analysis of these structures is the focus of this paper. All parts of the fossil turtle (collection number JM SCHA 101), including the thin section, are housed at the Jura-Museum, Eichstätt, Germany.

2. Material and Methods

As described above, the fossiliferous concretion was cut three times resulting in two larger end pieces and two medial slices, which combined exhibit six surfaces. All surfaces were macroscopically examined for the distribution of the bones and the putative eggs. One surface was polished and a thin section was produced from another that contains minor parts of bone and roughly half of a spherical structure believe to be an egg. During preparation, one of the medial slices broke, revealing parts of the carapace.

A sample of suspected eggshell was removed from one of the surfaces for X-ray powder diffraction analysis using a micro drill. The resulting powder was carefully packed onto a glass sample holder to present a flat powder-pack surface. Diffraction data was acquired over a range of angles from 2 to 65 degrees, with a step size of 0.05 degree and a dwell time of two seconds per step using a Phillips XRG3100 X-Ray Diffraction System. X-radiation was produced by a long fine focus Cu X-ray tube running at 40 kV and 30 mA. The Phillips goniometer was equipped with theta-compensating slit optics and a Cu monochromator. A MDI Databox in conjunction with MDI DataScan 3.1 software handled goniometer movement and data acquisition. The resulting diffraction data was then analyzed

Fig. 1.
Transverse section through the Schamhaupten turtle. For point of reference, the specimen is oriented anatomically with the carapace at the top and the plastral elements at the bottom. The fossil eggs are clearly visible within the body cavity.

Abb. 1.
Querschnitt durch die Schamhaupten Schildkröte. Zum besseren Vergleich ist das Fossil in der Abbildung anatomisch angeordnet mit dem Rückenpanzer oben und dem Bauchschild unten. Die fossilen Eier sind innerhalb der Körperhöhle deutlich sichtbar.

using the industry standard MDI Jade software package and the ICDD PDF-2 powder diffraction database.

3. Results

The carapacial side can be confidently identified because it exhibits clear traces of the vertebral column. In addition, the broken surface reveals a rib fragment. Paired bony elements are tentatively identified as plastral bones, based on their position and shape. They are visible in all slices, but whether they are articulated remains unclear. By observing the relative position of the vertebral column throughout the slices, it is apparent that the turtle was cut at an angle of about 70 degrees relative to the midline and that the exposed rib stands perpendicular relative to the vertebral column. In all known Late Jurassic turtles, the ribs only stand perpendicular to the vertebral column along the cranial two thirds of the carapace (JOYCE 2000). Combined with the fact that none of the slices expose any bridge elements, this may indicate that the turtle was cut cranial to the bridge.

The body cavity of the turtle is filled with carbonate sediments that grade from a micritic mudstone (sensu DUNHAM 1962; EMBRY & KLOVAN 1972) along the plastral side to a coarse-grained rudstone (sensu EMBRY & KLOVAN 1972) along the carapacial side that is composed primarily of coarse echinoderm and calcareous sponge fragments (Fig. 1). Together with the documented orientation of the concretion from the field, this sedimentary gradation convincingly indicates that the turtle was deposited on its back after death.

Comparison of the cranial and caudal surfaces of all slices reveals that the circular structures do not represent two elongate cylinders that lay parallel to the vertebral column, but rather four separate spheres. Additional spheres may be hidden in the remaining parts of the concretion, but further preparation is required to expose them. The largest observed diameter is 39 mm, the smallest 26 mm. Thin white “crusts”, ca. 0.30 to 0.34 mm thick, partially surround the spheres. The crusts are cleanly broken in some areas and even overlap in others, indicating that they were brittle and mobile at one time. X-ray diffractometry measurements show no trace of aragonite or high magnesium calcite. A white, coarse crystalline sparite fills the spheres as in a geode, but three of the four observable spheres are hollow in their center. The size of the spheres and the thickness of the crusts both lay within the range of observed values for eggs and eggshell in extant turtles of similar size (EWERT 1979).

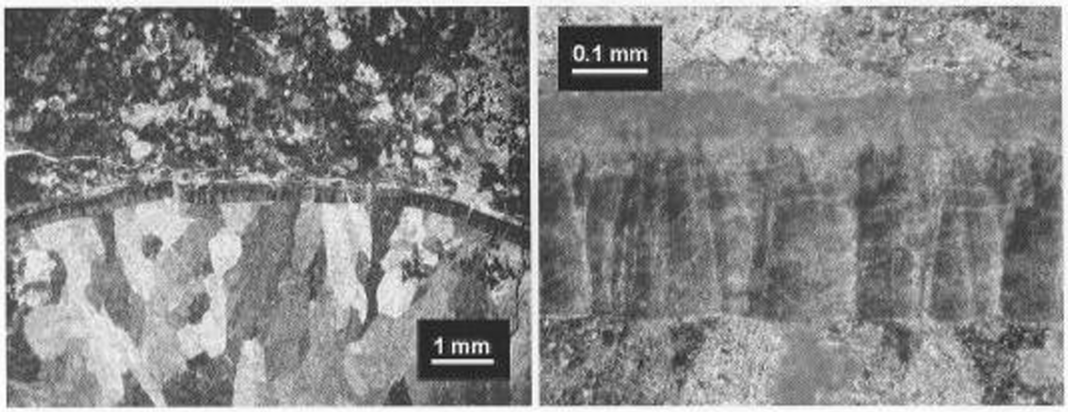

Fig. 2.
Details of the turtle eggs in thin section under crossed Nichols. The top represents the micritic matrix outside of the eggs and the bottom represents the blocky, calcitic infilling. Note that the "eggshell" comprises an outer micritic layer and an inner fibrous layer.

Abb. 2.
Detailaufnahme der Schildkröteneier im Dünnschliff mit gekreuzten Polarisatoren. Das obere Feld stellt die mikritische Matrix dar, welche außerhalb der Eier liegt, das untere die grobkörnige kalzitische Füllung. Zu beachten ist, dass die »Eierschale« aus einer äußeren mikritischen Lage und einer inneren faserigen Lage besteht.

In thin section, the crusts reveal two layers (Fig. 2). The outer layer is micritic and only 60 to 80 µm thick. The inner layer is about 220 to 260 µm thick and consists of dense, botryoidal to columnar crystal bundles that originate from the inside of the outer layer and radiate towards the center of the sphere. The two layers combined superficially resemble fossil turtle eggshell (HIRSCH 1983, 1996), with a replaced membrane layer and structured crystalline layer. However, consistently shaped units with concentric growth rings, evident in turtle eggshell (HIRSCH 1983, 1996) are lacking in the crystalline layer. Furthermore, these fossil structures stand in contrast to modern eggs, because the arrangement of layers and the direction of crystal growth are reversed.

4. Discussion

Three competing hypotheses can be formulated to explain what the Schamhaupten spheres are: the false-egg, the original-egg, and the egg-pseudomorph hypotheses. The false-egg hypothesis suggests that these structures are true *ludi naturae* – games of nature, or coincidental inorganic formations that happened to occur within the body cavity of the fossil turtle. The remaining two hypotheses suggest that the structures indeed are fossilized eggs, but they postulate different diagenetic pathways. According to the original-egg hypothesis, the spheres represent the unaltered or recrystallized fossil remains of turtle eggs. In contrast, the egg-pseudomorph hypothesis suggests that the spheres are the result of complex diagenetic processes during which the eggshell of the original eggs was replaced by inorganic precipitations that resemble inside-out turtle eggs. Other possible hypotheses, such as fossilized gut contents or internal organs, are not considered here because they seem implausible.

The false-egg hypothesis is the most difficult to falsify because it makes the fewest predictions and because it can be corroborated with any given number of *ad hoc* explanations. Nevertheless, we feel confident in interpreting the Schamhaupten spheres as fossilized eggs due to the following reasons. First, as expected from the fossilized eggs of a gravid female turtle, a "shell" surrounds the spheres and their insides are not filled with organic deposits such as bone or plant remains. Furthermore, both the "eggshells" and the "eggs" are within the range of size values observed among recent turtles of similar size (EWERT 1979). To date, no fossilized eggs have been reported from *within* the body cavity of any fossil vertebrate, indicating that this type of preservation is extraordinary. This absence from the fossil record is certainly a taphonomic bias, because the eggs of a gravid female are still in the process of being shelled and because eggs are subject to predation and decay and, consequently, as unlikely to be preserved as internal organs. Nevertheless, because the majority of tetrapods found in the Solnhofen region were not scavenged upon before burial (KEMP 2001), it is feasible that a gravid female may be found in this formation. While it is possible that egg-sized and "shelled" geodes did form symmetrically in the abdominal region of this fossil turtle, we conclude it more likely that these structures represent true fossil eggs. Based on this conclusion, modest inferences can be made about the reproductive ecology of Eurysternidae. Assuming that the remaining concretion is evenly filled with additional eggs, the total clutch size may be conservatively estimated to be between 10 to 15 eggs. Not surprisingly, this is comparable to the clutch size of modern turtle females of similar body size (WILBUR & MORIN 1988). To our knowledge, this represents the first estimate of the clutch size for a fossil turtle taxon.

Of the remaining two hypotheses, the original-egg hypothesis is the easiest to falsify because it makes the most explicit predictions regarding the composition and microstructure of the alleged eggshell. Although the microstructure of the purported eggshell superficially resembles the morphology of recent turtle eggshells, it lacks certain diagnostic microstructural features. Furthermore, it is apparent that these spheres cannot represent unaltered turtle eggs, because they appear to be preserved inside-out (i.e., the succession of layers and direction of crystal growth are reversed) and their composition is calcite rather than aragonite. Therefore, of the remaining two hypotheses, the original-egg hypothesis can be clearly dismissed.

The egg-pseudomorph hypothesis postulates that the original aragonitic eggshell was removed during diagenesis and that inorganic processes reproduced structures that look like inside-out eggshell. Carbonate cements are known to exhibit a large variety of morphologies depending upon the pore water chemistry from which they are precipitated (see papers in SCHNEIDERMANN & HARRIS 1985). However, we were unable to find any cement type that closely mimics turtle eggshell.

The formation of eggshell is an inorganic process during which supersaturated fluids excreted by the uterus precipitate carbonate onto organic cores formed by the shell membrane (e.g., PACKARD et al. 1984). If the membrane or original eggshell is preserved long enough, it is perhaps possible that pore water fluids deposited eggshell-like carbonate onto the inside of the membrane or the eggshell. Having the egg remain intact within the body cavity of the female may at first seem implausible, however, personal observations (WGJ) on macerating turtles reveal that the eggs of a gravid female will remain intact inside the body cavity long after all internal organs have decomposed. More rigorous experiments with modern turtle eggshells may be able to test this assertion.

5. Conclusions

We conclude that the Schamhaupten spheres represent the fossilized remains of turtle eggs that have been altered during diagenesis, but we remain puzzled as to their exact diagenetic history, because no plausible mechanism is know that produces carbonates that resemble inside-out turtle eggshell. Despite these difficulties, it remains safe to conclude that Late Jurassic turtles of the Eurysternidae laid moderately sized clutches similar to many living turtles of comparable body similar size. As the eggshells must be regarded as a pseudomorph, no eggshell characteristics can be derived for this group.

Acknowledgements

We would like to thank Dr. GÜNTHER VIOHL of the Jura-Museum Eichstätt for providing us with access to the Schamhaupten turtle concretion. We are indebted to Ms. MIMI REICHENBACH and Mr. ALAN GORDON of the GR Petrology Consultants Inc., Calgary, Alberta, whose company provided access to analytical equipment. JASON DOWNS, Dr. JENNEY HALL, JEFFREY RAHL, Dr. ADOLPH SEILACHER, CLAUDIA TRÖGL, KRISTER SMITH, and OLIVER WINGS provided useful discussion and comments regarding the manuscript. The Paleontological Society and a Yale University Graduate Student Fellowship provided funding to WGJ. DKZ was supported by a research grant from the Natural Sciences and Engineering Research Council of Canada to PHILIP J. CURRIE.

6. References

DUNHAM, R. J. (1962): Classification of carbonate rocks according to depositional texture. – A. A. P. G. Mem., **1**: 108-121.

EMBRY, A. F. & KLOVAN, J. E. (1972): Absolute water depth limits of Late Devonian paleoecological zones. – Geol. Rundsch., **61**: 672-686.

EWERT, M. A. (1979): The embryo and its egg: Development and natural history. – In: HARLESS, M. & MORLOCK, H. (Hgr.): Turtles: Perspectives and Research: 333-413, New York (John Wiley & Sons).

HIRSCH, K. F. (1983): Contemporary and fossil chelonian eggshells. – Copeia, **1983**: 382-397.

– (1996): Parataxonomic classification of fossil chelonian and gecko eggs. – J. Vertebr. Paleontol., **16**: 752-762.

JOYCE, W. G. (2000): The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications. – J. Paleontol., **74**: 684-700.

KEMP, R. (2001): Generation of the Solnhofen tetrapod accumulation. – Archaeopteryx, **19**: 11-28.

LAPPARENT DE BROIN, F. DE, LANGE-BADRÉ, B. & DUTRIEUX, M. (1996): Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. – Rev. Paléobiol., **15**:533-570.

MEYER, H. VON (1839a): *Idiochelys Fitzingeri*, eine Schildkröte aus dem Kalkschiefer von Kelheim. – Beiträge zur Petrefacten-Kunde, **1**: 77-89.

– (1839b): *Eurysternum Wagleri*, eine Schildkröte aus dem Kalkschiefer von Solnhofen. – Beiträge zur Petrefacten-Kunde, **1**: 89-95.

– (1843): Mittheilungen an Professor Bronn gerichtet. – N. Jb. Min. Geogn. Geol. Petrefakten-Kunde, **1843**: 579-590.

– (1860): Zur Fauna der Vorwelt. Reptilien aus dem lithographischen Schiefer des Jura in Deutschland und Frankreich. – 142 S., 21 Taf.; Frankfurt (Heinrich Keller Verlag).

– (1864): *Parachelys Eichstättensis* aus dem lithographischen Schiefer von Eichstätt. – Palaeontographica, **11**: 289-295.

PACKARD, M. J., IVERSON, J. B. & PACKARD, G. C. (1984): Morphology of shell formation in eggs of the turtle *Kinosternon flavescens*. – J. Morphol., **181**: 21-28.

RENESTO, S. & VIOHL, G. (1997): A sphenodontid (Reptilia, Diapsida) from the late Kimmeridgian of Schamhaupten. – Archaeopteryx, **15**: 27-46.

RÖPER, M. (1992): Beitrag zur Deutung des Lebensraumes der Plattenkalke der Almühlabl (Malm Epsilon 3 bis Malm Zeta 3). – Unveröff. Diss. Univ. Bonn.

SCHNEIDERMANN, N. & HARRIS, P. M. (1985): Carbonate Cements. – 379 S.; Tulsa (Society of Economic Paleontologists and Mineralogists).

SCOFFIN, T. P. (1987): An introduction to Carbonate Sediments and Rocks. – 274 S.; Glasgow and London (Blackie & Son).

WAGNER, A. (1859): Über einige, im lithographischen Schiefer neu aufgefundene Schildkröten und Saurier. – Gelehrte Anzeigen, **49**: 553-555.

WELLNHOFER, P. (1967): Ein Schildkrötenrest aus den Solnhofener Plattenkalken. – Mitt. Bayer. Staatssamml. Paläont. hist. Geol., **7**: 181-192.

WILBUR, H. M. & MORIN, P. J. (1988): Life history evolution in turtles. – In: GANS, C. & HUEY, R. B. (Hgr.): Biology of the Reptilia: 387-439, New York (Alan R. Liss, Inc.).

Addresse der Autoren:

WALTER G. JOYCE, Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New Haven, Connecticut 06511, USA; e-Mail: walter.joyce@yale.edu.

DARLA K. ZELENITSKY, Department of Geology and Geophysics, University of Calgary, Calgary, Alberta T2N 1N4, Canada; e-Mail: zelenits@geo.ucalgary.ca.