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SONTIOCHELYS CRETACEA STACHE, 1905 AND NEW DESCRIPTION OF THE FAMILIES EURYSTERNIDAE DOLLO, 1886 AND THALASSEMYDIDAE RÜTIMEYER, 1873 (TESTUDINES: CRYPTODIRA)

[*Sontiochelys cretacea *Stache, 1905 y redescripción de las familias Eurysternidae Dollo, 1886 y Thalassemydidae Rütimeyer, 1873 (Testudines: Cryptodira)]

Hans-Volker KARL[1,2]
Gottfried TICHY[3]
Diana VALDISERRI[3]

[1] Thüringisches Landesamt für Denkmalpflege und Archäologie. Humboldtstraße 11. D-99423 Weimar, Germany. Correo-e: hvkarl@web.de
[2] Geoscience Center of the University of Göttingen. Department of Geobiology. Goldschmidtstraße 3. D-37077 Göttingen, Germany
[3] University of Salzburg. Department of Geography and Geology. Hellbrunner Straße 32. A-5020 Salzburg. Correo-e: gottfried.tichy@sbg.ac.at and diavaldiserri@yahoo.it

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RESUMEN: Se describen nuevamente y revisan taxonómicamente los taxones de la familia Thalassemydidae publicados hasta ahora, teniendo en cuenta material nuevo y completo. Ahora, la familia Thalassemydidae Rütimeyer, 1873 no se divide, como de costumbre, en las dos subfamilias Idiochelyinae Oertel, 1915 y Thalassemydinae Rütimeyer, 1878. Aquí solo contiene los géneros *Eurysternum* Fitzinger, 1836; *Idiochelys* Meyer, 1839; *Solnhofia* Gaffney, 1975, y *Thalassemys* Rütimeyer, 1858. Los demás taxones descritos se consideran etapas ontogenéticas o casos de dimorfismo sexual. Se presenta una revisión histórica y un análisis de los caracteres. Por otra parte, el holotipo de *Sontiochelys cretacea* Stache, 1905 se ha perdido, pero se conserva un molde en el Museo Cívico di Storia Naturale de Trieste. La revisión de este *Sontiochelys* lo sitúa dentro de la familia Thalassemydidae, próximo a Idiochelys Meyer, 1839.

Palabras clave: Eurysternidae, Thalassemydidae, Jurásico Inferior a Cretácico Inferior, Europa Central y Oriental, Hauteriviense a Barremiense (Cenomaniense), Cretácico Superior, Monte Santo cerca de Görz (Dalmacia), revisión, descripción, *Sontiochelys cretacea* Stache 1905, redescripción.

ABSTRACT: The taxa of the family Thalassemydidae published up to now are newly described and revised taxonomically taking into account new and complete material. Here, the family Thalassemydidae Rütimeyer, 1873 is not divided in the two subfamilies Idiochelyinae Oertel, 1915 and Thalassemydinae Rütimeyer, 1878 as usual. It only contains the genera *Eurysternum* Fitzinger, 1836; *Idiochelys* Meyer, 1839; *Solnhofia* Gaffney, 1975, and *Thalassemys* Rütimeyer, 1858, so far known. The former taxa are here considered as ontogenetic stages or sexual dimorphism. A historical overview and a character analysis are also given. The holotype of *Sontiochelys cretacea* Stache, 1905 is lost, however a cast of a mould is preserved and stored at the 'Museo Civico di Storia Naturale di Trieste'. The revision of this *Sontiochelys* provided a position within the family Thalassemydidae, close to *Idiochelys* Meyer, 1839.

Key words: Turtles, Eurysternidae, Thalassemydidae, Lower Jurassic to Lower Cretaceous, Middle to Eastern Europe Hauterivian to Berremian (formerly Cenomanian), Lower Cretaceous, Monte Santo near Görz in Dalmatia, revision and description, *Sontiochelys cretacea* Stache, 1905, redescription.

INTRODUCTION

The Thalassemydidae belong to an extinct basal group of the infraorder Eucryptodira which also includes the families Plesiochelyidae, Hylaeochelyidae, and Xinjiangchelidae. While H. v. MEYER (1860) mentioned the following species *Platychelys oberndorferi* H. v. Meyer, *Eurysternum wagleri* H. v. Meyer, *Achichelys redtenbacheri* H. v. Meyer, *Palaeomedusa testa* H. v. Meyer, *Hydropelta meyeri* Thiollière and *Parachelys eichstaettensis* H. v. Meyer (1860), WAGNER (1863) came to the result, that *Eurysternum wagleri* H. v. Meyer, *Achichelys redtenbacheri* H. v. Meyer, and *Palaeomedusa testa* H. v. Meyer belong to the single genus with formerly two species: *Eurysternum wagleri* H. v. Meyer and *Eurysternum crassipes* Wagner, 1859 (nomen nudum). Furtheron, he added the species *Euryaspis radians* Wagner, 1863, and *Euryaspis approximata* Wagner. Later, MAACK (1869) joining this synonymy for *Eurysternum*. According to RÜTIMEYER (1873), also *Achelonia formosa* and *Euryaspis radians* should be included in this genus. Rütimeyer's revision resulted in a reduction of the numerous Bavarian and Cirin genera to only five: *Platychelys, Idiochelys, Eurysternum, Aplax* and *Hydropelta*. This revision is also shared by ZITTEL (1889). OERTEL (1915) summed up all previously published *Hydropelta* H. v. Meyer (not 1852!) remains and found some problems in the correlation among the material. The following remains were related to the genus *Hydropelta*:

1. Severely damaged right Hyo-and Hypoplastron, right edge of the disc with the anterior six Pleuralia. Quoted from H. v. MEYER (1860: 139, fig. 9, pl.) (XVI), and LORTET (1892: 18-23, fig. 3, pl.) (II). The Plastron was already named by THIOLLIÈRE (1851) as *Chelone meyeri*, and a new name, *Hydropelta,* was given by H. v. MEYER (1860) as a result of incorrect orientation of the plastron-plates (breast plates).

2. A right hyo-, hypo- and entoplastron, fragments of pleuralia, and a right foot. Cited by ZITTEL (1889: 330, fig. 498);

3. Carapace, posterior half of the plastron (breast) and extremities (Paris specimen). Quoted by a plaster cast in the Munich collection of WAGNER (1860: 394), and further,

4. a damaged carapace in ventral view with the remains of peripheralia, pleuralia, inguinal pillar, pelvis and limb fragments. Cited by MAACK (1869: 314, pl. XL).

OERTEL (1915) mentioned a still unpublished fossil from Kelheim in the collection of Leik without any further information. According to this author all these remains, described as *Hydropelta*, are belonging to the genera *Idiochelys* and *Eurysternum*. This statement was taken over by all the following manual authors. The approach to the problem was made even more difficult by the usually fragmentary material, and loss of type specimens due to the war. *Eurysternum crassipes* Wagner, 1859 was also correlated with the same specimen as later *Palaeomedusa testa* by H. v. MEYER (1860). Therefore that taxon should have to be called *Palaeomedusa crassipes* (Wagner, 1859) and not *Palaeomedusa testa* (see JOYCE, 2003). But nevertheless, it has to be considered as a nomen nudum. *Solnhofia parsonsi* Gaffney, 1975b, a further species, was also described; now that species is almost completely known by JOYCE (2000).

The first known tortoise from the Frankonian Lithographenschiefer of Brunn near Regensburg was published by RÖPER, ROTHGÄNGER & ROTHGÄNGER (1996), as well as the hitherto known, fragmentary material which was illustrated by Hatchlings (plate 6, fig. 1 in this paper). The former specimen is preserved in the Solnhofen Museum, the latter in an unnamed private collection. It was found in the *subeumela*-subzone of the Kimmeridgian (Upper Jurassic).

So far known Thalassemydid turtles are recovered mainly from the European Upper Jurassic (Callovian, Kimmeridgian and Thithonian) the oldest known evidence comes from the Lower Jurassic (Sinemurian), the most recent one from the lower/upper Cretaceous boundary (? Aptian/early Cenomanian) from Central Asia.

The turtles from the Upper Jurassic of the lithographic shale have been often described and illustrated. The focus of this work is on new and unpublished material,we also give references to those depicted in fossil handbooks. Besides the original work, *Sontiochelys* never was illustrated and was scarcely mentioned in scientific publications. A detailed description of the new genus, as it was announced by STACHE (1905), did not appear.

Fossils from the limestones of the Karst area have been described for a long time, such as the fishes *Belonostomus* and *Holcodon lesinensis* Kornhuber, 1882 and the fern *Sphenopteris lesinensis* Kornhuber, 1895. Further fishes are described by BASSANI (1882), KNER (1863), KORNHUBER (1873, 1893, 1901), KRAMBERGER-GORJANOVIĆ (1895), and, more recently, Amiopsis (Amiiformes) (DALLA VECCHIA *et al.*, 2008). Dalmatia and the Friuli area are widely known for their primitive mosasaurians such as *Pontosaurus lesinensis* Kornhuber, 1873 (syn.: *Hydrosaurus lesinensis*), *Aigialosaurus dalmaticus* Kramberger, 1892, *Aigialosaurus bucchichi* Kornhuber, 1901 and *Carsosaurus marchesettii* Kornhuber, 1893. *Aigialosaurs* is one of the oldest and most primitive ancestors of *Mosasaurs* (DUTCHAK, 2005; DUTCHAK & CALDWELL, 2009; DALLA VECCHIA *et al.*, 2008; GRANDE & BEMIS, 1998; MÚSICO & VENTURINI, 1990; NOPCSA, 1903). CALDWELL & LEE (2001) could prove embryos inside the body of *Carsosaurus marchesettii* Kornhuber 1893. *Aigialosaurus* was a semi-aquatic primitive form which lived in warm, shallow seas during the Lower Cretaceous. Under these same conditions, *Sontiochelys cretacea* also evolved a high degree of adaptation to marine life. Probably no turtle tracks are the problematic fossils from the flysch of Oláhlaposbána in Transylvania and the *Inoceramus*-layer or "Inoceramenschichten" (Cenomanian/Turonian) of Waidhofen at Ybbs/Lower Austria, and Steyer/Upper Austria (ABEL, 1904).

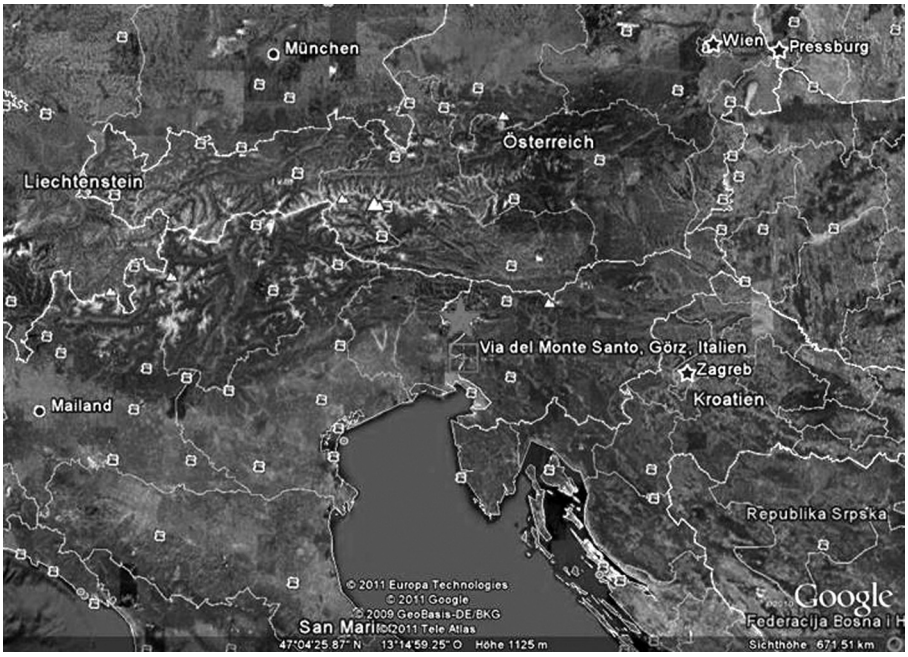

Figure 1. Geographical positition of the type locality of Sontiochelys cretacea *by © Google-Earth.*

Collection codes: BMMS-Bürgermeister Müller Museum (Mayor Muller Museum) Solnhofen, IGPS-Institute of Geology and Palaeontology of University Salzburg, JME-Juramuseum (Jurassic Museum) Eichstätt, JUMA-JUMA GmbH & Co. KG (Juma conpany) in Gungolding, MCL-Musée des Confluences, 86 Perrache, F-69002 Lyon, MCST-Museo Civico di Storia naturale di Trieste, MSS-Museum der Stadt Solothurn (Museum of the city Solothurn), MSL-Museen der Stadt Landshut (Museums of the city Landshut), RGH-'Red Gallery Hamburg' (D-20459 Hamburg, Rödingsmarkt 19), SM-Mineralogy-Geology Collection of the Solothurn Museum (see MSS), TM-Teyler Museum Haarlem, ZNIGR-ЦНИГР музей.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758

Infraorder Cryptodira Cope, 1868

Capaxorder Eucryptodira Gaffney, 1975a sensu Gaffney, 1984

Family Eurysternidae Dollo, 1886

Genus *Eurysternum* Fitzinger, 1836

[non Wagler without year, non H. v. Meyer, 1839]

ORIGINAL NAME: *Eurysternum*. Wagl., Fitzinger, 1836: 127 (non page 107 according Meyer, 1860 and Kuhn, 1964).

SYNONYMS: *Achelonia* Wagner, 1860, *Acichelys* Meyer, 1843, *Aplax* Meyer, 1843, *Changisaurus* Young, 1959, *Euryaspis* Wagner, 1859, *Hydropelta* Meyer, 1860, *Palaeomedusa* Meyer, 1860, *Parachelys* Meyer (1864).

KNOWN DISTRIBUTION: Upper Jurassic of Southern Germany, Switzerland and France.

DESCRIPTION: Neural row 6P/4/6A/6A/6A/6A/6A/6, all 6A are much wider at the anterior than at the posterior side. Plastron is cruciform, anterior plastron lobe much shorter than posterior; epiplastra and entoplastron reduced.

***Eurysternum wagleri* (Fitzinger, 1836)**

[non Compte of Münster, non H. v. Meyer, 1839]

ORIGINAL NAME: *Clemmys*? *Wagleri*, Fitzinger, 1836: 127.

SYNONYMS: See Kuhn (1961, and 1964): *Aplax oberndorferi* H. v. Meyer, 1843; *Acichelys redtenbacheri* H. v. Meyer, 1846; *Acrochelys approximata* Wagner, 1856; *Acrochelys redenbacheri* Wagner, 1856; *Eurysternum crassipes* Wagner, 1859; *Palaeomedusa testa* H. v. Meyer, 1860; *Achelonia formosa* Wagner, 1860; *Euryaspis radians* Wagner, 1863; *Euryaspis approximata* Wagner, 1863 and *Chelone planiceps* Quenstedt, 1885; *Changisaurus microrhrinus* Young, 1959 (BAIRD, 1964) and *Eurysternum ignoratum* Bräm, 1965.

Figure 2. Sexual dimorphism in sea turtles as in WYNEKEN *(2001). 1: skeleton of tail in male* Chelonia mydas*, 2: tail of a male and 3: tail of a female* Lepidochelys kempi*, 4: plastron of a male* Lepidochelys kempi *showing an elongated tail, long cuved claws, and during breeding season, the midventral plastron becoming soft (temporary re-ossified).*

TYPE LOCALITY: Solnhofen.

TYPE HORIZON: Upper Jurassic.

HOLOTYPE: According to WELLNHOFER (1967) destroyed during WW II.

NEW MATERIAL: Tithonian, Upper Jurassic of Eichstätt.

DESCRIPTION OF THE ONTOGENETIC STAGES:

Hatchling: Carapace rounded with the largest width in the middle part and very flat; carapace not ossified, ribs separately, plastron elements Hyo-, Hypo- and Xiphiplastra developed as slim clips; skull in relation to the shell is much larger than in adults; tail very long. See H. v. MEYER (1860): pl. XVIII, fig. 2, FRICKHINGER (1994): p. 241, fig. 242, and *Changisaurus microrhrinus* Young, 1959. YOUNG (1959) described and figured an anterior half of typical juvenile turtle in ventral view (fig. 3).

Juvenile: Carapace shield-shaped with the largest width in the rear third; very flat. Dorsal surface on each Centralia is ribbed radially at its anterior side. Nuchal-notch very flat, caudal-notch broad and flat; large fontanelles are present, horn plates furrows ontogenetically and individually variable, centrals very wide, about 1/2 of the width of the Carapace. The classic morphs of *Eurysternum* (figs. 4, 7) and *Eurysternum ignoratum* Bräm, 1965 are here included.

Female: Carapace long oval with the largest width in the first third, very flat; dorsal surface vermicular rougous; nuchal-notch very flat, caudal-notch small with sharp incision. No fontanelles present. Horn plates furrows very flat; tail short with about 13 vertebrae. Among these morphs are included the synonyms *Palaeomedusa* and *Hydropelta* (plate 1). Refer also to the figures in BARTHEL (1978: 224-225+cover), LEICH (1996: 44) and FRICKHINGER (1994): p. 136, fig. 244; p. 242, figs. 502-504; p. 244, figs. 507, 509; pp. 245-246, fig. 508.

Male: Carapace shield-shaped with the greatest width in the rear area, very flat; Dorsal surface vermicular rugos; nuchal-notch very flat, caudal-notch large with flat incision. No fontanelles present, horn plates furrows very flat, centrals moderately wide, approximately 1/3 of the width of the carapace. Tail very long with about 23 vertebrae and with cross laying rows of large horny scutes (plate 3). See also the figures in FRICKHINGER (1994): p. 245, fig. 508; p. 246, fig. 511 and plate 2 here.

REFERENCES: One complete skeleton from the Mörnsheim formation of Mühlheim (zone "Erste Rosa", C19-C22 according to HEYNG [2011] held in the RGH, the localities of the Mühlheim material are illustrated in the plate 3; IGPS, coll. Stefan Schäfer, Fürstenfeldbruck) n.º 649 (female, plate 1) and 651 (male, plate 2); JME Scha 97, 70: Upper Kimmeridgian, Schamhaupten/Eichstätt; JME SOS 02456 a+b, 02457: Lower Tithonian/Solnhofen layer, Sappenfeld near Eichstätt; JME SOS 03995 a+b: lower Tithonian, Birkhof (north of Eichstätt); one hatchling and one juvenile (ex coll. Johannes Högel, Regensburg), LEICH (1977: 158-159) and one adult specimen from Painten are presented in the BMMS, an adult specimen from the Müller-collection is the oldest turtles fossil in that

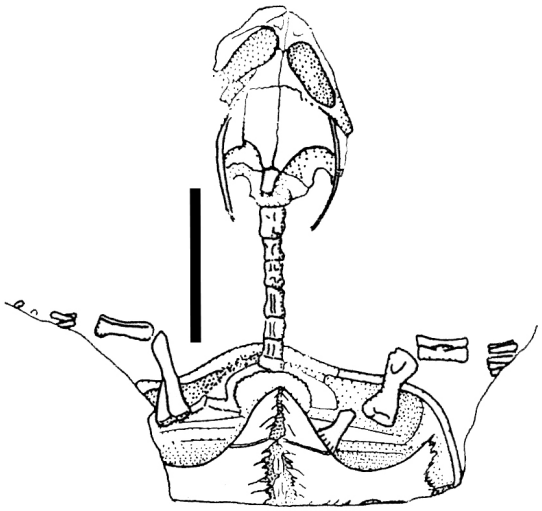

Figure 3. Eurysternum wagleri, *syn.* Changisaurus microrhrinus *according to* BAIRD *(1964).*

Figure 4. Eurysternum wagleri, *syn.* Hydropelta meyeri *according to* MAACK *(1869).*

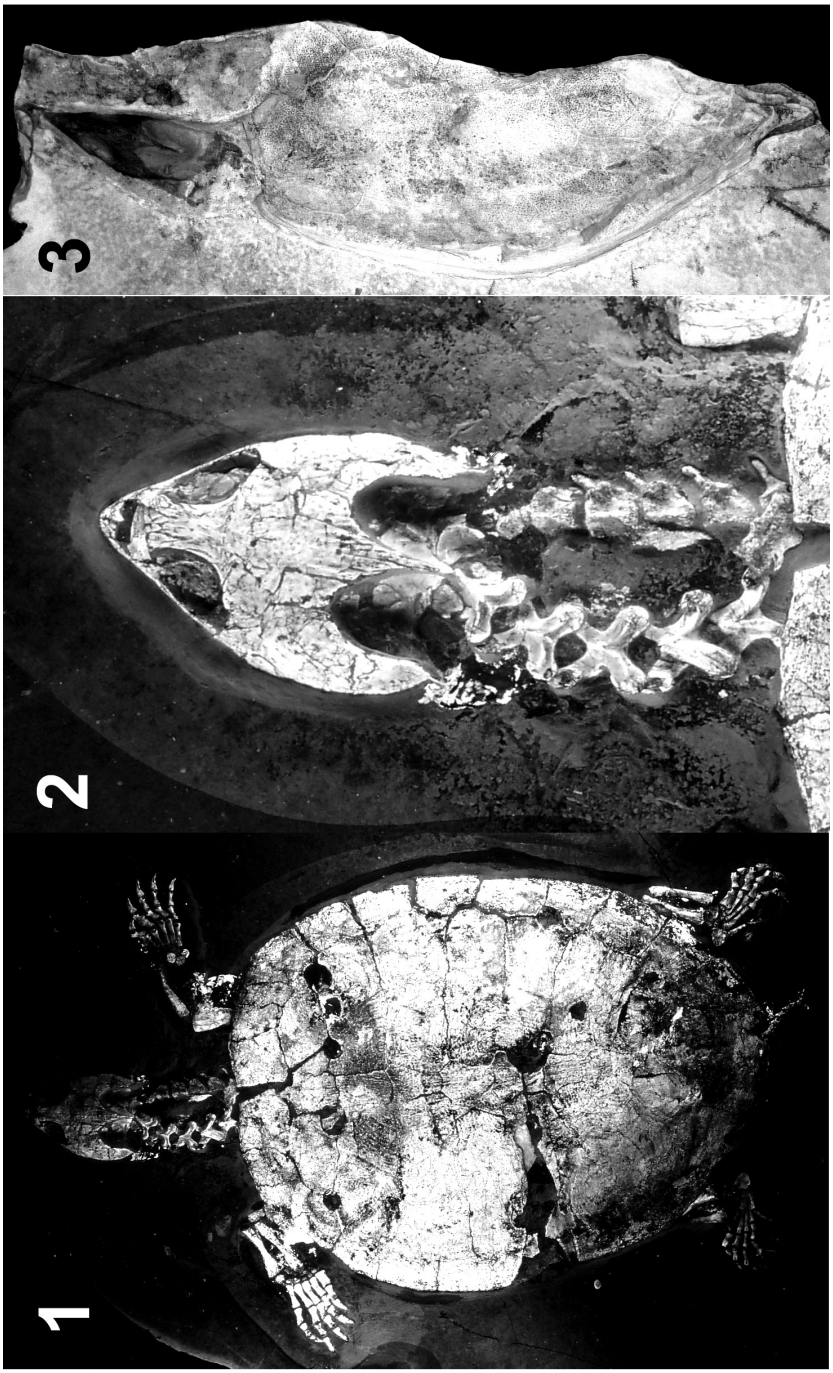

Plate 1. 1: Eurysternum wagleri, *female, Eichstätt, IGPS 649. 2. Skull and neck region. 3:* Eurysternum wagleri *female, Schernfeld, in dorsal view, coll. FTB (Fossilium Tierpark Bochum), length 36 cm. Photo Helmut Leich (Bochum-Wiemelhausen).*

Museum. Helmut Leich referred the existence of a fragmentary specimen from Schernfeld in the company JUMA whose counterpart is still held in "Fossilum Bochum". According to Heike Karg, who kindly informed us about the current whereabouts of this fossil, it is no longer in the JUMA-company. There is no information about the current owner. The dorsal surface of the carapace of this specimen shows a pustular structure, which was produced by chalky algae (plate 5).

Family Thalassemydidae Rütimeyer, 1873
(as Thalassemyden, p. 140)

SYNONYMS: Tribe Idiochelyidini (Oertel, 1915 as subgroup Idiochelyden) according KARL (1997).

Genus *Idiochelys* H. v. Meyer, 1839

ORIGINAL NAME: *Idiochelys*, H. v. Meyer, 1839: 59.

SYNONYMS: See KUHN (1961, 1964), *Yaxartemys* Riabinin, 1948.

KNOWN DISTRIBUTION: Upper Jurassic of Kazakhstan, Southern Germany and France.

DESCRIPTION: Neural row reduced, neurals tetragonal; plastron cruziform, anterior plastral lobe slightly shorter than the posterior one; epiplastrals and entoplastron present.

***Idiochelys fitzingeri* H. v. Meyer, 1839**

ORIGINAL NAME: *Idiochelys Fitzingeri*, H. v. Meyer, 1839: 59.

SYNONYMS: See KUHN (1964), *Yaxartemys longicaudata* Riabinin, 1948.

TYPE LOCALITY: Kelheim.

TYPE HORIZON: Upper Jurassic.

HOLOTYPE: According to WELLNHOFER (1967) destroyed during WW II.

DESCRIPTION OF ONTOGENETIC STAGES:

Hatchling: Carapace longoval and very flat, not ossified, ribs separated, plastron elements hyo-, hypo- and xiphiplastrals widened; skull in relation to the shell is much larger than in adults; tail very long. *Yaxartemys longicaudata* Riabinin, 1948 belongs to this stage. RIABININ (1948) described and illustrated an anterior half of typical juvenile turtle in ventral view (fig. 5).

Juveniles: Carapace rounded with the largest width in the middle part, very flat. Carapace not ossified, ribs separated, plastron elements hyo-, hypo- and xiphiplastra developed as slim clips; skull in relation to the carapace is larger than in adults. Refer also to the material of Brunn (plate 6).

Adults: Shell strongly ossified, but with large fontanelles, centralia are in width more than the half of the carapace; plastron very wide, but with lateral fontanelles between hyo-and hypoplastra; the large bridge with wing

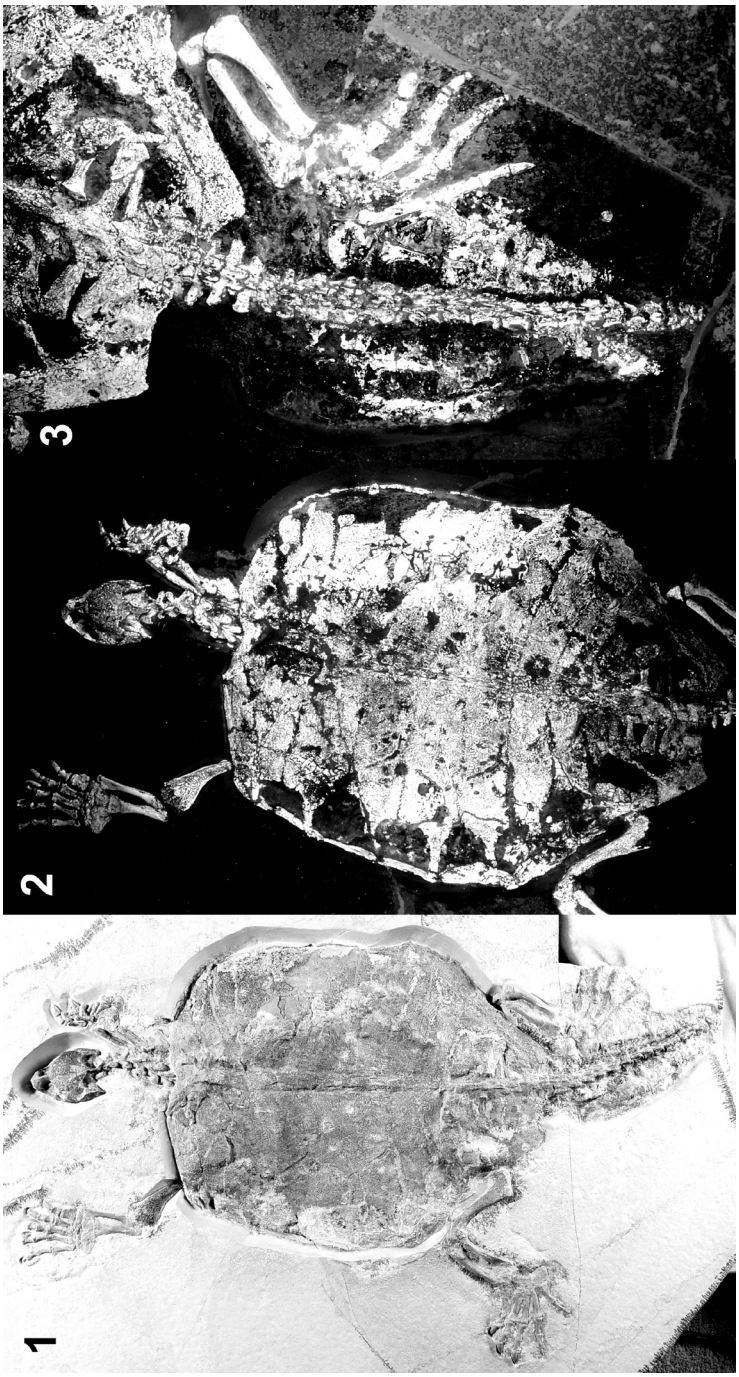

Plate 2. Eurystemum wagleri, *male, Eichstätt, IGPS 651. Photo Dirk Urban, Erfurt, UV - Photo Helmut Tischlinger (Stammbam), design H.-V. Karl & Heike Künzel, TLDA. 1: dorsal view; 2: carapace detail; 3: tail detail with scutes.*

like processes are in cartilagineous connection with the carapace; carapace length is 18 cm (KARL, 1997; DE LAPPARENT DE BROIN, 2001; MŁYNARSKI, 1976).

REFERENCES: France Original material of *Idiochelys fitzingeri* from Cérin (Ain) preserved in the MCL, n.º 15634 and 15635 (online: museedesconfluences.fr).

Genus *Solnhofia* Gaffney, 1975

ORIGINAL NAME: *Solnhofia* Gaffney, 1975b: 59.

SYNONYMS: None.

KNOWN DISTRIBUTION: Upper Jurassic of Southern Germany and France.

DESCRIPTION: Neural row 4/6A/6A/6A/6A/6A/6B, nuchal-notch deep, plastron cruziform, anterior and posterior plastron lobes are about equal in size. Epiplastrals and entoplastron are not known, refer also to GAFFNEY (1975), JOYCE (2003) and MŁYNARSKI (1976). In the specimen JM SCHA 70 the original position of the bones of the extremities are partly destroyed. Only one part of the metatarsals (1<2<3=4>5) and phalanges formula could be reconstructed.

***Solnhofia parsonsi* Gaffney, 1975**

ORIGINAL NAME: *Solnhofia parsonsi* Gaffney, 1975b: 59.

TYPE LOCALITY: Solnhofen.

TYPE HORIZON: Upper Jurassic.

HOLOTYPE: *Solnhofia* was first described based on a skull by PARSONS & WILLIAMS (1961) and named by GAFFNEY (1975): SM 137, TM 4023.

DESCRIPTION: As for the genus, first visceral view of carapace from Painten in plate 7.

REFERENCES: JME SOS 2429 a+b from Zandt, JME 03552 from the lower Tithonian of Zandt, ex coll. Josef Reitzer; JME Moe 9 from the Mörnsheim formation, lower Tithonian of Daiting. Refer also to the figures in FRICKHINGER (1994): p. 241, fig. 243; p. 247, figs. 510, 512; two adult specimens from Eichstätt and Langenaltheim are presented in the BMMS.

Genus *Thalassemys* Rütimeyer, 1858

ORIGINAL NAME: *Thalassemys* Rütimeyer, 1858: 57.

SYNONYMS: See BRÄM (1965), KARL *et al.* (2007) and KUHN (1964), *Parathalassemys* Nessov, 1984.

KNOWN DISTRIBUTION: Upper Jurassic of Southern Germany, Switzerland and France; Early Cenomanian of Middle Asia.

DESCRIPTION: Refer to BRÄM (1963), KARL *et al.* (2007) and MŁYNARSKI (1976), skull described by RIEPPEL (1980). Epiplastrals and entoplastron present, see also ZITTEL (1898, 1918) and figure 6 here.

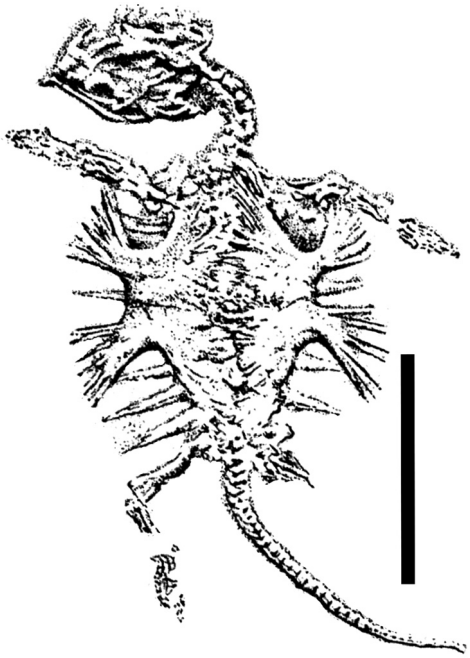

Figure 5. Idiochelys fitzingeri, *syn*. Yaxartemys longicaudata, *according to SUKHANOV (1964)*.

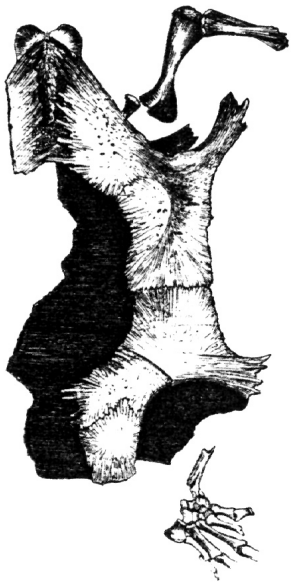

Figure 6. Thalassemys hugi, *syn*. Hydropelta meyeri *according to ZITTEL (1889)*.

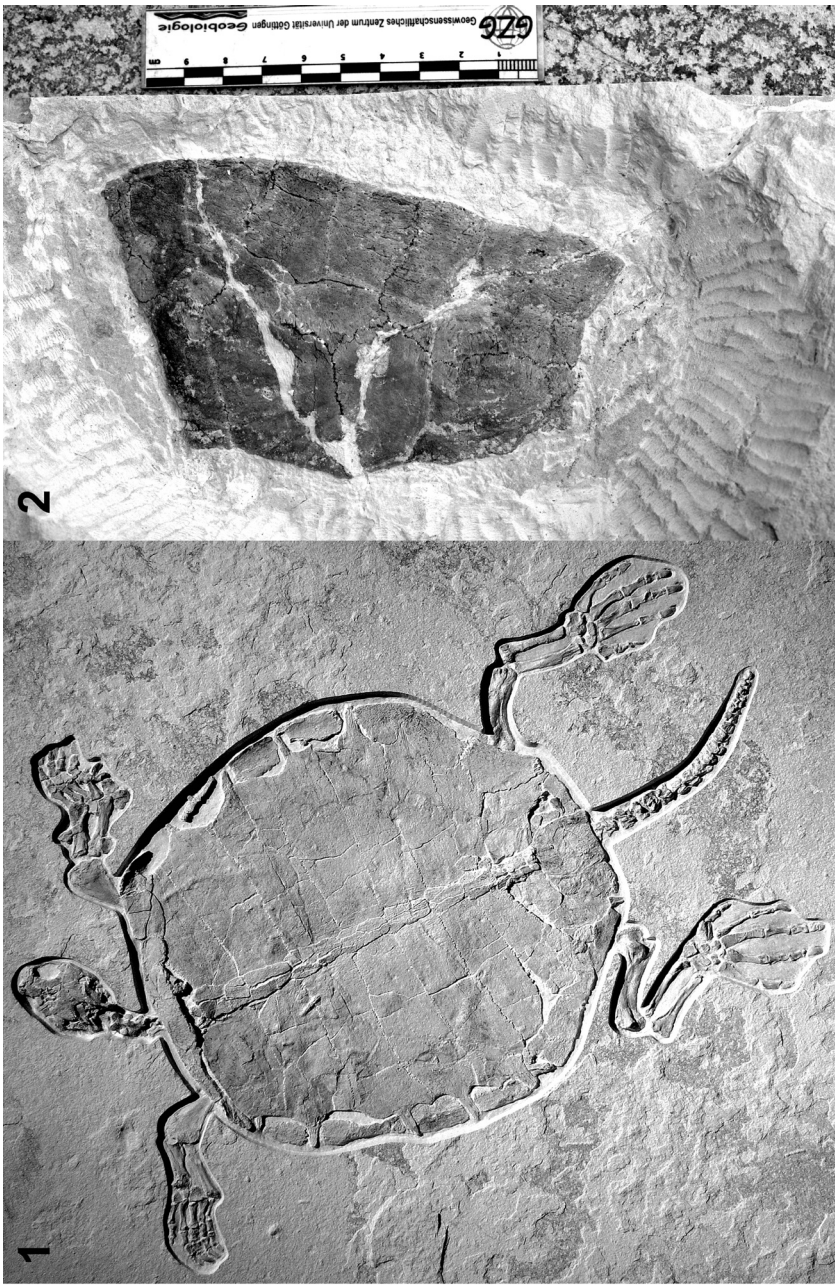

Plate 3. Eurysternum wagleri, *male, Mörnsheim formation of Mühlheim, coll. Red-Gallery Hamburg. Photo Krautworst Natursteine; 2. carapace remain, Mörnsheim formation of Mühlheim, coll. Krautworst Natursteine, photo H.-V. Karl, design Heike Künzel, TLDA.*

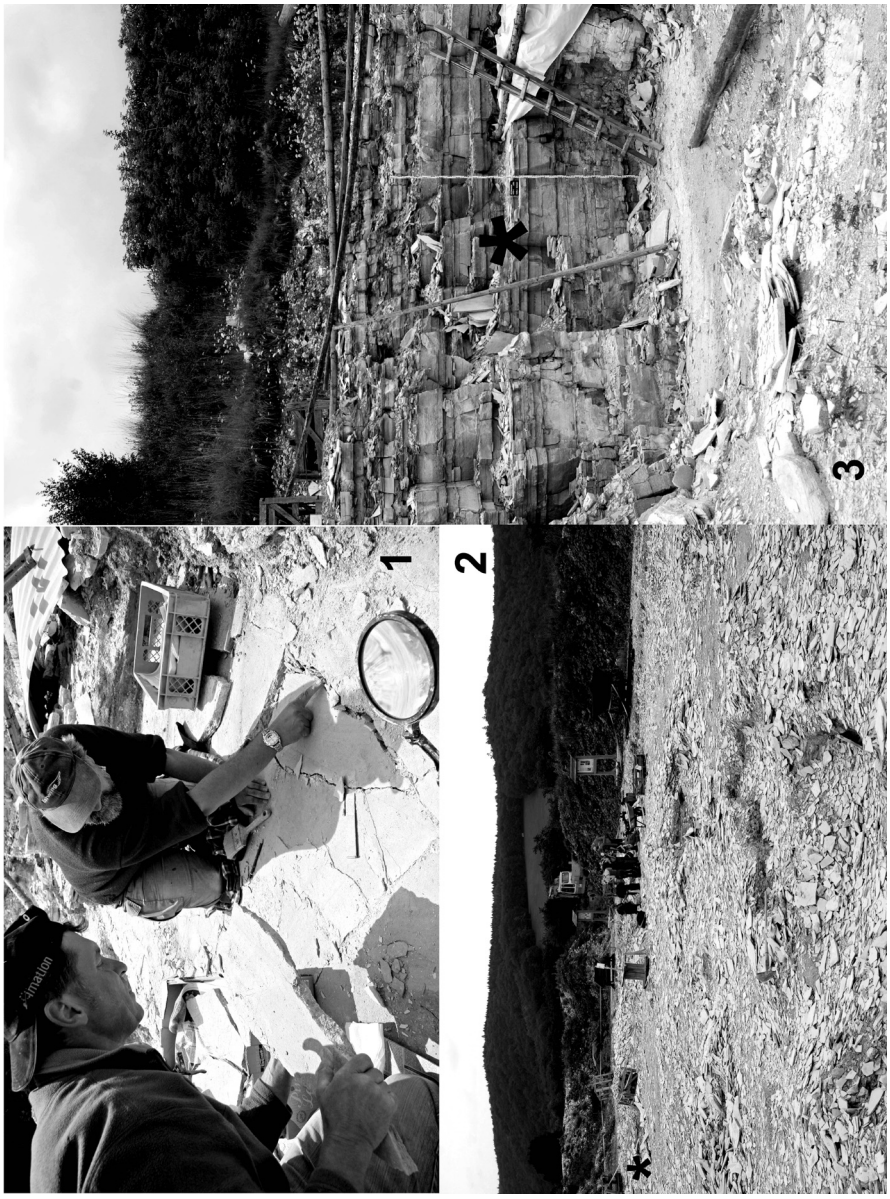

Plate 4. 1: Roland Pöschl (left) and Ulrich Leonhardt (rigth) during the excavation of the complete skeleton of a Eurysternum wagleri *male (plate 2) in the Mühlheim quarry; 2: stratigraphical position (*) of the Mühlheim specimen in the zone "Erste Rosa" C19-C22 at lower quarry of Mühlheim, 3: finding position (*) of the second Mühlheim specimen in the zone "Erste Rosa" C19-C22 at upper quarry of Mühlheim. Photos 1: 'Uwe-Krautworst natural stones Company', 2+3: H.-V. Karl, the last during the student excavation 2011 of the Geocenter Göttingen.*

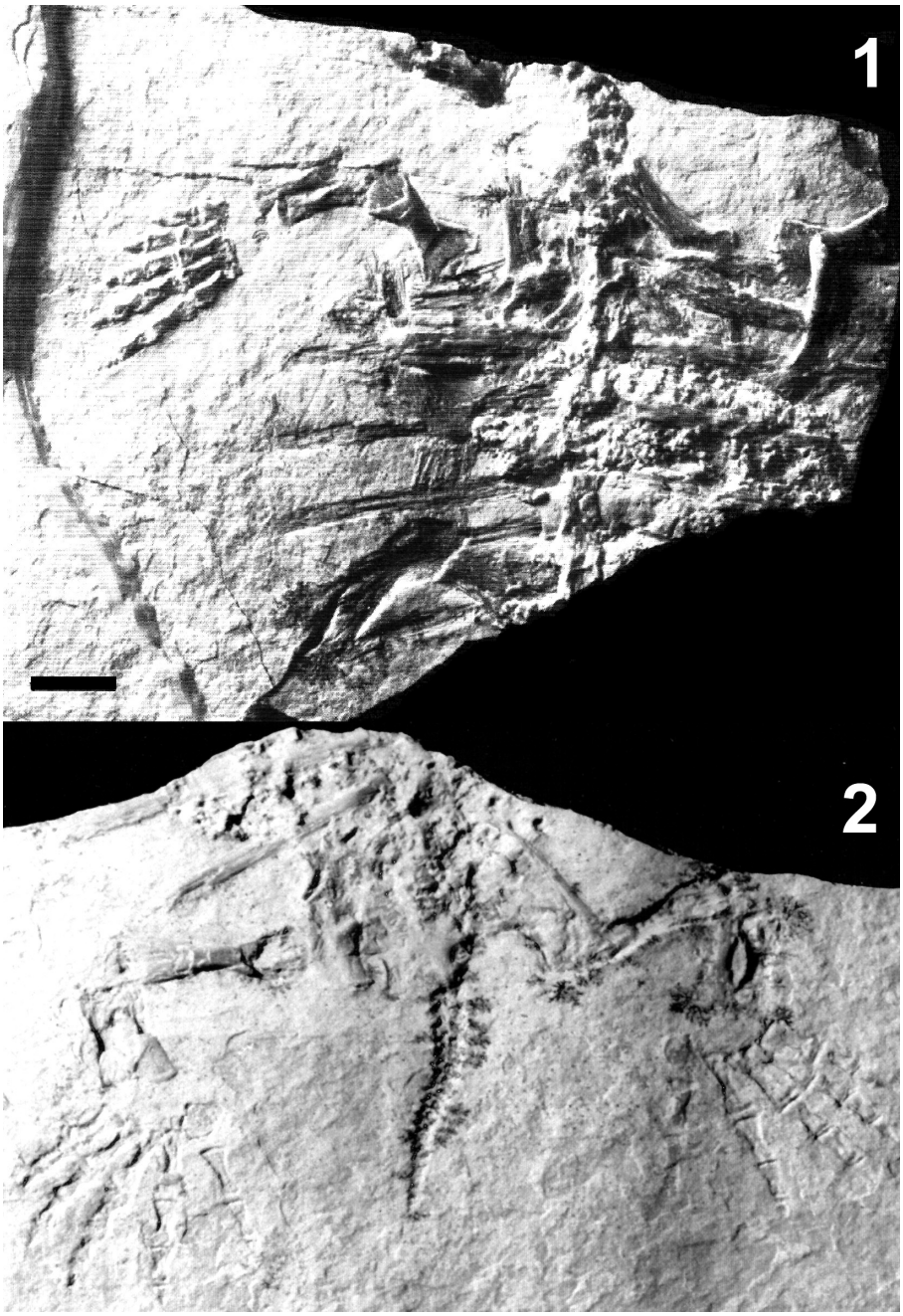

Plate 5. Idiochelys fitzingeri, *juvenile, Brunn, 1: anterior part in dorsal view, NMOR (Naturkundemuseum Ostbayern, Regensburg); 2: posterior part in dorsal view, coll. Ursula Penner, Kallmünz.*

Plate 6. Solnhofia parsonsi*, Painten, Coll. Dieter Kümpel (Wuppertal). Photo Dirk Urban, Erfurt, design H.-V. Karl & Heike Künzel, TLDA.*

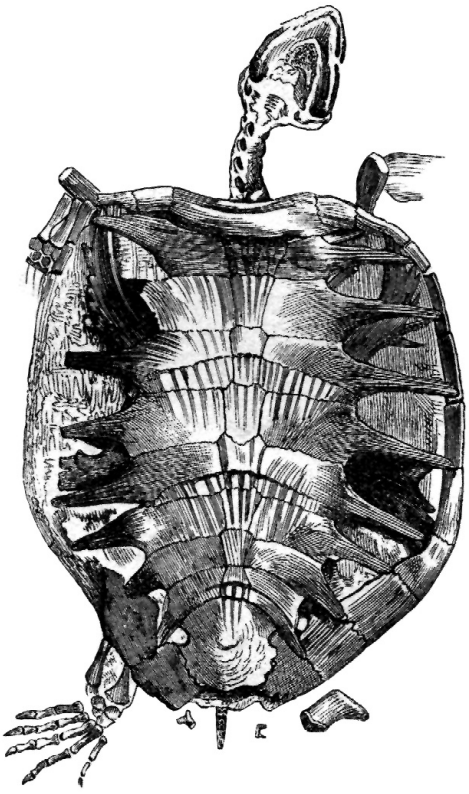

Figure 7. Eurysternum wagleri*, according to ZITTEL (1918).*

Thalassemys hugii (Gray, 1831)

ORIGINAL NAME: *Emys Hugi* Gray, 1831: 33.

SYNONYMS: Refer to BRÄM (1965), KARL *et al.* (2007) and KUHN (1964), *Thalassemys moseri* Bräm, 1965.

TYPE LOCALITY: Cirin, France.

TYPE HORIZON: Upper Jurassic.

DESCRIPTION: The same as the genus.

REFERENCES: Holotype preserved in MSS n.º 1, carapace with imprint and bones according to BRÄM (1965).

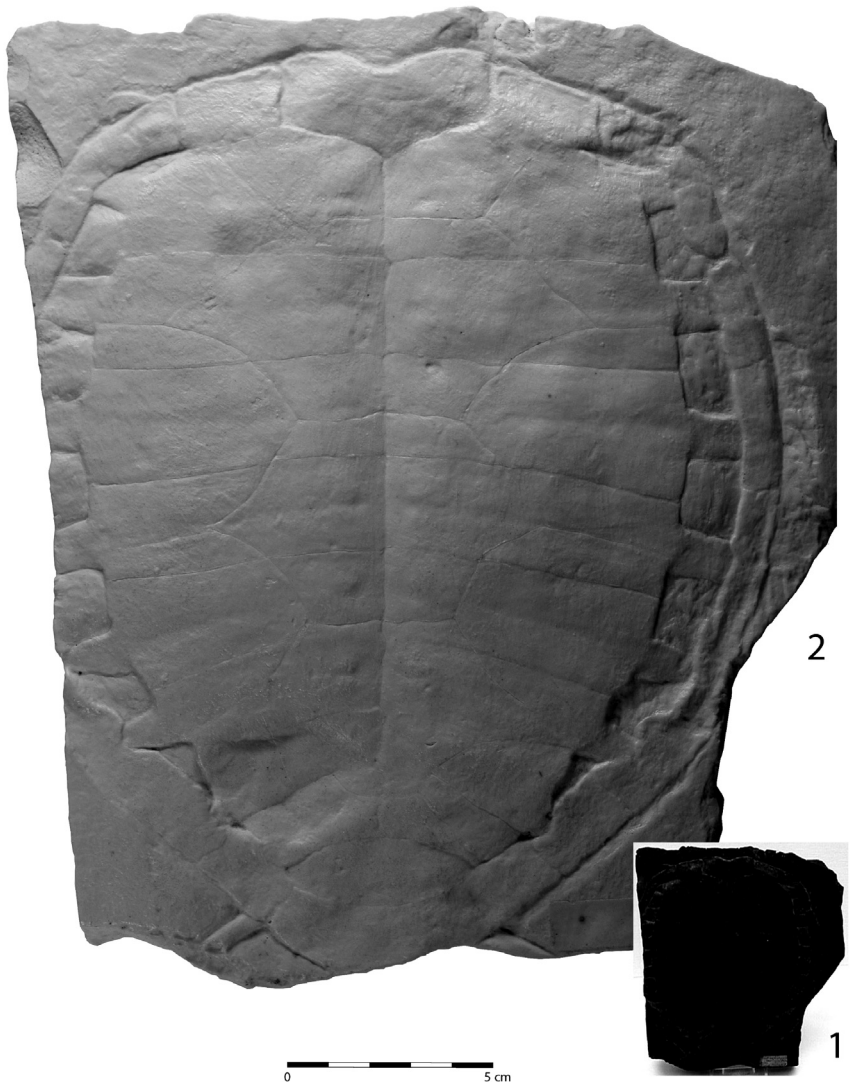

Plate 7. Figure 1: Original mould from the holotype of Sontiochelys cretacea *Stache, 1905 preserved in the Museo Civico di Storia Naturale di Trieste. Photo Deborah Arbullà; Figure 2: Actual resin mould by the original gypsum mould of* Sontiochelys cretacea *Stache, 1905 (plate 1). Photo Heike Künzel, TLDA.*

Thalassemys carva Nessov, 1984

ORIGINAL NAME: *Parathalassemys carva* Nessov, 1984 in NESSOV & KRASSOVSKAYA (1984); *Parathalassemys carva* Nessov, 1984, refer also to DANILOV, 1999.

TYPE LOCALITY: Itemir (Итемир), Kazakhstan, Kyzilkum, Middle Asia.

TYPE HORIZON: Early Cenomanian, (?Albian), Kulbikinskaya pack a (кулъбикинская пачка).

DESCRIPTION: All characters of *Parathalassemys* according to NESSOV & KRASSOVSKAYA (1984) are present also in the other groups of Thalassemydidae, such as: turtles with shell length to 50 cm; sulci of horny shields deep; centrals broad, within their borders there are numerous folds, crossed by concentric lines; last costal with two widely separated free ribheads, laterally with respect to them there are large elevated areas for the connection of the ilium; two metaneurals; the full range of vertebras is present in front of their elongation; heads of the trunk ribs are strong, at the last costal plate two of these heads are widely apart from each other and the plastron in large specimens is moderately developed and shows other central fontanelles.

REFERENCES: Holotype ZNIGR, n.º 1/12086, carapace and plastron remains according to NESSOV & KRASSOVSKAYA (1984), plate 4, figs. 9-12= carapace remains and 13= plastron remain, holotype figs. 10-13.

Genus *Sontiochelys* Stache, 1905

ORIGINAL NAME: *Sontiochelys* nov. genus, STACHE, 1905: 285.

SYNONYMS:

- 1905 *Sontiochelys* n.gen, Stache, p. 285.
- 1955 *Sontiochelys*, Bergounioux, p. 522.
- 1956 *Sontiochelys*, Romer, p. 500.
- 1956 *Sontiochelys*, Huene (sic), p. 208.
- 1956 *Sontiochelys*, Romer, p. 581.
- 1964 *Sontiochelys*, Kuhn, p. 32.
- 1975 *Sontiochelys*, Pritchard, p. 27.
- 1979 *Sontiochelys*, Pritchard, p. 873.

KNOWN DISTRIBUTION

Lower Cretaceous of Dalmatia, ABEL (1919) erroneously mentioned *Sontiochelys* from the Lower Cretaceous (Wealden) of Bernissart (Belgium).

DIAGNOSIS: Free rib end of pleural I alternating between peripheral II and III; nuchal notch not very deep; neural row is completely reduced; metaneural single and wide; pygal much wider than long.

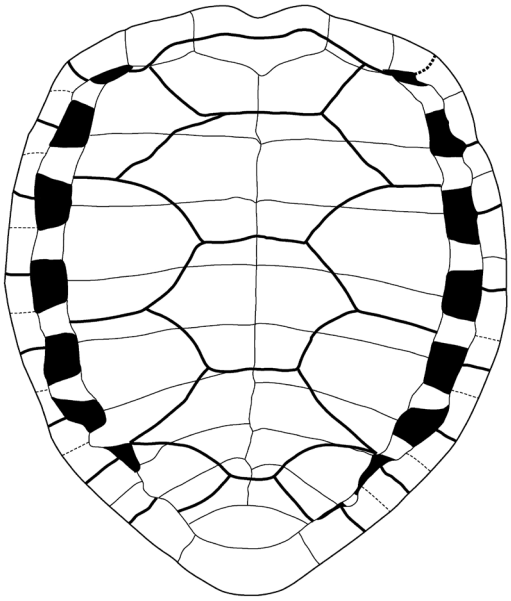

Figure 8. Actual reconstruction of the carapace of Sontiochelys cretacea *based on the new resin mould.*

Sontiochelys cretacea Stache, 1905

ORIGINAL NAME: *Sontiochelys cretacea*, Stache, 1905: 292.

SYNONYMS:

- 1905 *Sontiochelys cretacea*, Stache, pp. 292.
- 1964 *Sontiochelys cretacea*, Kuhn, pp. 32.

TYPE LOCALITY: Ancient quarry at Mrzlek, close to Salcano/Solkan at the south-eastern flank of Monte Santo near Görz/Gorizia (Slovenia); Gefürstete Grafschaft Görz and Gradisca, former Austria-Hungary, now Italy and Slovenia, Görz, Gorika, Gorizia in the region of Friuli-Venezia-Giulia in Italy.

TYPE HORIZON: Black limestone ("Fischschiefer") of the lower Cretaceous of Karst, Gorizia in Veneto Friuli, Hauterivian to Berremian (formerly Cenomanian). The black limestones of Mzrlik were originally classified as Lower Creatceous by KNER (1863), also STACHE (1905) located it the 'lower Karst chalk'. Later the layers have been considered as lowermost Upper Cretaceous (Cenomanian). According to the geological map of Yugoslavia, the limestone is Aptian in age. But, in the opinion of the Italian geologists, the

black fossiliferous limestone is considered to be Hauterivian up to Berremian in age (DALLA VECCHIA *et al.*, 2008).

HOLOTYPE: Originally preserved in the Museum of Görz, today lost. A cast of the holotype is in the permanent collection of Museo Civico di Storia naturale di Trieste and was available for the investigation.

Gen. et sp. indet.

LOCALITY: Neumarkt in the Upper Palatinate (German: Neumarkt i. d. Oberpfalz), Bavaria, Southern Germany.

HORIZON: Sinemurian (Liassic α-β), Lower Jurassic.

MATERIAL: Pleural (plate 8).

DESCRIPTION: Thalassemydid type with large peripheral fontanells and width centrals (SCHLEICH, 1984).

REFERENCE: MSL, inventary number Nm 4 according to SCHLEICH (1984).

CHARACTER ANALYSIS

For the analysis the following characters were selected:

SKULL

1. Primary palatine=0, or secondary palatine=1 presence;

2. orbits oriented dorsolaterally=0, or dorsofrontal=1;

3. snout bluntly rounded=0, or extended rostrally=1;

4. temporal notch moderate=0, or large=1;

5. primary palatine presence=0, or extensive secondary palatine developed=1;

CERVICAL AND CAUDAL VERTEBRAE

The number of cervical vertebrae is constant, the number of tail vertebrae may varies between genders.

CARAPACE

6. carapace outline long oval=0, shieldlike=1;

7. nuchal much wider than long: absent=0, present=1;

8. nuchal notch flat=0, deep=1;

9. neural row connect=0, interrupted=1;

10. cocervicals present=0, absent=1;

11. neural row 6P/4/6A/6A/6A/6A/6A/6=0, or 4/6A/6A/6A/6A/6A/6B=1;

12. caudal notch present=0, absent=1;

PLASTRON

13. epiplastrals and entoplastron present=0, absent=1;
14. anterior plastrallobe as long as the posterior=0, anterior shorter as the posterior=1;
15. intergular present=0, absent=1;
16. mesoplastrals present=0, absent=1;
17. submarginals present=0, ansent=1;

EXTREMITIES

18. first finger and first toe with two phalanges: absent=0, present=1;
19. second toe and second finger with three phalanges: present=0, with only two phalanges=1;
20. third finger and toe with three phalanges: present=0, absent=1;
21. fourth finger and toe with three phalanges: present=0, absent=1;
22. fifth finger and toe with three phalanges: present=0, absent=1;
23. fifth toe with four phalanges: present=0, absent=1;
24. third finger is the longest=0, fifth finger is the longest=1;
25. third toe is the longest=0, fourth toe is the longest=1;
26. first finger is the shortest: present=0, absent=1;
27. first toe is the shortest: present=0, absent=1;

DATAMATRIX: Pleurosternidae 00000000010000000??????????; Plesiochelyidae 00000000001000010??????????; Hylaeochelyidae 0000000001100001 0??????????; Chengyuchelyidae ?????000011000010??????????; *Indochelys* ?????1100110010101??? ???????; *Kayentachelys* 00010001011000010??????????; *Eurysternum* 00010110011 111?1?1000010001; *Idiochelys* 01101101111 0011101100011110; *Solnhofia* 1111 1101011001?11??????????; *Thalassemys* 0000010001100111100000100011001111??? ???????

RESULT: The character differentiation with DOLMOVE (Interactive Dollo and Polymorphism Parsimony by Joseph FELSENSTEIN, 1986a) shows only one simple tree (fig. 8a): (*Thalassemys*, (*Solnhofia*, (*Idiochelys*, (*Eurysternum*, (*Kayentachelys*, (*Indochelys*, (Chengyuchelyidae, (Hylaeochelyidae, (Plesiochelyidae, Pleurosternidae))))))))).

The tree obtained with PARS (Discrete character parsimony algorithm, version 3.6a3 by Joseph FELSENSTEIN, 1986b) for selected central European turtle taxa is conform with the previously quoted tree and shows a larger distance of *Eurysternum* and *Solnhofia* to *Idiochelys* and *Thallasemys*. Fig. 8b shows one of the most simple trees found (fig. 8b): ((*Thallasemys*: 3.00, (*Idiochelys*: 2.00 (*Solnhofia*: 4.50, *Eurysternum*: 2.00): 4.50): 4.00): 2.00, Hylaeochelyidae:

0.00, Plesiochelyidae: 1.00, Pleurosternidae: 3.00). One most parsimonious tree requires a total of 26.000.

BETWEEN	AND	LENGTH
1	4	2.00
4	*Thallasemys*	3.00
4	2	4.00
2	*Idiochelys*	2.00
2	3	4.50
3	*Solnhofia*	4.50
3	*Eurysternum*	2.00
1	Hylaeochelyidae	0.00
1	Plesiochelyidae	1.00
1	Pleurosternidae	3.00

CHARACTER ANALYSIS WITH *SONTIOCHELYS* (MCST): For the analysis of the carapace the following characters were selected:

28. carapace outline long oval=0, shieldlike=1;
29. nuchal much wider than long: absent=0, present=1;
30. nuchal notch flat=0, deep=1;
31. neural row connected=0, interrupted=1;
32. neural row complete reduced=1; neurals present= 0;
33. cocervicals present=0, absent=1;
34. neural row 6P/4/6A/6A/6A/6A/6A/6=0, or 4/6A/6A/6A/6A/6A/6B=1;
35. caudal notch present=0, absent=1;

DATAMATRIX: *Pleurosternon* 00000111, *Plesiochelys* 00000001, *Hylaeochelys* 00000111, *Eurysternum* female 01000110, *Eurysternum* male 11000110, *Idiochelys* 11110111, *Solnhofia* 10100111, *Thalassemys* 10000111, *Sontiochelys* 111011?1.

RESULT: The character differentiation with DOLMOVE (Interactive Dollo and Polymorphism Parsimony by Joseph FELSENSTEIN, 1986a) shows only one simple tree (fig. 4): (*Sontiochelys*, (*Thalassemys*, (*Solnhofia*, (*Idiochelys*, (*Eurysternum* male, (*Eurysternum* female, (*Hylaeochelys*, (*Plesiochelys*, *Pleurosternon*)))))))).

The tree obtained with PARS (Discrete character parsimony algorithm, version 3.6a3 by Joseph FELSENSTEIN, 1986b) is conform with the one mentioned before and shows a nearer relation of *Sontiochelys*, *Solnhofia* and *Idiochelys* inside the Thallasemydidae. Three parsimonious trees were found:

1): (((*Eurysternum* male: 0.00, *Eurysternum* female: 1.00): 2.00, ((*Sontiochelys*: 1.00, *Idiochelys*: 1.00): 1.00, *Solnhofia*: 0.00): 1.00, *Thalassemys*: 0.00): 1.00, *Hylaeochelys*: 0.00, *Plesiochelys*: 2.00, *Pleurosternon*: 0.00) [0.3333];

2): ((*Eurysternum* male: 1.00, *Eurysternum* female: 0.00): 2.00, (((*Sontiochelys*: 1.00, *Idiochelys*: 1.00): 1.00, *Solnhofia*: 0.00): 1.00, *Thalassemys*: 0.00): 1.00, *Hylaeochelys*: 0.00, *Plesiochelys*: 2.00, *Pleurosternon*: 0.00) [0.3333];

3): (((*Sontiochelys*: 1.00, *Idiochelys*: 1.00, (*Eurysternum* male: 0.00, *Eurysternum* female: 1.00): 2.00): 1.00, *Solnhofia*: 0.00): 1.00, *Thalassemys*: 0.00): 1.00, *Hylaeochelys*: 0.00, *Plesiochelys*: 2.00, *Pleurosternon*: 0.00) [0.3333].

The first parsimonious tree requires a total of 10.000.

BETWEEN	AND	LENGTH
1	2	1.00
2	3	2.00
3	*Eurysternum* male	0.00
3	*Eurysternum* female	1.00
2	4	1.00
4	5	1.00
5	*Sontiochelys*	1.00
5	*Idiochelys*	1.00
4	*Solnhofia*	0.00
2	*Thalassemys*	0.00
1	*Hylaeochelys*	0.00
1	*Plesiochelys*	2.00
1	*Pleurosternon*	0.00

DISCUSSION

ZITTEL (1877) and OERTEL (1915) had already stressed that different age stages are represented among the described material and the development of the fontanellae of the carapace depends on them.

The number and position of the phalanges of the fingers and the toes are homologues and can be reconstructed easily; this parameter is also applicable for the determination, due to his specimen specification. According to these preliminary known relations only one turtle species is represented in the Jurassic fauna of Brunn. In the hand and foot anatomy also reveals a closer relationship between the two genera *Idiochelys* (mono-typical species *I. fitzingeri*) and *Solnhofia* (mono-typical species *S. parsonsi*) (JOYCE, 2000). The taxonomic relationship between the genera *Idiochelys* and *Solnhofia* is clearly defined by the shell. The holotype of *Idiochelys* as well as that of *Eurysternum* are missing (WELLNHOFER, 1967). The next relation is probably given between Joyce's specimen on *Solnhofia* and Wellnhofer's specimen of Thalassemydidae indet., primarily in the morphology of the metatarsus V and

the toe V. *Eurysternum* shows a structure of the toe V similar to the present posterior specimen of Brunn, but the hand structure and the structures of the humerus and femur is clearly different from *Idiochelys* and from the Brunn material, it is in fact shorter and more compact. The tail of *Idiochelys* is much shorter than that of male *Eurysternum* which has still evident widenings and a row of broad scutes (KARL & TICHY, 2006). The foot of *Idiochelys* of Brunn shows well developed claws on all five toes.

The genus *Sontiochelys* Stache 1905, with the only known species *Sontiochelys cretacea* Stache 1905 is known from the early Cretaceous of Monte Santo area in Gorizia in Dalmatia. It is the last and most recent stage of the genuine marine evolution of Plesiochelyoidea and represents the complete reduction of the Neuralia as the last consequence of the evolution of the *Idiochelys*, which is nearer to the Thalassemydidae. Despite the attribuition of *Sontiochelys* into the Thalassemydidae no reason subsist to split this family into subfamilies, but because of the distribution of the separated clades of the genera *Thalassemys*, *Solnhofia*, *Idiochelys* and with *Eurysternum* in the cladogram, a split of the families Thalassemydidae and Eurysternidae is useful.

STACHE (1905) considered the fully reduced neuralia as the only characteristic of recent Chelidae (Pleurodira). Especially in consideration of the South American so-called frog head-turtle or toad head turtle *(Batrachemys*, *Phrynops)*. Certain similarity in the construction of the carapace of *Sontiochelys* with *Platemys platycephala,* which can be studied in BOULENGER (1889: fig. 61, p. 226) may be the reason for this assumption. He introduced *Sontiochelys* as a new type of so-called amphibian turtles ("Lurchschildkröten"), as Pleurodira was called at that time. The presence of a depression along the median line was also crucial to his theory, this is instead not nearly so deep as STACHE (1905) figured out. A closer relationship with the Pleurodira is not demonstrated. CADENA (2011) describes the first oldest shell remains of an probable podocnemidoid turtle from the Rosablanca Formation, Early Cretaceous (Valanginian) of Zapatoca town in Colombia.

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to publish the fossil. For the help with information on the search of the type specimen of *Sontiochelys* we thank Mag. Dr. Andreas Kroh (Natural History Museum Vienna) and Dr. Irene Zorn (Geological Survey of Austria). We are very grateful to Mrs Deborah Arbullà (Museo Civico di Storia Naturale di Trieste) who supported us with a high-quality resin mould of *Sontiochelys*.

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