

NEW OLIGOCENE TURTLE REMAINS OF THE OBERLEICHTERSBACH DOLINE FILLING (LOWER FRANCONIA, GERMANY) AND REVISION OF THE GENUS *PALAEOMAUREMYS* (TESTUDINES: GEOEMYDIDAE)

[*Nuevos ejemplares del Oligoceno superior de los sedimentos lacustres de la dolina Oberleichtersbach (Baja Franconia, Baviera, Alemania)*]

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ABSTRACT: New Late Oligocene (Chattian) remains of the terrapins *Palaeoemys bessiaca* Schleich, 1994 and *Palaeomauremys tuberculata* (Portis, 1882), the soft-shelled turtles *Allaeochelys parayrei* Noulet, 1867 and *Trionyx* cf. *triunguis* Forskål, 1775, and the snapping turtle *Cbelydrasia decheni* (H. V. Meyer, 1852) from lacustrine sediments of the Oberleichtersbach doline (Lower Franconia, Bavaria, Germany) are reported. The morphological features of these five species, their taxonomic position and their palaeobiological implications are discussed. The new *Palaeomauremys* material suggests that *P. mlynarskii* (Hervet & Lapparent de Broin, 2000) is a junior synonym of *P. tuberculata* (Portis, 1882).

Key words: Testudines, *Palaeoemys bessiaca* Schleich, 1994, *Palaeomauremys tuberculata* (Portis, 1882), *Allaeochelys parayrei* Noulet, 1867, *Trionyx* cf. *triunguis* Forskål,

1775, *Chelydrasia decheni* (H. V. Meyer, 1852), Late Oligocene, Chattian, Oberleichtersbach, Lower Franconia, description, palaeobiology.

RESUMEN: En este artículo se estudian nuevos ejemplares del Oligoceno superior de los sedimentos lacustres de la dolina Oberleichtersbach (Baja Franconia, Baviera, Alemania), determinados como de los galápagos *Palaeoemys hessiaca* Schleich, 1994 y *Palaeomauremys tuberculata* (Portis, 1882), las tortugas de caparazón blando *Allaechelys parayrei* Noulet, 1867 y cf. *Trionyx triunguis* Forskål de 1775, y la tortuga mordedora *Chelydrasia decheni* (V. H. Meyer, 1852). Se discuten las características morfológicas de estas cinco especies, su posición taxonómica y sus implicaciones paleobiológicas. El nuevo material de *Palaeomauremys* sugiere que *P. mlynarskii* (Hervet y Lapparent de Broin, 2000) es un sinónimo de *P. tuberculata* (Portis, 1882).

Palabras clave: Testudines, *Palaeoemys hessiaca* Schleich, 1994, *Palaeomauremys tuberculata* (Portis, 1882), *Allaechelys parayrei* Noulet, 1867, *Trionyx* cf. *triunguis* Forskål, 1775, *Chelydrasia decheni* (H. V. Meyer, 1852), Oligoceno superior, Chattianse, Oberleichtersbach, Baja Franconia (Alemania), descripción, paleobiología.

INTRODUCTION

From the German terrestrial and limnic deposits of Late Oligocene (Chattian) age the terrapin turtle *Palaeomauremys mlynarskii* (Hervet & Lapparent de Broin, 2000) was already described from Rott (North Rhine-Westphalia), Enspel (Westerwald: Rhineland-Palatinate), and Oberleichtersbach (Bavaria: Lower Franconia). In the meantime, additional material is available from the Walter Heck collection (Oberleichtersbach) which enables the revision of *Emys tuberculata* Portis, 1882, a species of previously uncertain status which was assigned to *Palaeomauremys* Hervet, 2004 by HERVET (2004) and KARL & WETTLAUER (2010). Based upon the now known morphological features in the new specimens, both taxa can easily be synonymized on generic level.

The genesis and topography of the Late Oligocene (Chattian) doline filling of Oberleichtersbach near Bad Brückenau (fig. 1) is discussed in detail by MARTINI (2008) which contribution is explicitly referred to. In the same volume BÖHME (2008) presented a compilation of 43 taxa of fish, amphibians and reptiles. The first consist of six species in two families: five species of Cyprinidae and the new *Cobites primigenus* Böhme, 2008 (Cobitidae). The amphibians include eight species of Allocaudata and Urodela as well as six species of Anura. The reptiles are present with one species of *Diplocynodon* (Crocodylia) and 15 species of Squamata: Lacertilia, Anguimorpha, and Ophidia, the latter with the new *Texasophis hecki* Böhme, 2008. Many of these species present the most ancient record of their groups, one of them is the latest one. With this content of fossils, this locality shows the highest diversity of ectothermic vertebrates of the Late Oligocene world-wide. Additionally there are six species of Testudines. One pleural of "*Palaeomauremys mlynarskii*" is figured (pl. 4, fig.

7a-b), the other taxa are listed without figures and catalogue numbers. Here it is referred to under the discussion of the species in question.

This paper is supplement 180 of chapter “C. Fourth faunal change: Paleogene-Neogene (P/N) boundary/V. Rise of stream terrapins”, in: *Studia Palaeocheloniologica*, IV (KARL, 2011).



Figure 1. Geographical positions of the *Palaeomauremys*-localities: 1= Rochette near Lausanne, Switzerland, type locality of *Emys tuberculata* Portis, 1882; 2= Trbovlje (former Trifail) in Slovenia, type locality of *Testudo riedli* Hoernes, 1892; 3= Wuberg south of Windischgarsten, Austria; 4= Rott, Germany, type locality of *Palaeochelys mlynarskii* Hervet & Lapparent de Broin, 2000; 5= Enspel, Germany; 6= Oberleichtersbach, Germany. Among the localities 4 and 5, see also the Geological Map of the Tertiary Westerwald, which was taken by KARL & WETTLAUER (2011) in SCHINDLER & WUTTKE (2010).

SYSTEMATIC PALAEOONTOLOGY

Ordo Testudines Linnaeus, 1758

Suprafamilia Testudinoidea Batsch, 1788

Familia Geoemydidae THEOBALD, 1868 (= Bataguridae Gray, 1869)

Subfamilia Palaeochelyinae Karl & Wettlaufer, 2011

Genus *Palaeoemys* Schleich, 1994

- 1994 *Palaeoemys* n. g. Schleich: 82-87.
- 2004 *Palaeoemys* Schleich, 1994 - HERVET: 65-70.
- 2004 *Palaeoemys* Schleich, 1994 - CLAUDE & TONG: 6.
- 2011 *Palaeoemys* Schleich, 1994 - KARL & WETTTLAUFER: 179.

Type species: *Palaeoemys hessiaca* Schleich, 1994: 82.

Additional species: *Palaeoemys occitana* Hervet, 2004, *Palaeoemys testudiniformis* (Owen, 1842) emend. CLAUDE & TONG (2004).

Geographic and stratigraphic distribution:

Early Eocene (MP9 to MP 10 boundary), Saint-Papoul near Castelnaudary (Aude, France) and Monthelon near Epernay (Marne, France: MP 19). Middle Eocene (MP11 to MP 13), Borken (northern Hesse, Germany).

Original diagnosis: SCHLEICH (1994: 82). With the present specimen the stratigraphic distribution is extended to the Late Oligocene and thus to the late Palaeogene.

3.1.1. *Palaeoemys* cf. *hessiaca* Schleich, 1994

- 2008 Emydidae indet. Böhme: 168.

New material: OLB 2-1, righth epiplastron in ventral view (plate 4, figs. 1-2); OLB 2-2, righth pleural I remain (plate 4, figs. 3-4); OLB 2-3, pleural remain (plate 4, figs. 5-6); OLB 4-1, phalanx III (plate 4, fig. 7); OLB 4-2, scapula remain (plate 4, fig. 8); OLB 2-4, left hyoplastron remain (plate 4, figs. 9-10); OLB 2-4, left hyoplastron remain (plate 4, figs. 9-10).

Discussion: The hitherto single record of *Palaeoemys*. Further specimens possibly belonging to this taxon are too fragmentary for a definite assignment. The ventral and visceral course of the gular suture, the furrow of the skin margin and the extremely weak gular bulge exactly resemble the known morphology of this genus (see HERVET, 2004; SCHLEICH, 1994), but due to the preservation the specimen is only tentatively assigned to *P. hessiaca*.

New oligocene turtle remains of the Oberleichtersbach doline filling (Lower Franconia, Germany) and revision of the genus *Palaeomauremys* (Testudines: Geoemydidae)

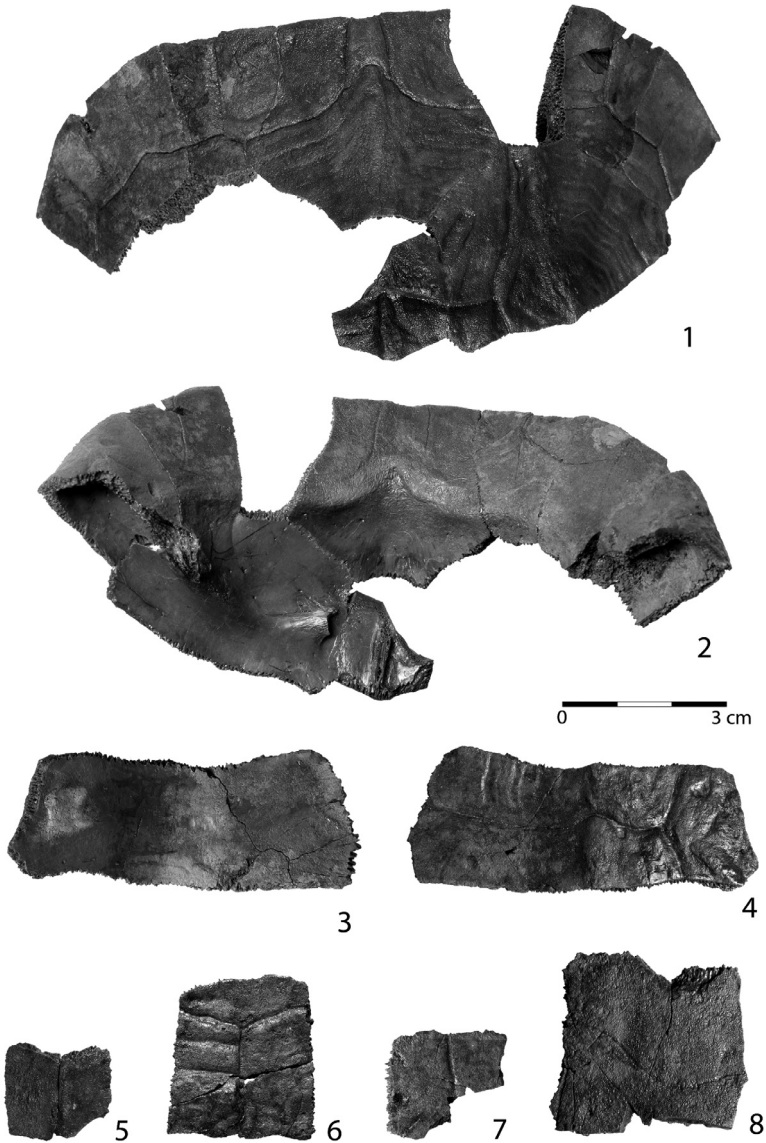


Plate 1. *Palaeomauremys tuberculata* (Portis, 1882) from Oberleichtersbach, ex Coll. Walter Heck, carapace remains: 1= OLB 1-1, anterior carapace remain in dorsal view, 2= in visceral view; 3= OLB 1-2, left pleural II in dorsal view; 4= in visceral view; 5= OLB 1-3, pygal in dorsal view; 6-8= OLB 1-4, OLB 1-5, OLB 1-6, bridge peripherals in dorsal view. Scale bar 3 cm. Photo Brigitte Stefan, design Heike Künzel (TLDA).

3.2. Genus *Palaeomauremys* Hervet, 2004

Selected synonymy:

- 1882 *Emys* - PORTIS: 19-20.
- 2000 *Palaeochelys* Schleich 1994 - HERVET & LAPPARENT DE BROIN: 563.
- 2004 *Palaeomauremys* n. gen. HERVET: 54-56.
- 2011 *Palaeomauremys* Hervet, 2004 - KARL & WETTTLAUER: 175.

Type species: *Emys tuberculata* Portis, 1882.

Original description: PORTIS (1882: 19-20, pl. 4).

Type locality: Rochette near Lausanne (Switzerland).

Type stratum: Subalpine Molasse (Molasse d'eau douce inférieure, USM), Late Oligocene: MP 28-30 (ENGESSER, 1990), MP 29 (ENGESSER & MÖDDEN, 1997).

Holotype: MGL 8901 (= PORTIS, 1882, pl. 4), anterior fragment of carapace + fragments of plastron (pl. 76, figs. E, F, G and H).

Emended description by HERVET (2004): "Le repli ventral de la cervicale est de longueur moyenne sur la face interne de la nucale, il est très large (Pl. 76, fig. G). Le repli ventral des M1 est assez long et il à présence de deux légers bourrelets transversaux sur la face interne de la nucale. La face interne de la PL1 montre l'insertion du pilier axillaire sur environ un tiers de la largeur de la pleurale (Pl. 76, fig. H); il y a un léger bourrelet osseux sur la PL1, médialement à cette insertion". For the generic diagnosis of the carapace: see HERVET (2003, 2004), in particular map 4.11 and chapter 4 in the paper in 2004.

Remarks: Most important synonym for the region in question is *Palaeochelys mlynarskii* (Hervet & Lapparent de Broin, 2000) from the Late Oligocene (MP 30: BÖHME & LANG, 1991; MÖRS, 1995) of the lignites of Rott near Bonn (North Rhine-Westphalia, Germany; see: HERVET & LAPPARENT DE BROIN, 2000; HERVET 2003 and 2004, with generic diagnosis). For the Enspel specimen Exemplar: see KARL & WETTTLAUER (2011). A small species with a carapace length of originally only 125 mm, but the present material suggests a length of more than 200 mm.

New oligocene turtle remains of the Oberleichtersbach doline filling (Lower Franconia, Germany)
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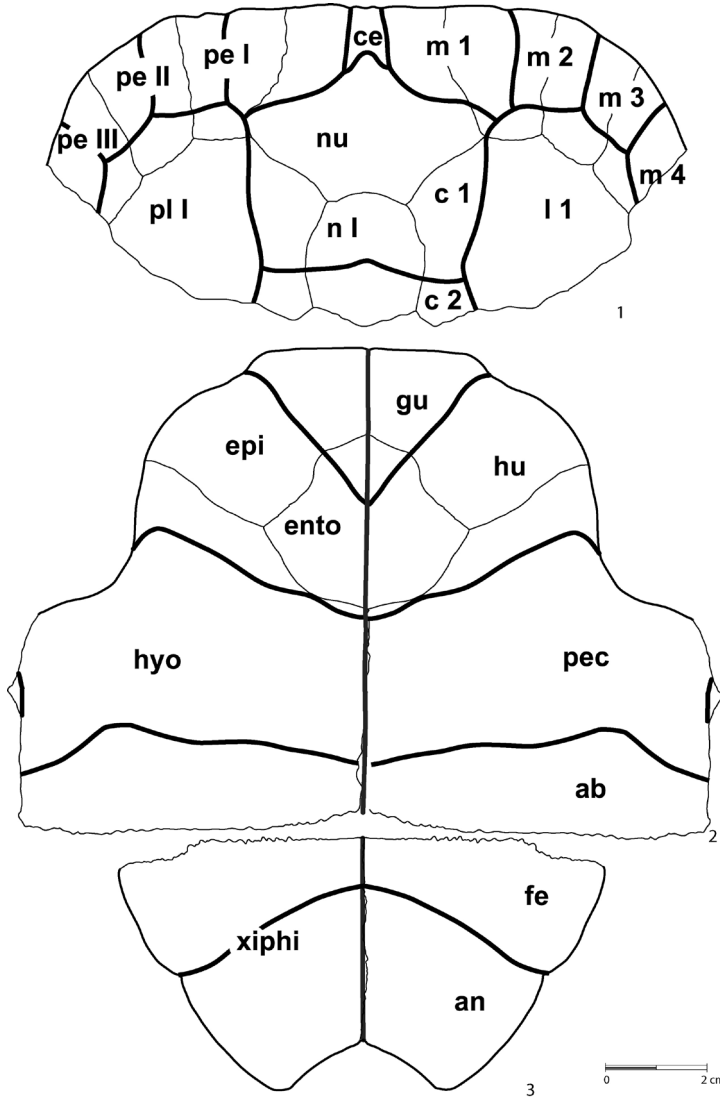


Figure 2. Reconstruction of *Palaeomauremys tuberculata* (Portis, 1882) from Oberleichtersbach: 1= anterior carapace region based on OLB 1-1 (plate 1, fig. 1); 2= anterior half plastron based on OLB 1-9 (plate 2, fig. 7); 3= caudal lobe of plastron based on OLB 1-12 (plate 2, fig. 10). Carapace plates (left side): nuchal = nu, neurals = n, pleurals = pl, peripherals = pe. Carapace scutes (right side): cervical = ce, centrals = c, laterals = l, marginals = m. Plastron plates (left side): epiplastrals = epi, entoplastron = ento, hyoplastron = hyo, xiphiplastron = xiphi. Plastron scutes (right side): gulars = gu, humeral = hu, pectorals = pec, abdominals = ab, femorals = fe, annals = an.
Graphic H.-V. KARL & Heike KÜNZEL (TLDA).

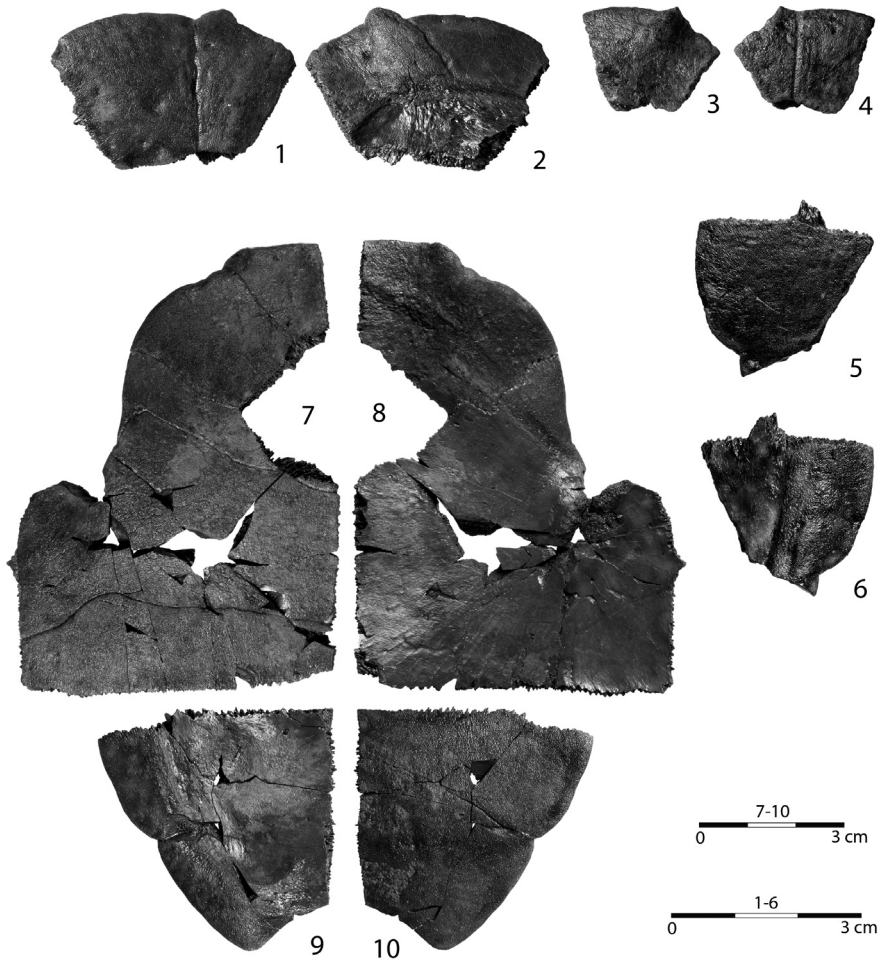


Plate 2. *Palaeomauremys tuberculata* (Portis, 1882) from Oberleichtersbach, ex Coll. Walter Heck, plastron remains: 1= OLB 1-10, right epiplastron in ventral view, 2= in visceral view;

3= OLB 1-11, left epiplastron in ventral view, 4= in visceral view; 5= OLB 1-12, left xiphiplastron in visceral view, 6= in ventral view; 7= OLB 1-9, right anterior plastral lobe in ventral view, 8= in visceral view; 9= OLB 1-13, right xiphiplastron remain in ventral view, 10= in visceral view. Scale bar 3 cm. Photo Brigitte Stefan, design Heike Künzel (TLDA).

3.2.1. *Palaeomauremys tuberculata* (Portis, 1882)

Selected synonymy:

- 1882 *Emys tuberculata* n. sp. Portis: 19-20; pl. 4.
- 1892 *Testudo Riedli* nov. form. Hoernes: 243 (synonyms in KARL, 1994/95).

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- 2000 *Palaeochelys mlynarskii* n. sp. Hervet & Lapparent de Broin: 563-569; figs. 1-3.
- 2004 *Palaeomauremys «tuberculata»* (Portis, 1882) - HERVET: 163.
- 2011 *Palaeochelys mlynarskii* Hervet & Lapparent de Broin, 2000 - KARL & WETTLAUER: 175-177.
- 2011 *Palaeomauremys «tuberculata»* (Portis, 1882) - KARL & WETTLAUER: 175.

Geographic and stratigraphic distribution: (i) Germany: Top of Late Oligocene (MP 30), Rott near Bonn (North Rhine-Westphalia); Enspel Maar (Rhineland-Palatinate: Westerwald); doline filling at Oberleichtersbach (Bavaria: Lower Franconia; KARL & WETTLAUER, 2011).

(ii) Slovenia: Trbovlje (former Trifail).

New material: OLB 1-1, anterior carapace remain (plate 1, figs. 1-2); OLB 1-2, left pleural II (plate 1, figs. 3-4); OLB 1-3, pygal (plate 1, fig. 5); OLB 1-4, OLB 1-5, OLB 1-6, bridge peripherals (plate 1, figs. 6-8); OLB 1-9, right anterior plastral lobe (plate 2, figs. 7-8); OLB 1-10, right epiplastron (plate 2, figs. 1-2); OLB 1-11, left epiplastron (plate 2, figs. 3-4); OLB 1-12, left xiphiplastron; OLB 1-13, right xiphiplastron remain (plate 2, figs. 9-10).

Main characters of the new material: Length of carapace = 200 mm. Cervical distinctly developed, visceral part larger than dorsal part; epiplastron strongly vaulted, with distinctly marked geoemydaloid gular bulge; gular furrows cutting entoplastron, humeropectoral furrows not; entoplastron 1,2 x broader than long, rhomb-like, anteriorly markedly pointed; anal notch obtuse-angled; pygal geoemydaloid; neurals emydoid and geoemydaloid; three (to maybe five) strong dorsal keels, no keel on bridge developed; bridge piers weak, inguinal piers inserting into pleural I via peripherals II and III, peripherals III with distinct visceral moschus channel, all marginal furrows situated on peripherals; typical geoemydaloid structure of areols on carapace present, surface of carapace with coarse sculpture, partly with very deep furrows on the horn-scutes. In fragmentary material the latter can feign the presence of terrestrial turtles: "Several plastron and carapace remains belong to an undetermined species of *Testudo*..., and a second land turtle known only by one plastron fragment (not figured). It differs from *Testudo* in having rising (= geocheilonid according to SCHLEICH 1988) sutural furrows, typical for large land turtles of the genus *Geochelone* sensu lato" (BÖHME, 2008).

KARL (1994/95) grouped *Testudo riedli* Hoernes, 1892 with *Clemmydopsis Boda*, 1927. Based upon the new material from Oberleichtersbach it is almost sure that it really belongs to *Palaeomauremys*. There are exactly the same morphological features in the anterior part of the internal mold from Trbovlje (former Trifail) in Slovenia and in the anterior visceral region of the carapax from Oberleichtersbach. Even the structure of the plastron is the same. The close stratigraphical age of the Slovenian and German specimens support their close relationships (plate 3, figs. 1-2). According to RIJAVEC & DOZET (2002) the limno-brackish

Socka Beds (former Sotzkaschichten) are subdivided into the Lower Socka Beds, the main coal horizon, and the Upper Socka Beds. They are overlain by the Late Oligocene Marine Marly Clay, dacite-andesitic tuff and pyroclastic breccia. The stratigraphical position is Egerian (= Late Oligocene: Chattian to the Oligocene/Miocene boundary beds). For a detailed description and the synonymy of the taxon see KARL (1994/95) and GROSS (1994). The Egerian in the Paratethys largely corresponds with the late Chattian and the complete Aquitanian (25,8-20,3 MY) (BALDI, 1975) and includes the “Gosau-Schichten”.

During railway constructions the visceral mold of a turtle carapace was discovered in a quarry for building stones in the “Gosau-Schichten” at the Wuhrberg S Windischgarsten (Upper Austria) and donated to the k. k. Geologischen Reichsanstalt in Vienna by Ing. Gross (Spital, Pahrn, Austria) in 1905. The comparable characters completely correspond with those of the steinkern from Trbovlje (former Trifail, Slovenia). Thus the Wuhrberg specimen has to be assigned to *Palaeomauremys*, too (plate 3, fig. 3). With a length of 254 mm and a width of 186 mm this carapace is the largest known.

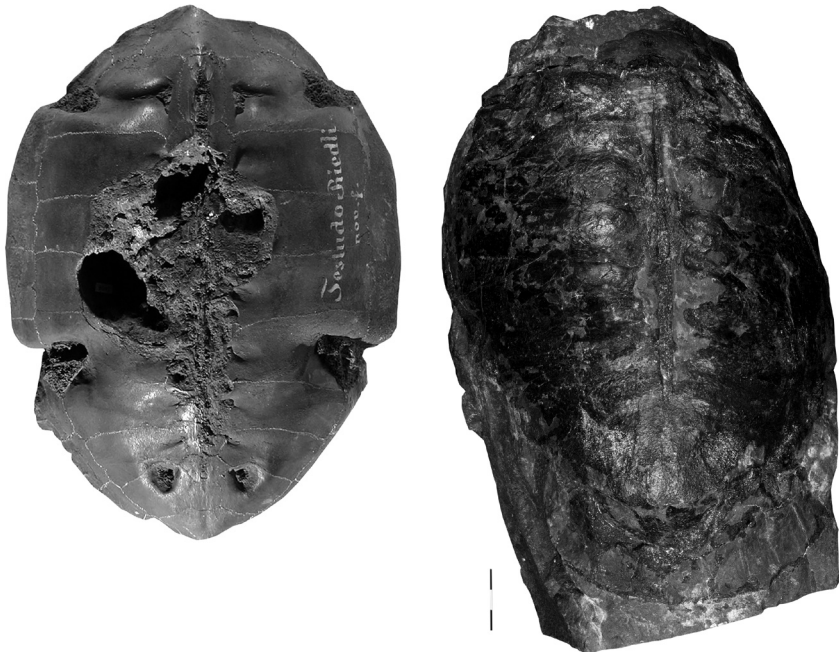


Plate 3. *Palaeomauremys tuberculata* (Portis, 1882): 1= Steiermärkisches Landesmuseum Joanneum, Graz n.º 5.908, Steinkern from Trbovlje (former Trifail) in Slovenia, holotype of *Testudo riedli* Hoernes, 1892 from GROSS (2002) with permission by the author; 2= Geological Survey of Austria/Department of Paleontology n.º #, visceral mold of carapace from Wuhrberg south of Windischgarsten/ Oberösterreich.

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Suprafamilia Trionychoidea Fitzinger, 1826

Familia Carettochelyidae Boulenger, 1887

Subfamilia Carettochelyinae Boulenger, 1887

3.3. Genus *Allaeochelys* Noulet, 1867

Synonymy: See KUHN (1964), BROIN (1977) and LAPPARENT DE BROIN (2001).

Type species: *Allaeochelys parayrei* NOULET, 1867 (original generic designation); originally described from Eocene deposits in southern France.

Diagnosis: See MŁYNARSKI (1976: 73-74).

Remarks: Neither the genus name *Allaeochelys* nor its author NOULET (1867) were listed in the "Fossilium Catalogus" on "Trionychia fossilia" (HUMMEL, 1932) (see KARL *et al.*, 2006).

Geographic and stratigraphic distribution: Early to late Middle Eocene in southern France, Spain, England, Belgium and Germany, in Germany up to the Late Oligocene (KARL *et al.*, 2006).

3.3.1. *Allaeochelys parayrei* Noulet, 1867

Selected synonymy:

- 1956 *Anosteira crassesculpta* Harrassowitz, 1922 - GRAMANN: 18.
- 1956 *Anosteira crassesculpta* = *gracilis* Harrassowitz, 1922 - KUHN: 181.
- 1986 "*Anosteira*" aff. *crassesculpta* Harrassowitz, 1922 - SCHLEICH: 285.
- 2006 *Allaeochelys parayrei* Noulet, 1867 (syn. *Anosteira crassesculpta* et *A. gracilis* Harrassowitz, 1922) - KARL, GRÖNING & BRAUCKMANN: 51-57.
- 2007 *Allaeochelys* Noulet, 1867 (syn. *Anosteira crassesculpta* Harrassowitz, 1922) - KARL, 2007: 61.

New material: Left dental (adult) and right xiphiplastron (juvenile).

Brief description: Sculpture on xiphiplastron flat and reticular, alveolar plain of dental without sculpture (without marked chewing ridges). Fossa meckeli open until symphysis. Labial margin with the typical porous structure of Trionychoidea.

Familia Trionychidae Fitzinger, 1826

Subfamilia Trionychinae Fitzinger, 1826

Subtribus Trionychina Fitzinger, 1826

3.4. Genus *Trionyx* Geoffroy Saint Hilaire, 1809

Synonymy: See KARL (1998), older synonymy in HUMMEL (1929, 1932), LOVERIDGE & WILLIAMS (1957), WERMUTH & MERTENS (1961), KUHN (1964), and IVERSON (1992).

Type species: *Testudo triunguis* Forskål, 1775.

Terra typica of type species: "In Nilo rarior" [= Nile River] (IVERSON, 1992).

Diagnosis: See KARL (1998).

Remarks: As pointed out by KARL (1999), the Eocene/Oligocene transition is marked by a change in the Trionychidae in Central Europe. The Eocene Nearctic *Rafetoides austriacus* (Peters, 1868) disappear and open wide space for the oriental species *Trionyx gregarius/triunguis*. The latter becomes the dominant species of the Neogene Palaearctic and is now restricted to a postglacial relict areal in Ethiopia (for the history of distribution see KARL, 1999). *Trionyx triunguis* is also known from the Early Oligocene sequence in the Weißelster Basin (Saxonia, Germany; KARL, 2007). On the other hand, in the Early Oligocene "Melanien-Ton" of Borken (Hesse, Germany) *Rafetoides austriacus* still occurs (KARL & MÜLLER, 2008).

Geographic and stratigraphic distribution:

- (i) Late Oligocene to Miocene: Austria, Slovenia, southern and Central Germany, France, Hungary, Romania, Bohemia, Switzerland.
- (ii) Miocene to Pliocene: Germany, Egypt.
- (iii) Tertiary (without exact data): Núrpur in Nepal.
- (iv) Prehistoric: Egypt.
- (v) Recent: Southern Turkey to Africa (Senegal to Angola, Somalia and Egypt) (IVERSON, 1992).

The additional species *Trionyx gregarius* (syn. *Amyda gregaria* Gilmore, 1931) was mentioned from the Early and "Middle" Oligocene Houldjin Formation at Camp Margetts, 25 miles SW Iren Babasu, Inner Mongolia (= Neimenggu, northern China).

3.4.1 *Trionyx* cf. *triunguis* (Forskål, 1775)

Remarks: According to BÖHME (2008) "the rearest turtle in Oberleichtersbach are the soft-shell or river turtle *Trionyx* sp., documented by one characteristically sculptured pleural fragment (not figured)". Here only a single free pleural cone, showing the structured transition of the proximal part to the pleural plate.

Superfamilia Chelydroidae Gray, 1831

Familia Chelydridae Agassiz, 1857

Subfamilia Chelydropsinae Młynarski, 1980

3.5. Genus *Chelydrasia* Chkhikvadze, 1999

Synonymy: See KUHN (1964), DE BROIN (1977), DE LAPPARENT DE BROIN (2001) and HUTCHISON in STEYERMARK *et al.* (2008).

Type species: *Chelydropsis minax* Chkhikvadze, 1971 (?= *Chelydra decheni* H. V. Meyer, 1852).

Diagnose: CHKHIKVADZE (1999).

Geographic and stratigraphic distribution: Early Eocene to Pliocene in Kazakhstan; Middle Eocene to Early Miocene in Europe (HUTCHISON in STEYERMARK *et al.*, 2008; KARL *et al.* in print).

Remarks: CHKHIKVADZE (1999) established *Chelydrasia* with its original type species *Chelydropsis minax* Chkhikvadze, 1971 from the Early Oligocene of the Zajsan Basin in Eastern Kazakhstan. He also assigned *Ch. sanctihenrici* and all the species of the so-called *decheni-sanctihenrici* group. Furthermore, he assumed an uncertain taxon from Artenay (MN4) to be closely related. According to HUTCHISON in STEYERMARK *et al.* (2008) *Chalydrasia* now includes *Ch. minax* Chkhikvadze, 1971, *Ch. poena* Chkhikvadze, 1971, *Ch. apellanzzini* (Murelaga *et al.*, 1999), *Ch. decheni* (H. V. Meyer, 1852), *Ch. sanctihenrici* (De Broin, 1977), "*Ch.*" *kusnetzovi* (Chkhikvadze, 1985). Judging from the preservation, the differences between *Ch. minax* and *Ch. decheni* seem to be not definitely clarified. If *Ch. minax* is regarded a junior synonym of *Ch. decheni* the latter becomes the type species.

3.5.1. *Chelydrasia decheni* (H. V. Meyer, 1852)

Synonymy: See KUHN (1964), DE BROIN (1977), DE LAPPARENT DE BROIN (2001), KARL *et al.* (in print).

New material: OLB 3-1, left pleural I in dorsal view in situ at grey chalky sediment (plate 4, fig. 11); OLB 3-2, pleural remains in dorsal view in situ at reddish chalky sediment with many gastropods (plate 4, fig. 12).

Brief description: The dimensions of pleural I are superficially similar to those of *Palaeomauremys*, but with a thickness with no more than 1 mm in its proximal region it is distinctly thinner. The plate thickens towards the margin but does not even approximately reaches the dimensions of the following one. The dorsal plain is smooth, with a few areoles only towards the lateral margin, but without any rudiments of keels. The latter first appear on a few smaller fragments of pleurals.

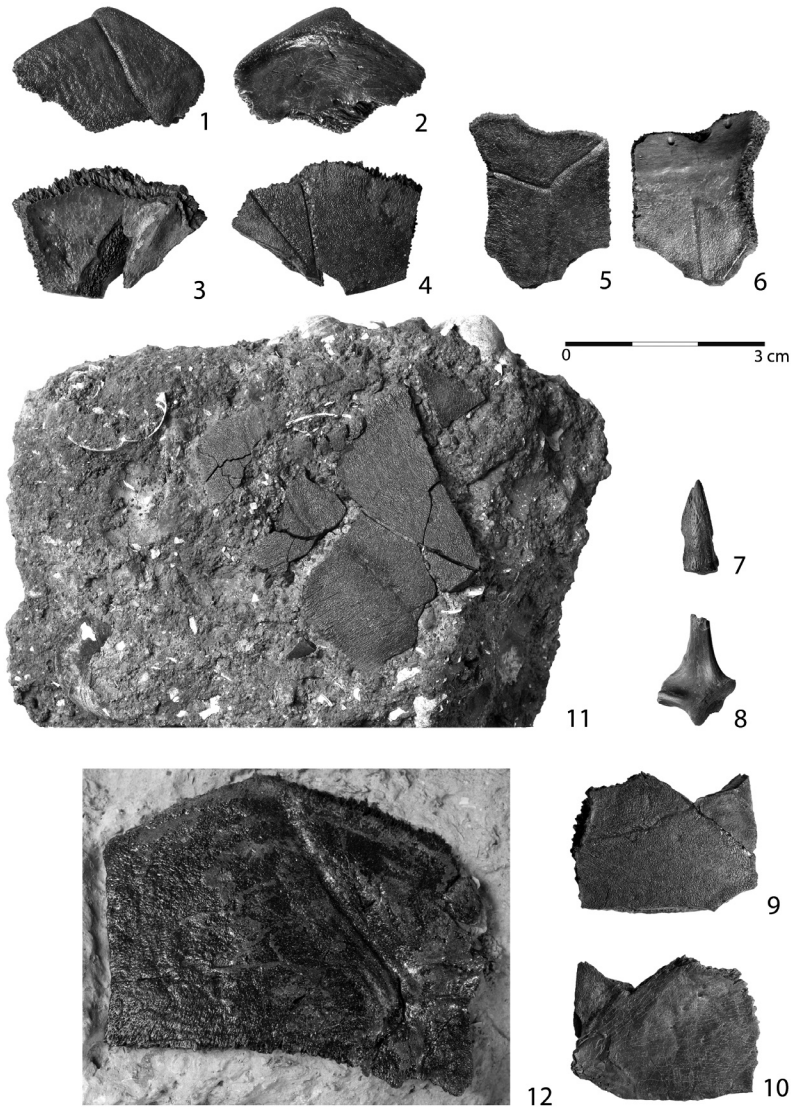


Plate 4. *Palaeoemys cf. hessiaca* SCHLEICH, 1994 from Oberleichtersbach, ex Coll. Walter Heck: 1= OLB 2-1, right epiplastron in ventral view; 2= in visceral view; 3= OLB 2-2, right pleural I remain in visceral view, 4= in dorsal view; 5= OLB 2-3, pleural remain in dorsal view; 6= in visceral view; 7= OLB 4-1, pbalanx III; 8= OLB 4-2, scapula remain; 9= OLB 2-4, left hyoplastron remain in ventral view, 10= in visceral view.

Chelydrasia decheni (H. V. Meyer, 1852) from Oberleichtersbach, ex Coll. Walter Heck: 11= OLB 3-1, left pleural I in dorsal view in situ at grey chalky sediment; 12= OLB 3-2, pleural remains in dorsal view in situ at reddish chalky sediment with many gastropods.

Scale bar 3 cm. Photo Brigitte Stefan, design Heike Künzel (TLDA).

CONCLUSIONS

PALAEOBIOLOGY

The palaeobiological conditions of the extinct genus *Palaeomauremys* are supposed to be very similar to those of the Recent and fossil *Mauremys*. Today these Palaeochelyiinae inhabit calm smaller water systems as pools, ditches, or muddy brooks from the lowland up to the mountainous regions. Recent species are omnivorous (see for example KARL & WETTLAUFER, 2011).

The most detailed climatic data, based upon plant remains, were presented by MAI (2008). The annual average temperature varied between 10 and 16 °C, the warmest month reached about 22 to 28 °C whereas the temperature of the coldest month changed from about –3 to –8 °C. The annual precipitation ranged presumably from 630 to 1040 mm, with one or two dry months of only 18 to 7 mm.

Comparable Recent conditions are known only from a few Chinese weather stations, as for example Enshi (= Engshih) in Hubei (= Hupeh) as well as Tai Shan and Jinan (= Tsinan) in Shandong (= Schantung). For the time interval between 23.5 and 25 million years ago MAI (2008) proposed a new and separate “floral complex Oberleichtersbach” which is a particular Carpino-Ostryon (MMF) assemblage including semihumid species, typical floral elements of dry summers and a great number of annual plants of open places.

According to BÖHME (2008), the fauna suggests the existence of a large, shallow, permanent and oxygen-rich lake with intensively structured shore and an afflux. The faunal climatic conditions were considered to be subtropical and humid which is not completely in accordance with the palaeobotanical data.

SYSTEMATICS AND PALAEOGEOGRAPHY

In contrast to other authors, CLAUDE & TONG (2004) synonymized a large number of generic names of the Palaeochelyiinae with *Palaeoemys* which is regarded as a taxon different from *Mauremys*. In particular they assign *Palaeoemys* to the so-called *Malayemys* complex, including *Malayemys*, *Geoclemys*, *Palaeoemys*, and *?Borkenia*. On the other hand, *Mauremys* is allocated to the *Melanochelys* complex, including *Melanochelys*, *Mauremys*, *Sacalia*, *Cuora*, *Cistoclemmys*, *Notochelys*, *Heosemys*, *Hieremys*, *Cyclemys*, *Leucocephalon*, *Ocadia*, *Chinemys*, *Palaeochelys*, *?Siebenrockiella* and *?Geoemyda*. These different views implicate a hotspot on the European spit during the Paleogene as it was already pointed out by KARL (1998, 1999) and DANILOV (2005) for the Trionychidae. Likewise this seems to be true for the Palaeochelyiinae. Within the whole relationship distinct tendencies can be recognized for splitting into the generic complex *Mauremys/Ocadia*, the Ptychogastrinae and the Geoemydinae, still combined with large overlapping (see for example KHOZATSKY & MLYNARSKI, 1966). Surely this problem cannot

yet finally dissolved since BROPHY *et al.* (2006) show twelve cases of intergeneric hybridisation, where the following genera are connected by genetic overlapping: *Mauremys* x *Chinemys*, *Mauremys* x *Cuora*, *Mauremys* x *Cyclemys*, *Mauremys* x *Heosemys*, *Mauremys* x *Sacalia*, *Cuora* x *Geoemyda* und *Cuora* x *Sacalia*, i.e. the complete complex with its fossil roots in the Palaearctic. Indeed, even recently often different “hybrid species” occur in open nature, as for example *Chinemys megacephala*, *Mauremys pritchardi*, *Ocadia glyphistoma*, *Ocadia philippeni*, *Mauremys iversoni* and others. The latter is even bred in Chinese turtle farms as a hybrid of *Mauremys mutica* x *Cuora trifasciata* and was already discussed under taxonomic respect (FONG & CHEN, 2010; PARHAM & CHI, 2001). Consequently, FRITZ & HAVAŠ (2007) regarded *Chinemys*, *Sacalia* und *Ocadia* etc. as synonyms of *Mauremys* as a conclusive result of a genetic analysis of single individuals, just in contrast to the comparison of morphologically studied series. Once more, this clearly shows that precipitate “results” based only on genetic analyses are not sufficient as they are not compatible with morphological conclusions.

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