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THE FOSSIL REPTILES (REPTILIA: CHELONII, CROCODYLIA) FROM THE MARINE EARLY OLIGOCENE OF THE WEISSELSTER BASIN (CENTRAL GERMANY: SAXONIA)

[Reptiles fósiles (Reptilia: Chelonii, Crocodylia) del Oligoceno inferior marino de la cuenca de Weisselster (Alemania Central: Sajonia)]

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RESUMEN: Se describen tortugas del Oligoceno inferior marino de la cuenca de Weisselster, comparándolas con especies vivientes y relacionadas de la misma edad. Se presenta la historia de las investigaciones, paleogeografía y situación estratigráfica así como las relaciones paleontológicas con otras especies de Trionychidae, Testudinidae, Cheloniidae y *Psephophorus*. Se presenta una nueva especie de *Allopleuron*. Se conservan escasos restos de cocodrilos, determinados a priori como *Diplocynodon* sp.

Palabras clave: Testudines, Cryptodira, *Trionyx triunguis* (Forskål, 1775), *Glarichelys knorri* (Gray, 1837), *Allopleuron lipsiensis* n. sp., *Psephophorus* cf. *rupeliensis* Van Beneden, 1887, *Cheirogaster* sp., gen. et sp. indet., Crocodylia, *Diplocynodon* sp., Oligoceno inferior, Rupeliense, cuenca de Weisselster, Sajonia, Alemania Central.

ABSTRACT: The fossil turtles and crocodiles from the marine Early Oligocene of the Weisselster Basin are described and compared with related species of the same stratigraphical age. Additionally, an overview is given on the history of research, the palaeogeographic and stratigraphic situation as well as on the relationships of the species mentioned. Beside the known representatives of the Trionychidae, Testudinidae, Cheloniidae and *Psephophorus*, the turtles include also a new species of *Allopleuron*. The crocodile remains are poorly preserved and therefore only tentatively assigned to *Diplocynodon* sp.

Key words: Testudines, Cryptodira, *Trionyx triunguis* (Forskål, 1775), *Glarichelys knorri* (Gray, 1837), *Allopleuron lipsiensis* n. sp., *Psephophorus* cf. *rupeliensis* Van Beneden, 1887, *Cheirogaster* sp., gen. et sp. indet., Crocodylia, *Diplocynodon* sp., Early Oligocene, Rupelian, Weisselster Basin, Saxonia, Middle Germany.

INTRODUCTION

Remains of turtles are known from Oligocene sediments in Europe (figure 1), Germany, and in particular in Central Germany (figure 2: W= Weisselster Basin, Saxonia) for a rather long time. However, the knowledge of the partly untypical material developed in a complicated way. In the older literature, remains of turtles from marine deposits of Central Germany were usually assigned to the genus *Chelyopsis* van Beneden, 1887. This genus was merely used by Pierre-Joseph van Beneden (born 1809 at Mechlin, died 1894 at Lauvain) in his lectures at the University of Lauvain, Belgium and was published by the Abbot Prof. Dr. G. SMETS (1887) from the "Collége èpistopal de Hasselt" with the type species *Chelyopsis littoreus* under his name. The type material of *Chelyopsis holsaticus* Dames, 1894, from the Rupelian of Itzehoe near Hamburg is lost by war.

The opinions concerning the validity of these taxa were already controverse from the very beginning. However, some authors held it for valid as for example LYDEKKER (1889); KARL (1989, 1995); KARL & SCHLEICH (1994); KUHN (1964); MLYNARSKI (1969, 1976); ROMER (1956) and PRITCHARD (1975, 1976). Difficulties arose, except for the type of *Chelone gwinneri* Wegner, 1918, from the fragmentary preservation in most cases and from the far scattered distribution of the materials. Only more recently, the knowledge increased due to new and better preserved materials.

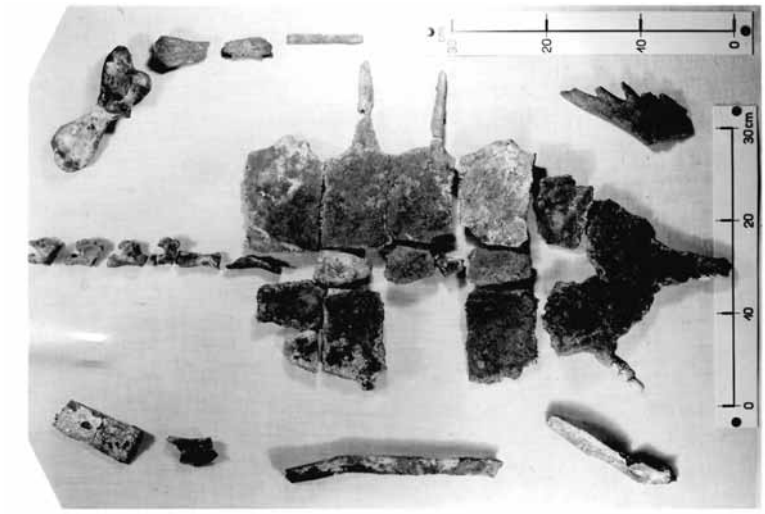
HISTORICAL SURVEY

The first findings of fossil turtles from the marine Early Oligocene of Central and Eastern Germany were collected from the Rupelian ("Rupel Clay" = Rupelton, Septarienton) in Brandenburg. The original materials of these collections are lost. According to RETTSCHLAG (1955), these are as follows:

1. Proximate part of a coracoid dex. of a cheloniid from Bad Freienwalde;

2. Tibiae or fibulae, radii or ulnae as well as metatarsals or metacarpals and phalanxes from Treplin;

3. Proximate parts of a femor of a sea turtle from Bad Freienwalde which was anatomically described by Dr. Wolfgang Haller (in RETTSCHLAG, 1955); according to informations by Dr. Schneider of the former Central Geologic Institute of Berlin (ZGI) (letter from 15.10.1986 and pers. comm. in summer 1988), these findings are, however, no more traceable within the old collections of the Prussian Geologic Survey.



Schildkrötenreste aus dem marinen Mitteloligozän des Tagebaues Böhlen bei Leipzig
(Bl. 26 der Geol. Karte von Sachsen).
Gefunden und präpariert von Markscheider Ob.-Ing. Schulz, 1929.
(Übermittelt von [Chef geologendienst] Prof. Pietzsch, Freiberg Sa., Schloßplatz 1, Geol. Z.-A.).

Chelonopsis sp.

Die Schildkröte gehört der Gattung Chelonopsis an, von der bisher nur 2 Arten in spärlichen Resten bekannt geworden sind, und zwar ausschließlich aus dem Mitteloligozän von Belgien (Ch. hibbertii von Beneden) und Ägypten (Ch. holandrica Dames). Namentlich die Rückenpanzer dieser Gattung war bisher so gut wie unbekannt. Nur von der belgischen Art wird ein Costalplatten-Fragment erwähnt, das über Form und Bau des Panzers keine Rückschlüsse gibt. Der Fund von Böhlen zeigt nun, dass die Rückenpanzer dieser Tiere im Verhältnis zu ihrer außerordentlich schmal ist, d. h. dass die Costalplatten sich nur sehr wenig distalwärts verbreitern, und dass mit sehr großen und breiten Fontanellen zwischen Costal- und Randplatten zu rechnen ist.

Die Bestimmung des vorliegenden Fundstückes als Chelonopsis ergibt sich aus der Form des Humerus, der mit dem von Ch. holandrica in der Größe und den wesentlichen Merkmalen, namentlich auch des von Chelonia unterscheidenden Nährloches (Foramen nutricium) gut übereinstimmt. Ein Unterschied zu der Holotypus Form ist aber bei dem Böhlener Humerus der Gelenkkopf im Umriss mehr ovaler gestreckt (bei der belgischen Art soll der Umriss nahezu kreisförmig sein). Es ist natürlich durchaus möglich, dass dieser Unterschied nur von individueller Bedeutung ist; bei dem wenigen bisher von der Gattung Chelonopsis vorliegenden Material empfiehlt es sich aber nicht, ihn durch vorbehaltlose Zurechnung des Böhlener Schildkröte zu Ch. holandrica zu verschleiern. Das Böhlener Exemplar ist daher bis auf weiteres als Chelonopsis sp. zu bezeichnen.

Eine eingehende, für eine Veröffentlichung ausreichende Bearbeitung des Fundes von Böhlen ist leider nicht möglich, da die hierzu nötige belgische Literatur (van Beneden, Smets, Rollo) durch die hiesigen Bibliotheken nicht beschafft werden konnte.

Dr. 27/10.50.

Plate 1. The first attempts of a scientific determination of the findings from Böhlen and the Weisselster Basin by K. STAESCHE in a response letter to the request by Prof. K. PIETZSCH. The photograph was prepared by Dr. Schulz; Pietzsch notices the incorrect arrangement of some bones on the reverse side of it. I am cordially grateful to my friend and colleague Dr. Ulrich Staesche for supplying me with the scientific estate of his father Dr Karl Staesche concerning the turtles.

Other materials were discovered in 1929 and 1936 within the Weisselster Basin during the development of the brown coal digging in the south of Leipzig (Saxonia, Central Germany, figure 3: L) by surveyor Dr. Schulz. The first site was Böhlen (figure 3: BÖ). From here PIETZSCH (1951, 1962) described the first material of turtles which, after the enduring determination by Karl Staesche, considered as *Cheliopsis* sp. (plate 1); it is deposited in the magazine of the former "Geologic Research and Investigation, Freiberg in Saxony". After comparison with the Espenhain materials in Altenburg, KARL (1991) recognized the Böhlen material as different; on the basis of characters in lower jaw, humerus and shell fontanelles he assigned it to *Dollochelys casieri* Zangerl, 1971 from the Landenian in Belgium. This is followed in the present article.

An very usefully survey of the vertebrates of the Tertiary North Sea Basin gave ROTHAUSEN (1986). He listed the follow taxa for this area: Testudinata, Cryptodira, Cheloniidae, *Puppigerus* cf. *crassicostatus* (Owen, 1849); ?*Caretta* sp.; ?*Chelyopsis holsaticus* Dames, 1894; ?*Chelyopsis* sp.; Dermochelyidae, ?*Pseudosphargis ingens* (von Koenen, 1891; *Psephophorus* sp.; Testudinata indet. According RUSSELL (1982) he remarks the unsuccessfully systematic position of the Böhlen-material (differs to *Chelyopsis* sp.).

HUNGER & MAGALOWSKI (1957) collected and described extensive sirenian materials (*Halitherium schinzi*) from Espenhain (figure 3: ES). Among them there was also the scapular fragment of a very large turtle, but which was recognized correctly only by FISCHER (1981) and which was described by KARL (1989b) as *Psephophorus* cf. *rupeliensis* van Beneden, 1887. The material is deposited in the palaeontological collection of the Technological University of Freiberg in Saxony (formerly Bergakademie).

MÜLLER (1983) mentioned several remains from Espenhain as *Chelyopsis* sp. which were described by KARL (1989a) as *Chelyopsis halleri* Karl, 1989, mainly based on the characters considered by Dr. Wolfgang Haller (in RETTSCHLAG, 1955). This was also used to point out to the temporary status of the genus *Chelyopsis* ("collective characters of the genus"). The type material is housed in the Museum Mauritianum in Altenburg, Thuringia. FREES (1991) gives a short overview of the higher taxa of the Weisselster basin without a reflection of that.

In a literature study the lost cranial fragment was grouped by KARL (1993) with *Pseudosphargis* Dames, 1894 (type specimen: *Chelone ingens* v. Koenen, 1891) from the Upper Oligocene of the Doberg near Bünde which was furthermore put into the synonymy of *Psephophorus* H. v. Meyer, 1847. Other shell materials of the same age of the Doberg belong to *Chelyopsis* as discussed in detail by KARL (1995). Already in 1994, *Chelyopsis raabei* was established by KARL & SCHLEICH on characters of the lower jaw from the Upper Eocene of Helmstedt near Braunschweig.

KARL & TICHY (1999) erected the new sea turtle genus *Rupelchelys* (type species: *R. breitkreutzi*) on very representative material from the Rupelian "Lower Marine Sand" (Unterer Meeressand) of Neumühle near Weinheim/Alzey which simultaneously represents a new tribus Rupelchelyini. The comparison of this material with the characters of *Chelone*

gwinneri Wegner, 1918 from the Middle Oligocene of Flörsheim shows that the whole material previously allocated to *Chelyopsis* species is co-specific and synonymous with the genus *Glarichelys* Zangerl, 1958.

In the overview on the fossil marine turtle families of Central Europe, KARL (2002) completed this difficult taxonomic process and compiled the synonymy and the hitherto known distribution of *Glarichelys knorri* (Gray, 1831). The soft-shelled tortoises of the Weisselster Basin found partial entrance in basic revisions of this group by KARL (1994, 1997, 1998, 1999).

And now, MOTHS (2003) referred cheloniid plastron remain from the Rupelian of Malliß as *Cheliopsis holsaticus* Dames, 1894 and a peripheral from the Eochattian of Kobrow ("Sternberger Gestein") as *Cheliopsis* sp., both localities are in Mecklenburg-Vorpommern, Northern Germany.

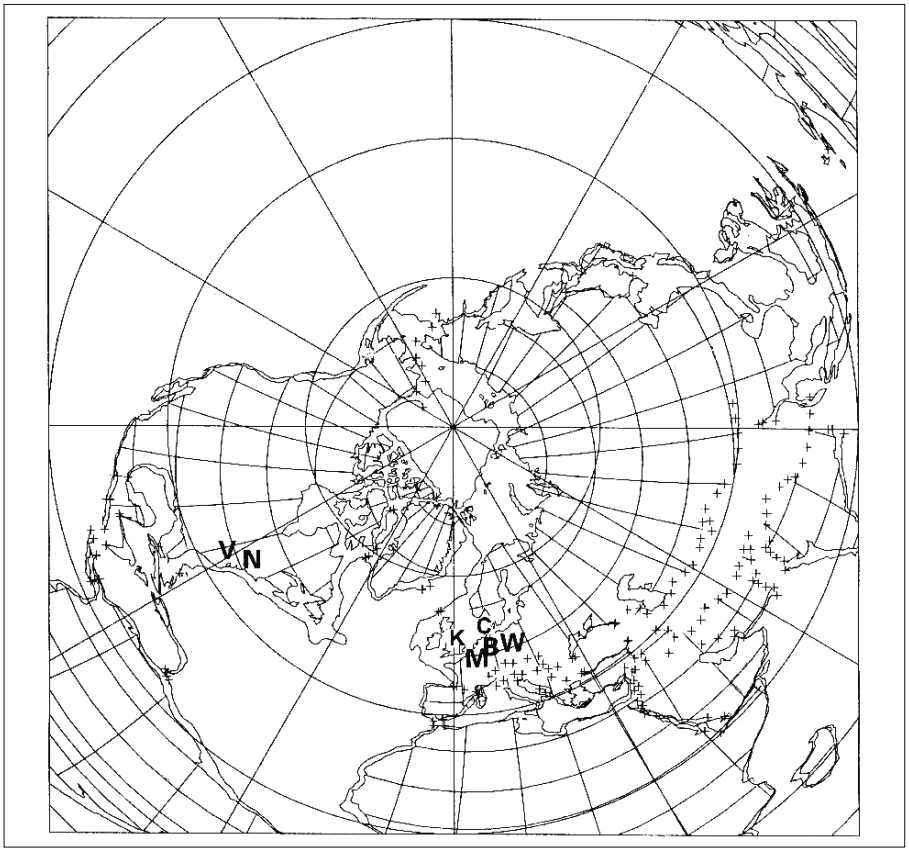


Figure 1. Lambert equal area projection in North Pole view for the Upper Eocene (40 million years), according to SMITH, HURLEY & BRIDEN (1982) to show the distribution of the continental plates; V = Virginia, N = New Jersey, K = County Kent (Great Britain), M = Maastricht (the Netherlands), B = Brabant (Belgium), C = Copenhagen (Danmark), W = Weisselster Basin (Germany).

PALAEOGEOGRAPHY AND STRATIGRAPHY

Geographic (figs. 1-3) and geologic-stratigraphic (fig. 4) relations were already shown and discussed by MÜLLER (1983). Nearly all turtle remains treated here are from the "Phosphoritknollen Horizon" which lies immediately at the base of the Early Oligocene Rupelian clay. Here an ideal section is added to the representation of the general depositional relations of the marine Oligocene in the Weisselster Basin according to MÜLLER (1983). The turtle remains were largely collected as findings from fragments of bedrock and came certainly from the horizon of phosphorite nodules ("Phosphoritknollenhorizont"). The age of this Rupelian horizon is 33,7 million years before present. A stratigraphic survey over the middle German Oligocene based on fish-otoliths associations gives MÜLLER (2000).

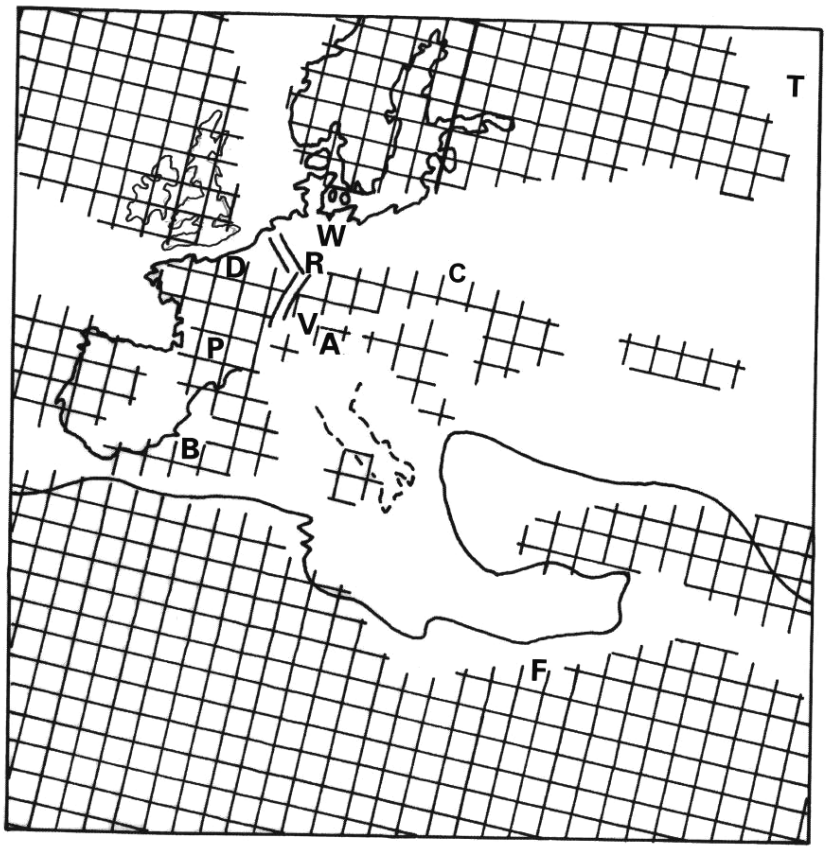


Figure 2. Distribution of land and sea in Central Europe during the Oligocene, according to STANLEY (2001). B = Betic Ranges, P = Pyrenees, D = Paris Basin, A = Alps, V = Alpidian Foredeep, R = Upper Rhine Valley, W = Weisselster Basin, C = Carpathian Mountains, F = Fayum Depression, Egypt (= Al Fayyum), T = Turgai Street.

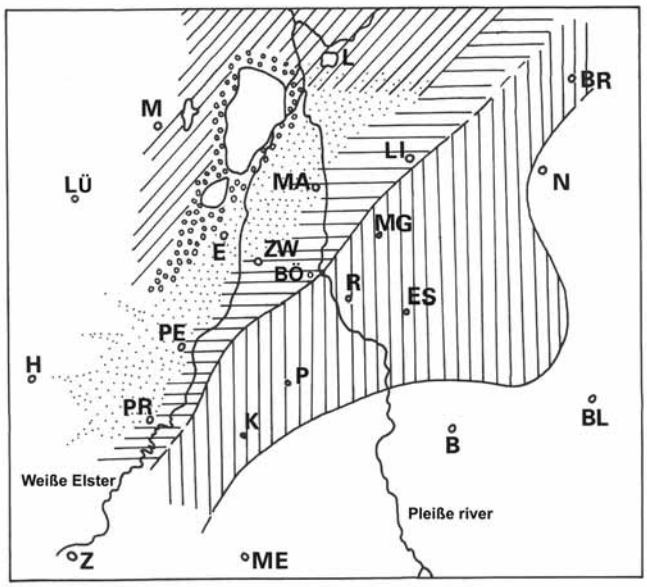


Figure 3. Palaeogeographic situation within the Weisselster Basin, with the most important sites, adapted from MÜLLER (1983). B = Borna, BL = Bad Lausik, BÖ = Böhlen, BR = Brandis, E = Eythra, ES = Espenhain, H = Hohenmölsen, K = Käferhain, L = Leipzig, LI = Liebertwolkwitz, LÜ = Lützen, M = Markranstedt, MA = Markleeberg, ME = Meuselwitz, MG = Magdeborn, N = Naunhof, P = Pödeleitz, PE = Pegau, PR = Profen, R = Rötha, Z = Zeitz, ZW = Zwenkau.

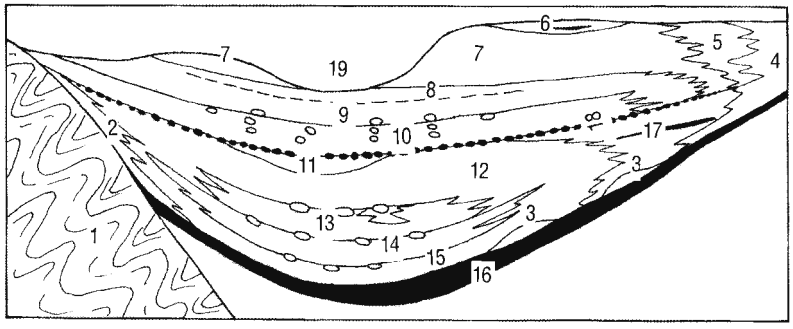


Figure 4. Facies differentiation of the "Böeblener Schichten" (Boehlen Beds) within the ideal section of the Weisselster Basin, according to MÜLLER (1983). 1 = Basement: Leipzig Greywacke (Leipziger Grauwacke), 2 = pretertiary coarse facies (prätertiäre grobe Fazies), 3 = White Sand ("Weißer Sand"), 4 = Younger Fluviatile Sand ("Jüngere Flußsande"), 5 = Pödelwitz Moulding Sand ("Pödelwitzer Formsande"), 6 = Late Oligocene Sand (oberoligozäne Sande), 7 = Grey Moulding Sand ("Graue Formsande"), 8 = Zwenkau Horizon (Zwenkauer Horizont), 9 = Shelly Sand ("Muschelsand"), 10 = Shelly Silt ("Muschelschluff"), 11 = Upper Grey Sand ("Oberer Grauer Sand"), 12 = Lower Grey Sand ("Unterer Grauer Sand"), 13 = Glauconitic Silt ("Glaukonitschluff"), 14 = Brown Silt ("Brauner Schluff"), 15 = Basal Sand ("Basissand"), 16 = Seam IV ("Flöz IV"), 17 = Seam y ("Flöz y"), 18 = Horizon of Phosphoritic Nodules ("Phosphoritknollenhorizont"), 19 = River Flood Plain ("Flußaue": Weiße Elster, Pleiße).

TERMINOLOGY

Figure 5 shows the schematic reconstruction of carapace and plastron of testudine turtles (e.g. *Testudo* according to KARL [STAESCHE, 1961, adapted]). Without scale.

Carapace plates: nuchal = nu, neurals = n I to n VIII, pleurals = pl I to VIII, peripherals = pe I to pe XI, metaneurals = mn I to II, pygal = py.

Carapace scutes: cervical = ce, centrals = c 1 to c 5, laterals = l 1 to l4, caudal = ca.

Plastron plates: epiplastrals = epi, entoplastron = ento, hyoplastron = hyo, hypoplastron = hypo, xiphiplastron = xiphi.

Plastron scutes: gulars = gu, humeral = hu, pectorals = pec, abdominals = ab, femorals = fe, annals = an (fig. 5).

Figure 6a shows the schematic reconstruction of carapace and plastron of trionychine turtles (e.g. *Pelodiscus sinensis* [Wiegmann, 1835] according to KARL [1998]). Without scale.

Carapace plates: N I to N VII = neurals I to VII, Nu = Nuchal, Pl I to Pl VIII = pleurals I to VIII, C I to C VIII = costae I to VIII, Fp = postnuchal foramina.

Plastron plates: Epi = epiplastrons, Ento = entoplastron, Hyo = hyoplastrons, Hypo = hypolpastrons, Xiphi = xiphiplastrons. (fig. 6a).

In figure 6b the schematic reconstruction of the plastron of trionychine turtles (e.g. *Amyda cartilaginea* [Boddaert, 1770] according to KARL [1998]) is shown. Without scale.

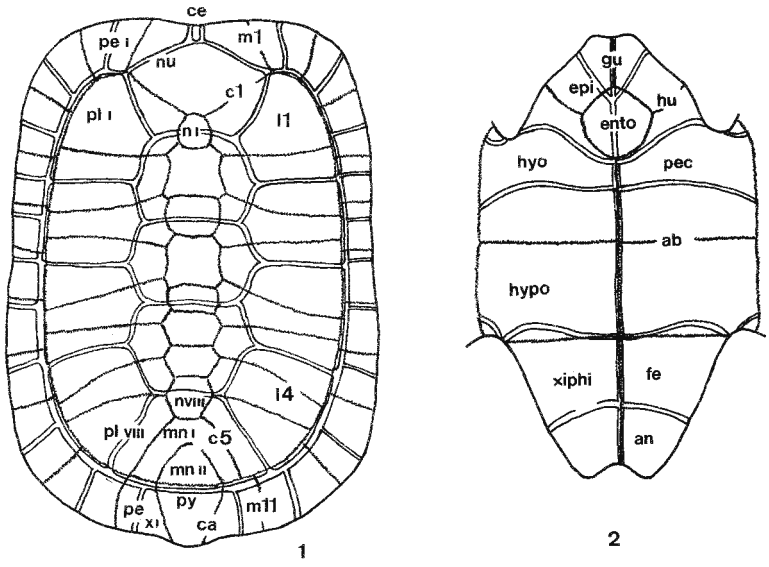


Figure 5. General terminology of a turtle shell, remarks: see in the text.

1 = Processus epiplastralis anterior, 2 = Processus epiplastralis posterior, 3 = Processus entoplastralis dexter, 4 = Processus entoplastralis sinister, 5 = Processus hyoplastrales media, 6 = Processus cardinus masculi anterior, 7 = Processus cardinus masculi posterior, 8 = Processus hypoplastralis medialis anterior, 9 = Processus hypoplastralis medialis posterior, 10 = Processus xiphiplastrales media, 11 = Processus xiphiplastrales anterior; I = Level of the Suturae hyohypoplastrales, II = Level of the Processus hypoplastrales media anterior, III = Level of the Processus epiplastrales posterior.

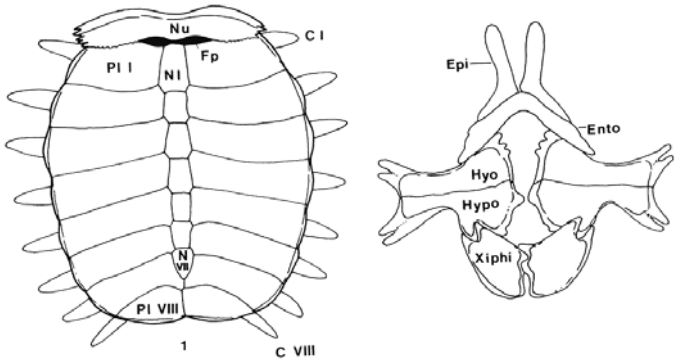


Figure 6a. General terminology of the trionychid shell, remarks: see in the text.

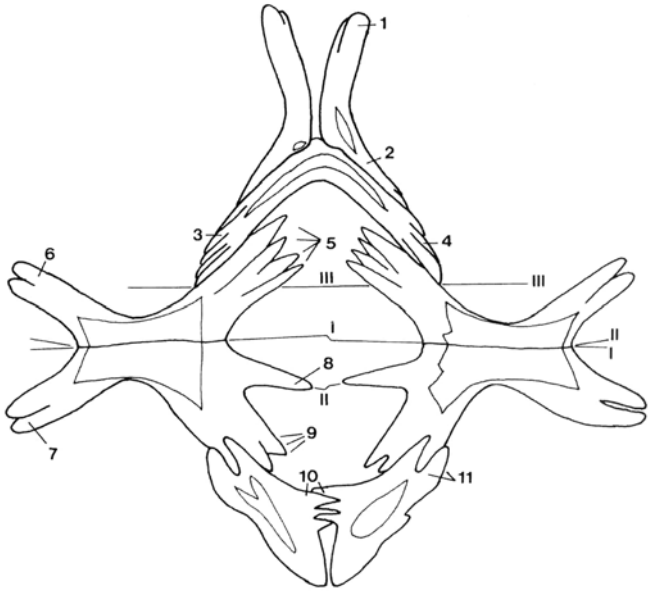


Figure 6b. Terminology of the trionychid plastron, remarks: see in the text.

SYSTEMATIC PALAEONTOLOGY

Order Chelonii Brongniart, 1800 (Latreille, 1800)

Infraorder Cryptodira Cope, 1868

Suprafamily Trionychoidea Fitzinger, 1826

Family Trionychidae Fitzinger, 1826

Subfamily Trionychinae Fitzinger, 1826

Tribe Trionychini Fitzinger, 1826

Subtribe Trionychina Fitzinger, 1826

Genus *Trionyx* Geoffroy Saint Hilaire, 1809

Trionyx triunguis (Forskål, 1775)

Synonyms:

– *Trionyx* cf. *hilberi* (Hoernes, 1892), KARL, 1989: 233, Abb. 16, Fig. 14 a-b;
– *Trionyx boulengeri* Reinach, 1900, KARL, 1993: 121, Taf. I, Fig. d;
– *Trionyx boulengeri* Reinach, 1900, KARL, 1994: 333;
– *Trionyx triunguis* (Forskål, 1775) [syn. *Trionyx boulengeri* Reinach, 1900], KARL, 1999: 43, Beil. 1, Fig. 2.

Known distribution: Early Oligocene of Spain, France, Belgium, Switzerland, Italy, Austria, Germany, Hungary, Romania, Slovenia and many other European localities up to the Pliocene; Recent in Minor Asia and Africa (KARL, 1999). For general remarks: see LAPPARENT DE BROIN (2001).

Description: Ornament flat tesselat to knoblike without elated bulges in C/IV according to KARL (1998); processus cardinus masculi anterior single, processus cardinus masculi posterior in pairs.

Remarks: According to KARL (1997, 1998, 1999), due to present knowledge, only two species of the Trionychinae, each of it representing a separate genus, seem to have existed in the Paleogene of Central Europe. *Rafetoides austriacus* (Peters, 1858) is typical for the Eocene to the Early Oligocene in southeastern Europe. The most important synonym is *Trionyx messelianus* Reinach, 1900. GRAMANN's (1956) species *Trionyx (Amyda) borkenensis* from the early Oligocene "Melanienton" of Borken (Lower Hassia) is a synonym of the present species also. Up from the late Early Oligocene (Rupelian), only *Trionyx triunguis* (Forskål, 1775) is recorded. Its most important synonym for the Rupelian/Oligocene (Meeressand of Alzey) of Germany is *Trionyx boulengeri* Reinach, 1900 (plate 2). Tho most important synonym for the Chattian/Oligocene (Trbovlje/Trifail in Slovenia formerly Styria) south of the Alps is *Trionyx stadleri* Teppner, 1913 (see plate 3, figure 1). Beside the absence of, in particular, high vertical structures in the ornament like in *Rafetoides* Karl, 1998 are typical. *Trionyx* differs clearly

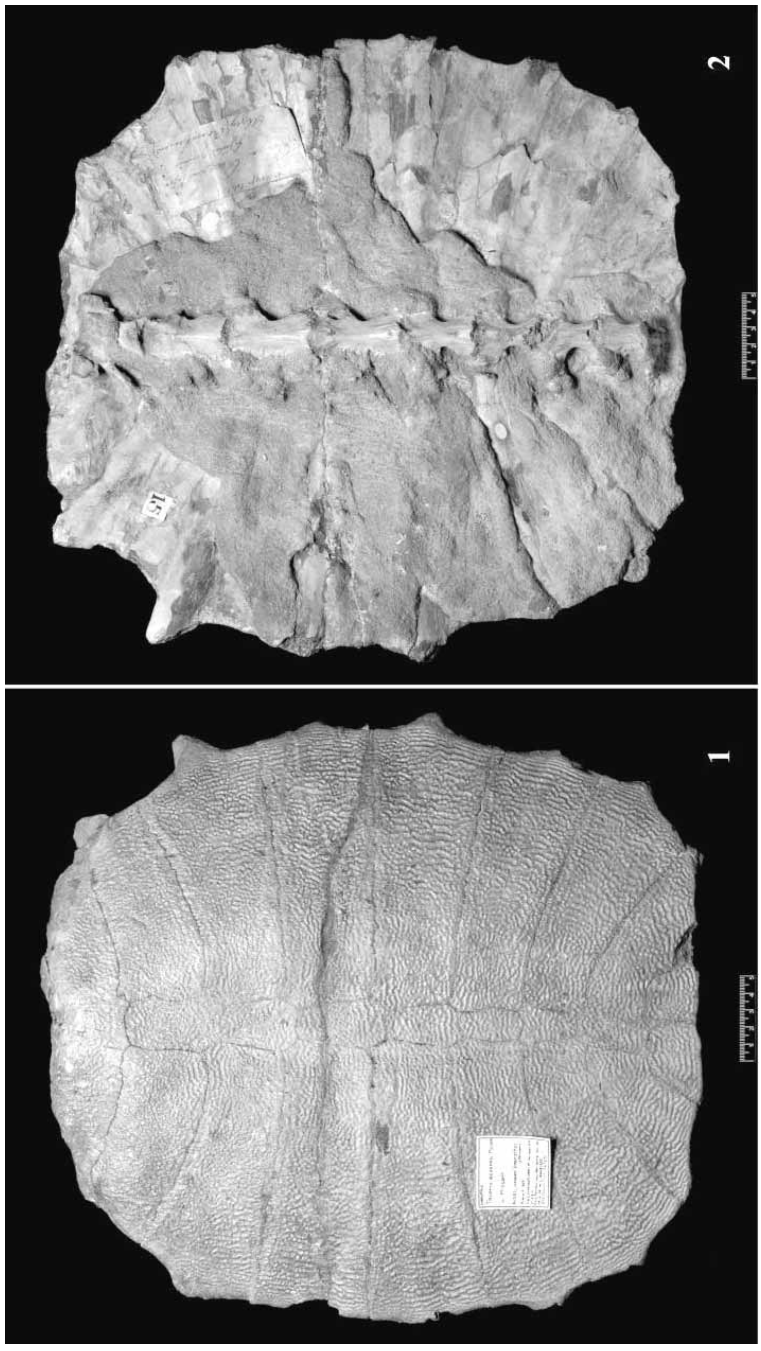


Plate 2. Trionyx triunguis *(Forskål, 1775) [syn.* Trionyx boulengeri *Reinach, 1900 and* Trionyx gergensi *H. v. Meyer, 1844, according to* LYDEKKER *(1889)], BMNH N.º 36765, complete discus, the type specimen selected by* HUMMEL *(1932), figure 1 = dorsal view, figure 2 = visceral view. Photograph: British Museum of Natural History, with kind permission by Dr Sandra Chapman. Scale bar 5 cm.*

by only one processus cardinus masculi anterior, whereas in *Rafetoides* and *Amyda* Geoffroy Saint Hillaire, 1809 it is commonly paired. These characters are steady and are regarded here as the most important arguments for grouping the present material.

References/material: Espenhain: PMUL: ES 1373 - nearly complete hyoplastron dex. (plate 3, figures 5-6); NML: Pal 5510 - pleural remain and two other without number (plate 3, figures 2-4); MMA: no number - pleural remain dist. (KARL, 1989: 233, fig. 16, fig. 14 a-b; KARL, 1993: 121, pl. I, fig. d; KARL, 1999: 43, addition 1, fig. 2).

Superfamily Chelonioidea Baur, 1893

Family Cheloniidae Gray, 1825

Subfamily Cheloniinae Dollo, 1886

Tribe Cheloniini Zangerl & Turnball, 1955

Figure 7 shows the phylogenetic relationships between the tribes of cheloniids according to KARL & TICHY, 1999.

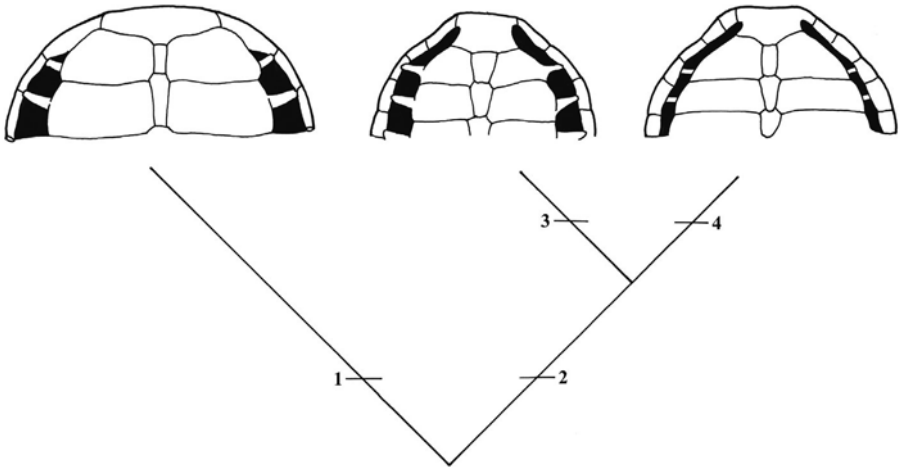


Figure 7. Dendrogram explaining the tribes of the Cheloniidae, according to KARL & TICHY (1999) and to KARL (2002); node 1 = Costa I penetrates between peripherals I and II (Rupelchelyini), node 2 = costa I penetrates more posteriorly: node 3 = at peripheral III (Chelonini) or node 4 = at peripheral IV (Carettini).

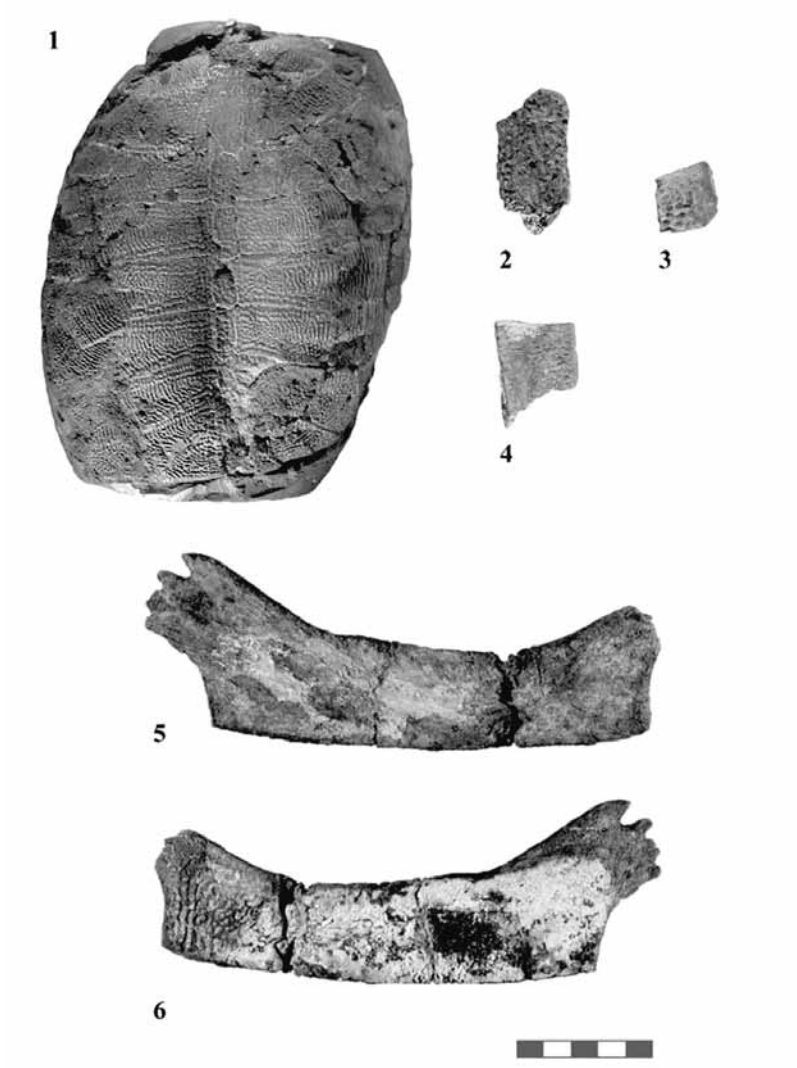


Plate 3. Trionyx triunguis *(Forskål, 1775): figure 1 = syn*. Trionyx stadleri *Teppner, 1913, according to* GROSS *2002: 39, plate 16, figure 1, SLMJ No. 1831, complete discus, the type specimen; photograph: Styrian Provincial Museum Joanneum, Dpt. Palaeontology, with kind permission by Dr. Martin Gross; figure 2 = dorsal view of pleural remain NML PAL No. 5510; figure 3 = dorsal view of pleural remain NML PAL, without number; figure 4 = dorsal view of pleural remain NML PAL, without number; photographs: Natural History Museum Leipzig, with kind permission by Dipl.-Geol. Reinhardt Baudenbacher; figure 5 = PMUL: ES 1373, visceral view of a nearly complete hyoplastron dex.; figure 6 = PMUL: ES 1373, dorsal view of the same specimen as in figure 5; photographs by Dirk Urban, Erfurt. Scale bar 5 cm, but not for figure 1.*

Genus *Glarichelys* Zangerl, 1958

Glarichelys knorri (Gray, 1831)

Synonyms:

- "*Cheliopsis* sp.", MÜLLER, 1983: 77, 141 (pl. XXVII, figs. 7-10);
- *Chelyopsis halleri* Karl, 1989a: 229, figs. 2-8, pl. XXIX-XXXIII;
- *Chelyopsis halleri* Karl, 1989a, KARL, 1995: 349-356, pl. I-IV;
- *Chelyopsis halleri* Karl, 1989a, KARL & SCHLEICH, 1994: 116, fig. 9;
- *Chelyopsis halleri* Karl, 1989, KARL, 1994: 333;
- *Glarichelys gwinneri* (Wegner, 1918), KARL & TICHY, 1999: 61-77;
- *Glarichelys knorri* (Gray, 1837), KARL, 2002: 177, 191, map 2.

Known distribution: Upper Eocene to Upper Oligocene of Belgium, Switzerland, Germany, Denmark and Poland (KARL, 2002). For general remarks: see LAPPARENT DE BROIN (2001).

Description: Skull of juvenile specimens enlarged; secondary palatine lesser developed (ZANGERL, 1958); lingual ridge of mandibula lesser developed as in *Chelonia*, but more as in *Eretmochelys*; dorsal scutes of head like in cheloniids, mostly *Eretmochelys*; postnuchal foramina present in juveniles; shell typical as cheloniids; flippers with extreme enlarged phalanxes of fingers 3 and 4; humerus "toxochelyid" (ZANGERL, 1953); end-phalanxes of finger 1 in comparison with other cheloniids strongly enlarged and thick (sexual dimorphism) (plate 4, figure 1).

Remarks: This monotypic genus is described in detail by WEGNER (1918) and ZANGERL (1958). At that time ZANGERL (1958, 1980) still considered such unimportant differences in the characters of dorsal head scutes and distal phalanxes for usable for taxonomic purposes. Today such differences are regarded as caused by individual variability or changes in the ontogenetic development. This particularly is true in comparison to the low individual age of the Glarner type materials of *Glarichelys* (plate 4, figure 2). *Glarichelys* is morphologically a stage between *Chelonia* and *Eretmochelys*, based on mandibular morphology (KARL & SCHLEICH, 1994), the dorsal head scutes and the possible presence of imbricate scutes. This aspect is remarkable in relation to the natural hybrids between *Chelonia mydas* and *Eretmochelys imbricata*, too. Physical patterns of the hybrids show a mix of *Chelonia mydas* and *Eretmochelys imbricata* scalation within one pair of prefrontal scales similar to *Chelonia mydas* and three post-orbital scales per lateral surface similar to *Eretmochelys imbricata* (figure 9). Mandibular dentition possessed a median ridge similar to that found in *Chelonia mydas*. The carapace scutes were imbricated as in *Eretmochelys imbricata*, however, the degree of overlapping was notably less than that characterizing hawksbill turtles of equivalent size. Marginal scute dentition was present and apparently intermediate between *Chelonia mydas* and *Eretmochelys imbricata*. One individual possessed a single claw on each flipper characteristic for *Chelonia mydas* (WOOD *et al.*, 1983; SEMINOFF *et al.*, 2003).

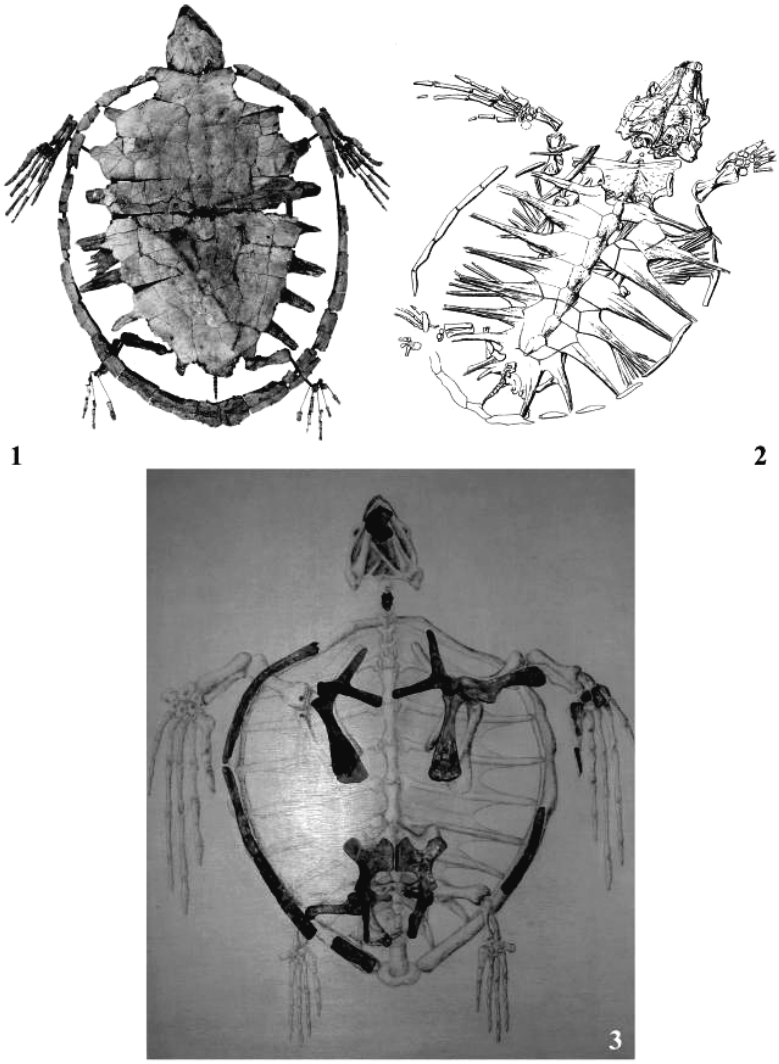


Plate 4. Glarichelys knorri *(Gray, 1837): figure 1 = type specimen of* Chelone gwinneri *Wegner, 1918, adult stage, according to* WEGNER *(1918) and* KARL & TICHY *(1999) (exhibited in the Senckenberg Museum, Frankfurt am Main, unknown number, Rupelian of Flörsheim/Germany); figure 2 = type specimen of* Chelonia knorri *Gray, 1831, juvenile stage, according to* ZANGERL *(1958) (deposited in the Zurich University, PIMUZ No. A/III 0596, Rupelian of Engi/Glarus/Switzerland); figure 3 = material from the Rupelian of Espenhain: NML PAL without number: mounted bones from a single adult specimen before the silhouette of* Chelonia mydas, *including palatine, peripherals II-VIII dex., peripherals VI-VII sin., pelvis girdle, shoulder girdle, humerus dex., femor dex., metacarpal remains, one cervical vertebra remain, one tail vertebra remain, epiplastron sin., diverse vertebrae remains indet.; photograph: Natural History Museum Leipzig, with kind permission by Dipl.-Geol. Reinhardt Baudenbacher.*

These patterns are likely that of *Glarichelys knorri*, but with lesser marginal scute dentition, a smoother mandibular median ridge and a larger single claw in the flippers. It may be an ancestor of the recent *Chelonia mydas* and *Eretmochelys imbricata*. For compare see figures 8 to 10.

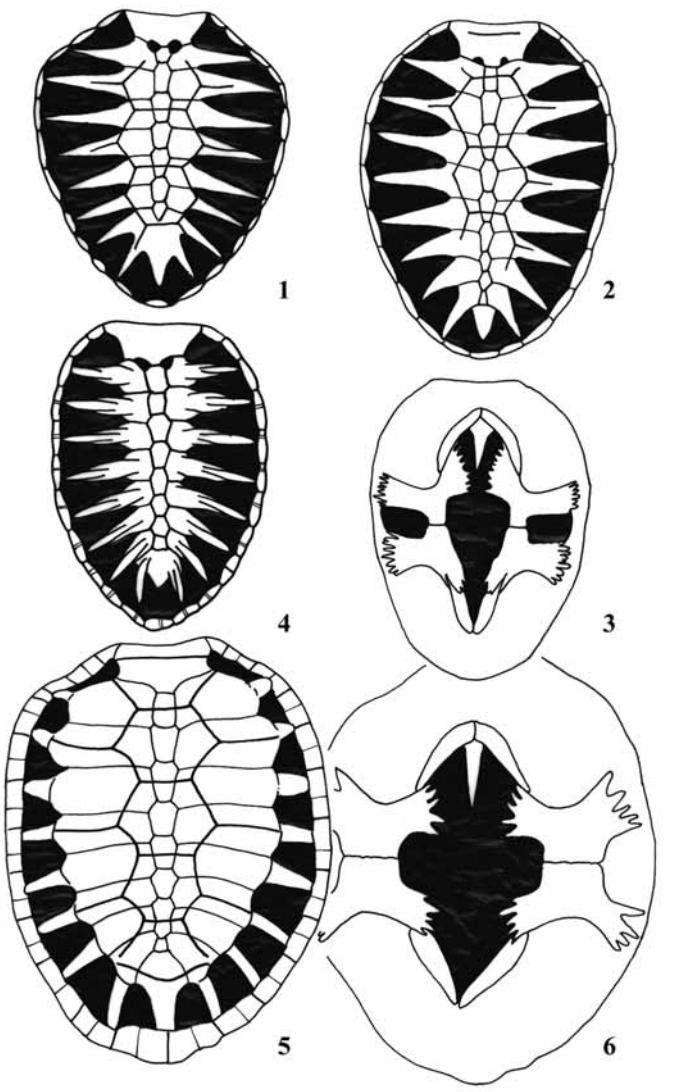


Figure 8. Schematic sketches of comparative shell morphology of Glarichelys knorri *(Gray, 1837); 1 = juvenile "*knorri*" specimen, according to ZANGERL (1958), 2 = juvenile "*ovata*" specimen, according to ZANGERL (1958), 3 = juvenile plastron, according to MLYNARSKI (1983), 4 = juvenile carapace, according to MLYNARSKI (1981), 5 = adult "*gwinneri*" carapace, according to WEGNER (1918), 6 = adult "*gwinneri*" plastron, according to WEGNER (1918).*

References/material: Espenhain: NML without number, finded in 2000: mounted bones from one individuum includes palatine, peripherals II-VIII dex., peripherals VI-VII sin., pelvis girdle, shoulder girdle, humerus dex., femor dex., metacarpal remains, one neck vertebra remain, one tail vertebra remain, epiplastron sin., diverse vertebrae remains indet.; NML Pal 3321, 3322, 3323, 3236, 3256, 3244a-b, 3241a-d, 3227a-e, 3328 pleural remains, ex coll. W. B. Freess; NML Pal 3227f neural, ex coll. W. B. Freess; NML Pal 3226a-d plastral remain, ex coll. W. B. Freess; NML Pal 3324 plastron remain, ex coll. W. B. Freess; NML Pal 3326 femor remain, ex coll. W. B. Freess; NML Pal 3327 shell remain indet., ex coll. W. B. Freess; NML Pal 5516, 5510 femur heads;

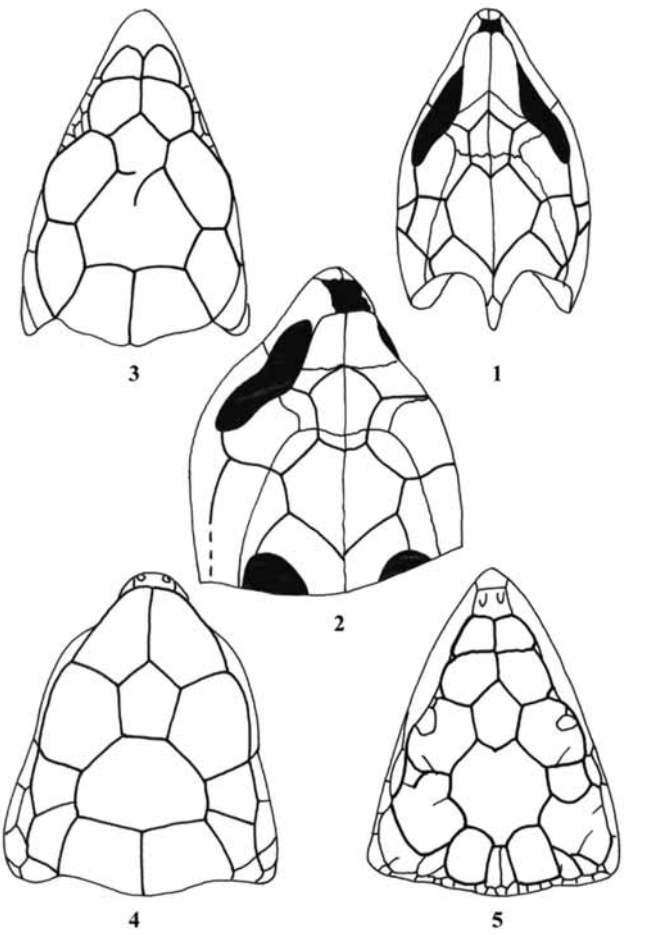


Figure 9. Schematic sketches of comparative dorsal head morphology of cheloniids: 1 = Glarichelys knorri *(Gray, 1837), juvenile, according to* ZANGERL *(1958), 2* = Glarichelys knorri *(Gray, 1837), adult, according to* WEGNER, *1918, 3* = Eretmochelys imbricata *(Linnaeus, 1766), 4* = Chelonia mydas *(Linnaeus, 1758), 5* = Lepidochelys kempi *(Garman, 1880), 3-5 according to* LEBUFF *(1990).*

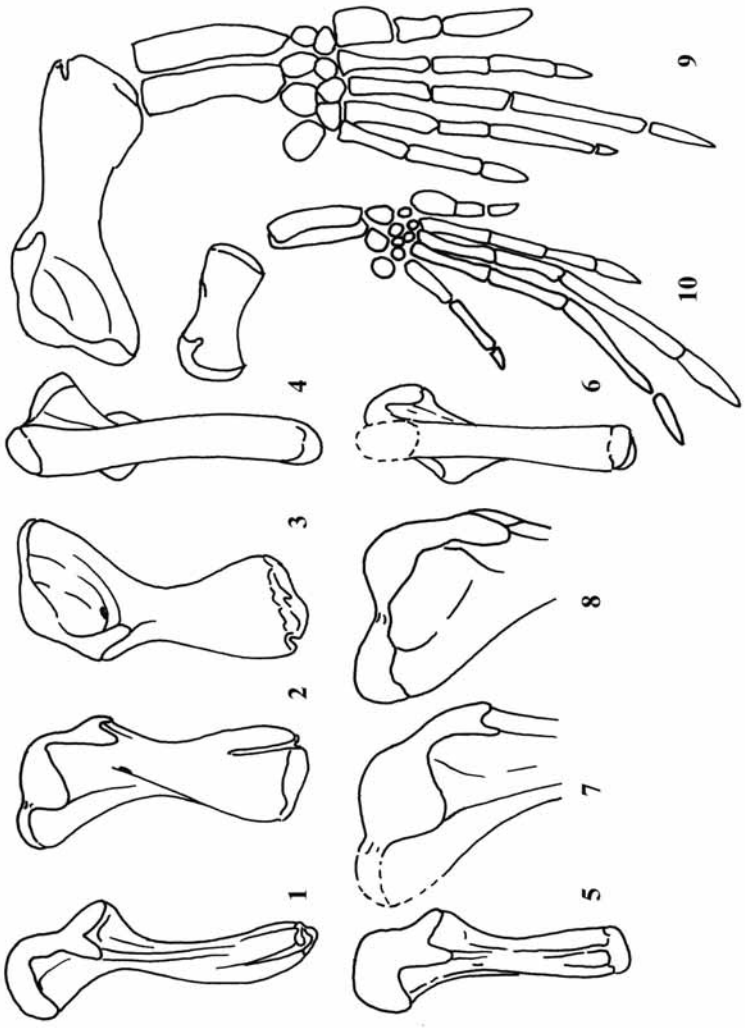


Figure 10. Schematic sketches of comparative morphology of humeri and forelimbs in Glarichelys knorri *(Gray, 1837); 1 = schematic sketch of NML PAL 3343 in frontal view, 2 = the same in visceral view, 3 = the same in dorsal view, 4 = the same in posterior view, 5 = schematic sketch of NML PAL 3329 in frontal view, 6 = the same in posterior view, 7 = caput humeri of* Chelone gwinneri *Wegner, 1918, according to WEGNER (1918), 8 = caput humeri of* Chelyopsis holsaticus *Dames, 1894, according to DAMES (1894), 9 = right forelimb (flipper) of the adult stage of "*knorri*", according to ZANGERL (1958), 10 = right forelimb (flipper) of the juvenile stage of "*gwinneri*", according to WEGNER (1918) and the new material.*

Plate 5. Glarichelys knorri *(Gray, 1837): figure 1 = humerus dex. from plate 4, figure 3, dorsal view, figure 4: frontal view; figure 2 = PMUL ES 1381, humerus dex., Rupelian of Espenhain, dorsal view, figure 3 same specimen, ventral view; photographs by Dirk Urban, Erfurt. Scale bar 5 cm.*

Plate 6. Glarichelys knorri *(Gray, 1837): figure 1 = humerus sin. NML PAL No. 3343, a = ventral view, b = dorsal view; figure 2 = humerus sin. NML PAL No. 3329, a = ventral view, b = dorsal view; figure 3 = humerus dex. NML PAL No. 5515, a = ventral view, b = dorsal view; figure 4 = humerus dex. NML PAL No. 3184, a = ventral view, b = dorsal view; photographs: Natural History Museum Leipzig, with kind permission by Dipl.-Geol. Reinhardt Baudenbacher. Scale bar 5 cm.*

NML Pal 3894 metacarpal remains; NML Pal 5513 lateral part of hyo-hypoplastron; NML Pal 5514 articulating part of scapula remain; NML Pal 3925 neural; NML Pal 3243 (finded before 1980), 3184, 3330, 5515 (all finded in 1995) humeri and remains from the lower Oligocene "Meeressande" (ca. 4 m under the Phosphorite nodule horizon); PMUL ES 1352 A02.06.02 two neurals; PMUL ES 1384-C, E proximate pleural remains, PMUL ES 1384-G metaneural remain, PMUL ES 1368 mandible remain sin. [symphysal length 29, symphysal high 20, symphysal deepth 4]; PMUL ES 1381 humerus without head; PMUL ES 1365 articulating part of scapula remain; PMUL ES 1371 femor; PMUL ES 1403 A03.01.02 two large carapace remains; PMUL ES 1416 three shell remains. Type materials of *Chelyopsis halleri* KARL, 1989 from Espenhain: MMA, without numbers, ex coll. Arnold Müller (1975-1982).

Messurements

Number	Bone	l_{caput}	d	b_{prox}	b_{dist}	b_{min}
NML PAL 3343	Humerus	125	12	50,5	45	23,5
NML PAL 3329	Humerus	75	95			
NML PAL 3330	Humerus	74				15
NML PAL wn 1	Humerus	157		84	53	30
NML PAL wn 2	Humerus	43		23,5	12,5	10
NML PAL wn 3	Femor	150		30	32	23

Subfamily Allopleuroninae Weems, 1988

According WEEMS (1988) the Allopleuroninae can be defined as large, relatively very thin-shelled, strongly fontanellized sea turtles having strongly reduced, anteroposteriorly elongate plastral elements, a deeply excavated nuchal element, but no development of dermochelyid epithecal shell.

Genus *Allopleuron* Baur, 1888

Type species: *Allopleuron hofmanni* (Gray, 1831) - figure 11

Known distribution: *A. hofmanni* is known only from the Maastichtian type area (SE Netherlands, NE Belgium). There are no Maastrichtian deposits in Kent. Eric Mulder (letter) advise to avoid to use the name "*Chelone camperi*". It is confusing, since it has two meanings: as a junior synonym of *A. hofmanni* in Owen (1851), and as a synonym of *Puppigerus camperi* in LYDEKKER (1889); the latter being another taxon. Maastricht (Netherlands), Brabant (Belgium), Kobenhaven (Danmark) and County Kent (Great Brittain). Type locality of the genus is the Pietersberg near Maastricht. General remarks see LAPPARENT DE BROIN (2001).

Horizon: Maastrichtian, Upper Cretaceous (e.g. middle to upper chalk of Kent).

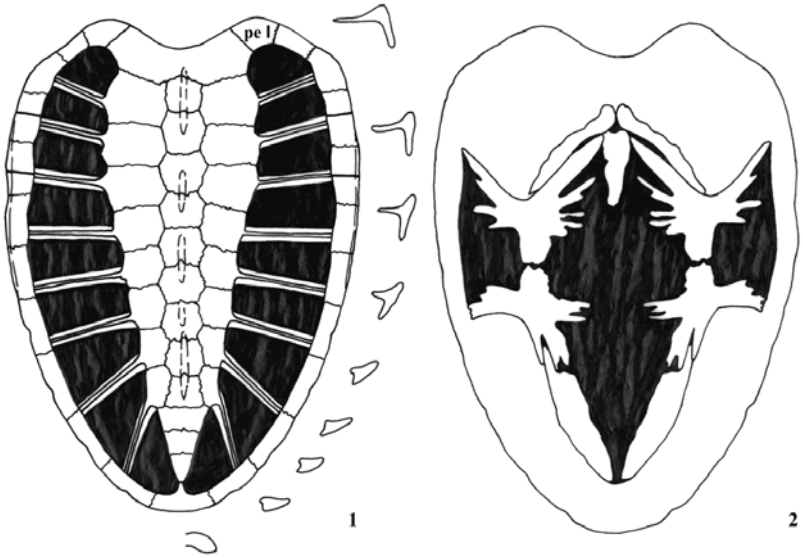


Figure 11. Schematic sketch of the shell of Allopleuron hofmanni *(Gray, 1831), according to* MULDER *(2003); 1 = carapace with the cross section of peripherals, 2 = plastron, pe I = peripheral I.*

Description: LYDEKKER (1889) induced to refer to this species OWEN's (1851) materials of *Chelone camperi* on account of their size, their shape, and especially their carinate structure. Carapace long and narrow, with deeply emarginate nuchal; neurals comparatively short and wide, with a type of hexagonals 6B according to KARL & TICHY (2005), and with a strongly knoblike keel. The pleurals are long antero-posteriorly, and extending only a short distance down the ribs, which are slender and sharply defined. The peripherals are long, and the posterior ones with a free entire border. Skull with a shorter and wider palate and a wider mandible in which the symphysis is shorter and flatter and without distinct prominence at the posterior border of the alveolar surface (plate 7, figure 3; plate 9, figure 1). The humerus morphology is characteristic according HIRAYAMA (1994) (plate 11, figure 4, 5). For descriptions and discussions: see GAFFNEY (1979), HIRAYAMA (1994) and MULDER (2003), for phylogenetic references: see GAFFNEY & MEYLAN (1988), HIRAYAMA (1994) and MULDER (2003).

Synonyms: See KUHN (1964) and MULDER (2003).

References/material: Redescribed original materials from the Pietersberg near Maastricht, see MULDER (2003).

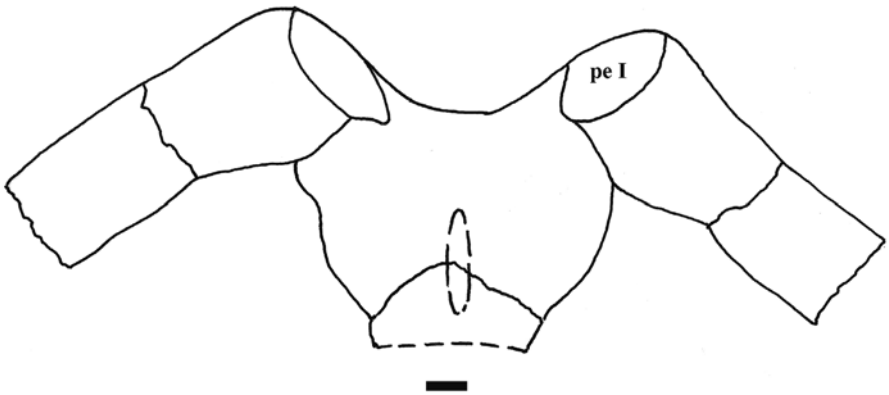


Figure 12. Schematic sketch of the anterior part of the carapace in Allopleuron insularis *(Cope, 1872), according to* WEEMS *(1988); pe I = peripheral I. Scale bar 1 cm.*

Other species: *Allopleuron insularis* (Cope, 1872) - figure 12

Known distribution: Bluff between Aquia creek and Potomac river, Stafford county, Virginia (Palaeocene); Formingdale, Monmouth county, New Jersey (Eocene).

Horizons: NP8, Zone 6, Picateway Member, Aquia Formation, Palaeocene to Greensand of Eocene.

Description: The synonyms of this taxon (*Lembonax insularis* [Cope, 1872], *Lembonax polemicus* Cope, 1870 and *Lembonax propulaeus* Cope, 1872) are based on too poorly preserved materials (discussion see WEEMS, 1988). *Allopleuron insularis* (synonym: *Lembonax insularis* [Cope, 1872]) is redescribed by WEEMS (1988): The carapace bones are extremely thin for their size, and built a very large keel. On base of its large size, its deeply indented nuchal, the forewardly projected position of the first peripherals, and its occurrence at only a slightly lower stratigraphic horizon (NP8) *Allopleuron insularis* is a valid taxon.

References/material: HAY (1908) and WEEMS (1988).

Synonyms: See KUHN (1964) and WEEMS (1988).

Remarks: Contrary to WEEMS' view, it seems to Eric MULDER (letter) not proven yet, that *Lembonax insularis* belongs to the genus *Allopleuron*. Note the differences in the abutment of the nuchal and peripherals I and II. Furthermore it seems that *Allopleuron* is not a dermochelyoid and a protostegid. Just to point out one important aspect: there is a profound difference beween the pelvic girdles of chelonioids and dermochelyoids. *Allopleuron* has a chelonioid pelvic girdle (MULDER, 2003). The same structure show PMULES ES 1376 from the Rupelian of Espenhain SE at plate 8, figs. 3 and 4, represents the following species.

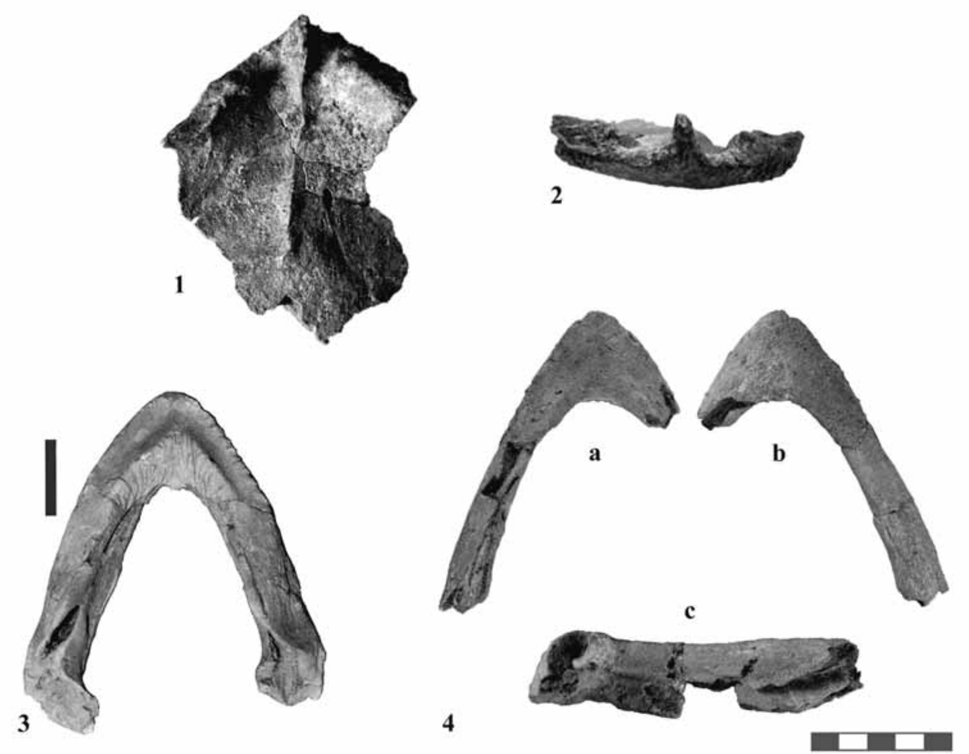


Plate 7. Glarichelys knorri *(Gray, 1837): figure 1 = remain of the secondary palatine, dorsal view, from plate 4, figure 3; figure 2: frontal view; figure 3 = lower jaw of* Allopleuron hofmanni *(Gray, 1831), Maastrichtian of Maastricht, dorsal view with proeminent dentary ridge, according to Mulder (2003); figure 4 = lower jaw remain PMUL ES 1368 with symphyseal area and the left ramus, Rupelian of Espenhain SE; a = dorsal view; b = ventral view; c = view of the broken Meckel's canal, inner side of the left ramus from below to the ventral edge; photographs by Dirk Urban, Erfurt. Scale bar 5 cm.*

Allopleuron lipsiensis n. sp.

Synonyms:

- *Chelyopsis* sp., PIETZSCH, 1956: 94;
- *Chelyopsis* sp., PIETZSCH, 1963: 450, fig. 160;
- *Dollochelys casieri* Zangerl, 1971, KARL, 1991a: 234-236, fig. 1b;
- *Dollochelys casieri* Zangerl, 1971, KARL, 1994: 333;
- *Dollochelys casieri* Zangerl, 1971, KARL, 2002: 190.

Diagnosis: Allopleuroninae. No keel elements present. Very large peripheral fontanelles in the carapace, free costae longer than pleural plate, lateral peripherals not as strongly as in *A. hofmanni*; humerus with short processus radialis (lateralis) and fascia; alveolar surface of the dental simple, without vertical differentiation, symphysis short and without cavern.

Holotype: PMUL ES (plate 9, figure 2): Carapace posterior up pleural III.

Description of holotype: Most parts of the posterior carapace area including neurals IV to VIII, pleurals III to VIII, right free costae III to VIII, left free costae V to VIII, right peripheral edge, single parts of left peripherals, left pubis, left coracoid and the right lateral wings of hyoplastron and hypoplastron.

Paratype: PMUL ES 1380 humerus, A02.07.01, Espenhain SE (plate 11, figure 2-3).

Description of paratype: A broken humerus with destroyed major and minor process and parts of epicondylus: length to head 170 mm, minimate broadth 38 mm, thickness at corpus 19 mm.

Locus typicus: Espenhain south of Leipzig, Saxonia, Middle Germany.

Stratum typicum: Phosphorite nodule horizon (Phosphoritknollenhorizont), "Böhlener Schichten", Rupelian (Stampian), Early Oligocene.

Ethymology: allo-, αλλοζ, greace: an other; pleuron-, πλευρον, greace: rib, side; *lipsiensis* - from Lipsia, latin name of Leipzig.

Differential diagnosis: The character analysis is restricted due to the conditions in *Allopleuron insularis*. Used characters can only be 1) presence of knoblike keels, 2) relative length of anterior peripherals and 3) the degree of reduction of the first peripheral. The character differentiation with DOLMOVE (Interactive Dollo and Polymorphism Parsimony by Joseph FELSENSTEIN, 1986a) shows a simple tree: (*Allopleuron lipsiensis*, (*Allopleuron insularis*, *Allopleuron hofmanni*); that with PARS (Discrete character parsimony algorithm, version 3.6a3 by Joseph FELSENSTEIN, 1986b) shows a larger distance of *Allopleuron lipsiensis* to the others. One most parsimonious tree found: (*Allopleuron lipsiensis*: 3.00, *Allopleuron insularis*: 0.00, *Allopleuron hofmanni*: 0.00); that is a clear specific differentiation of the new species described here and reconstructed in figure 13; further more only two metaneurals are present in *A. lipsiensis*, three in *A. hofmanni*.

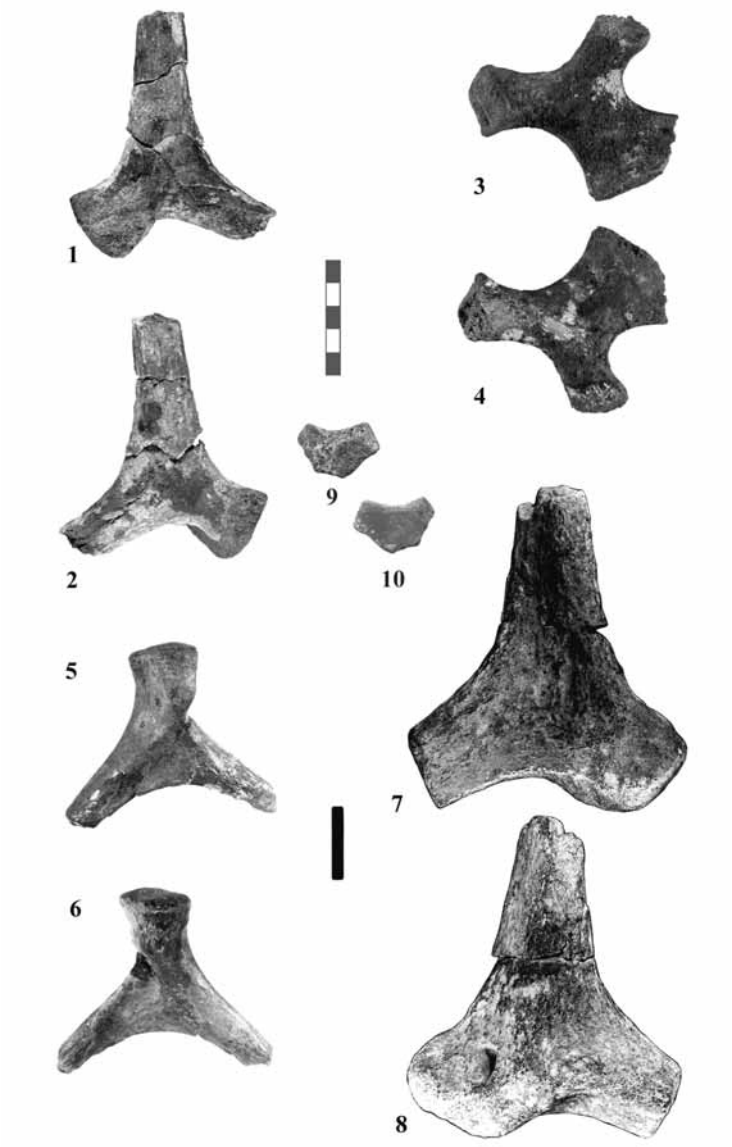


Plate 8. Glarichelys knorri *(Gray, 1837): figure 1 = PMUL ES 1365, Rupelian of Espenhain, remain of a juvenile scapula in visceral view; figure 2 = same specimen in lateral view; figure 5 = MMA, without number, Rupelian of Espenhain, remain of a juvenile scapula in visceral view; figure 6 = same specimen in lateral view;* Allopleuron lipsiensis *n. sp.: figure 3 = PMULES ES 1376, Rupelian of Espenhain SE, pubis in visceral view, figure 4 = same specimen in dorsal view, photographs by Dirk Urban, Erfurt;* Psephophorus *cf.* rupeliensis *van Beneden, 1887, BAF FG: 232/1, Rupelian of Espenhain, remain of a semiadult scapula, figure 7 = in lateral view, figure 8 = same specimen in visceral view, according to KARL (1989), figure 9 = single dermal placoid of* Psephophorus *cf.* rupeliensis *from Espenhain PMUL ES 1416a, dorsal and visceral. Scale bar 5 cm.*

+----------*Allopleuron lipsiensis*

|

1-*Allopleuron insularis*

|

+*Allopleuron hofmanni*

requires a total of 3.000

between and length

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1 *Allopleuron lipsiensis* 3.00

1 *Allopleuron insularis* 0.00

1 *Allopleuron hofmanni* 0.00

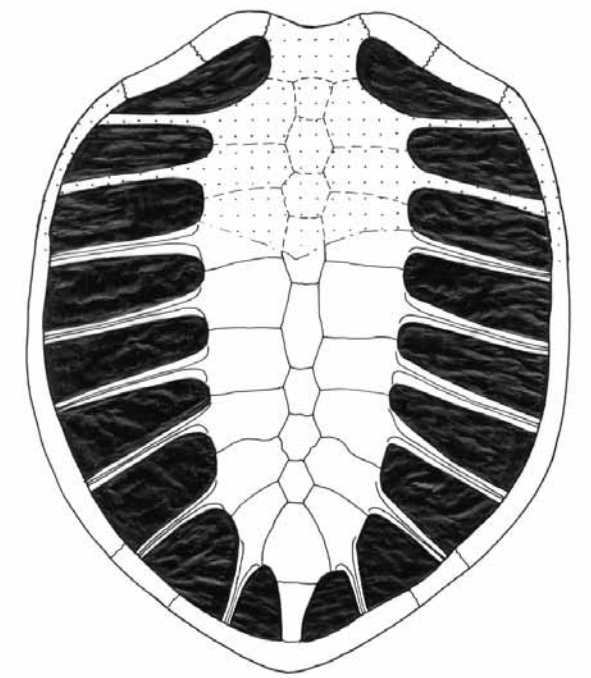

Figure 13. Schematic reconstruction of the carapace of Allopleuron lipsiensis *n. sp., based on the holotype specimen from Espenhain and the anterior peripheral from the Böhlen sample. Original.*

References/material: Original material from Böhlen of PIETSCH (1951, 1962) and KARL (1991): GFEF old number 37: remains of carapace e.g. pygal area (plate 10, figures 3-4), plastron, humerus (plate 11, figure 1), femor, half mandible, neck and tail vertebrae (see plate 1), peripherals I to II (plate 10, figures 1-2).

Materials from Espenhain located in the University of Leipzig: PMUL ES 178 distal pleural remain dist.; PMUL ES 1366 proximate pleural remain; PMUL ES 1367 two pleural remains and five free costa remains; PMUL ES 1383 A02.07.01 four plastron remains from Espenhain; PMUL ES 1384 A-F proximate pleural remains (A = A02.07.01 Espenhain); PMUL ES 1384 H juvenile eroded pleural and diversity pleural remains; PMUL ES 1378A proximate pleural I remain with costa I and II at viszeral surface; PMUL ES 1378B-A, B, D proximate pleural remains (e.g. plate 10, figure 7-8); PMUL ES 1365 posterior carapace remain dex. with the last four or five neurals (plate 10, figure 5-6); PMUL ES 1376 pubis (plate 8, figures 3-4).

Materials from Espenhain SE located in the University of Leipzig: PMUL ES 1379 diversity plate remains partly much swollen, fragmentary or transformed by markasite diagenesis (FeS_2). Some remains may be origin by inner skull, only four remains listed here: A-C proximate pleural remains, D neural.

Family Dermochelyidae Gray, 1825

Genus *Psephophorus* H. v. Meyer, 1847

Psephophorus cf. *rupeliensis* van Beneden, 1887

Synonyms:

– sea turtle (Seeschildkröte), FISCHER, 1981: 5-6;

– *Psephophorus* cf. *rupeliensis* van Beneden, 1887, KARL, 1989b: 124-129, figs. 1-3;

– *Psephophorus* cf. *rupeliensis* van Beneden, 1887, KARL, 1994: 333;

– *Psephophorus polygonus* H. v. Meyer, 1847, KARL, 2002: 192, map. 4.

Known distribution: Cosmopolitan. For general remarks: see LAPPARENT DE BROIN (2001), a detailed study gives KARL (2002).

Description: The main character of this genus is the epithecal mosaic shell, over a nearly fully reduced thecal shell. The single dermal placoids of this mosaic armour usually occur in many localities of the formerly Paratethys. Complete bones are rare and articulated skeletons are hitherto unknown. A survey is given by KÖHLER (1996), a special study of the Upper Oligocene materials from Süchteln in Germany gives ROTHAUSEN (1958).

Remarks: Here only two bones are grouped with *Psephophorus*: the scapula fragment (the largest up to now) from Espenhain from the Freiberg University collection and a single dermal placoid from Espenhain from the Leipzig University (plate 8, figure 9). The smaller specimen of the Altenburg

collection in the Mauritianum probably belongs to *Glarichelys* (plate 8, figure 5-6). Further remarks: see KARL (2002). The present scapula differs to *Glarichelys* in the larger size and to *Allopleuron* in the absence of a ridge along the processus like in MULDER (2003).

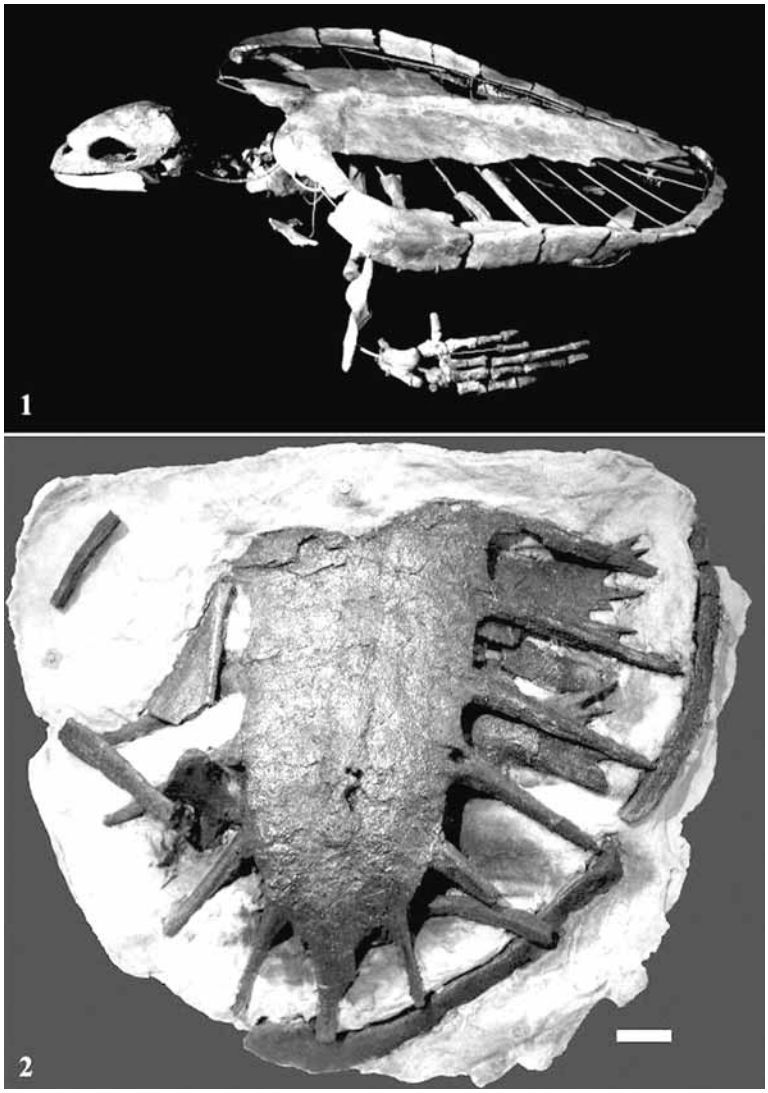

Plate 9. Allopleuron hofmanni *(Gray, 1831), Maastrichbtian of Maastricht: figure 1 = largely complete specimen in the Maastricht Museum, photograph by Anne Schulp;* Allopleuron lipsiensis *n. sp.: figure 2 = PMUL ES, without number, holotype specimen, Rupelian of Espenhain, photograph: PMUL. Scale bar 5 cm.*

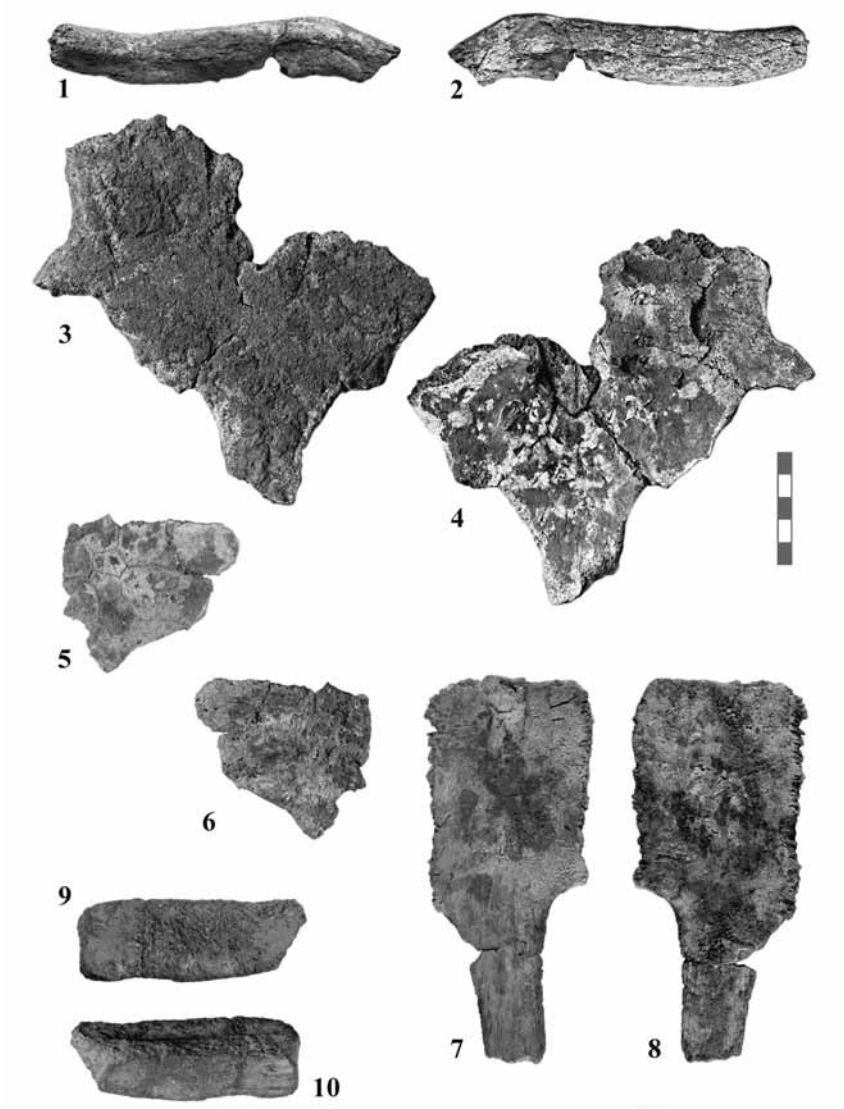

Plate 10. Allopleuron lipsiensis *n. sp.: figure 1 = GFEF, without number, Rupelian of Böhlen (see plate 1), peripherals I and II in visceral view, figure 2 = same specimen in dorsal view; figure 3 = pygal area of the discus including the last two pleurals and the metaneurals, in dorsal view, figure 4 = same specimen in visceral view; figure 5 = PMUL ES 1365, Rupelian of Espenhain, pygal area of the discus including the posterior two pleurals, the posterior neurals and the metaneurals, dorsal view, figure 6 = same specimen in visceral view; figure 7 = PMUL ES 1378, Rupelian of Espenhain, typical pleural of the posterior part of the left side in dorsal view, figure 8 = same specimen in visceral view;* Glarichelys knorri *(Gray, 1837): figure 9 = PMUL 1364, Rupelian of Espenhain E, anterolateral peripherals in dorsal view, figure 10 = same specimen in visceral view; figures 1 to 4 according to* KARL *(1991), photographs for figures 5 to 10 by Dirk Urban, Erfurt. Scale bar 5 cm.*

Plate 11. Allopleuron hofmanni (*Gray, 1831*), *Maastrichtian of Maastricht: figure 4 = right humerus in dorsal view, figure 5 = same specimen in ventral view, according to* MULDER *(2003);* Allopleuron lipsiensis *n. sp.: figure 1 = GFEF, without number, right humerus, Rupelian of Böhlen, after the original photograph by Dr. Schulz (plate 1), dorsal view; figure 2 = PMUL ES 1380 (A 02.07.01), paratype specimen, right humerus, Rupelian of Espenhain SE, dorsal view, figure 3 = same specimen in visceral view; photographs by Dirk Urban, Erfurt. Scale bar 5 cm.*

References/material: Scapula, according to Fischer (1981) and KARL (1989b, 2002): BAF FG: 232/1 (plate 8, figures 7-8); PMUL ES 1416a A03.01.03 a single dermalplacoid from Espenhain.

Cheloniid turtle remains from the last regulary excavations of the years 1996 and 1997.

PMUL ES - Working number 1: four large carapace remains; 2: some carapace remains includes proximate pleural; 3: three carapace remains and a distal humerus part; 4: one neural; 5: shell remain.

Superfamily Testudinoidea Batsch, 1788

Family Testudinidae Batsch, 1788

Genus *Cheirogaster* Bergounioux, 1935

Cheirogaster sp.

Synonyms: None.

Known distribution: According to LAPPARENT DE BROIN (2001): European Upper Eocene to Upper Pliocene of France, Germany, Spain, Switzerland, Turkey and Greece.

Description: Medium to large forms of land tortoises with the evolutional tendence towards dorsal enlargement the epiplastral lip.

Remarks: According to KARL (1996), the most ancient known species of that genus, from the Lutetian of Sankt Pankraz in Austria, *Cheirogaster steinbacheri* Karl, 1996 shows a very primitive neural fomula of ?/6/6/6/6/6/4, the Miocene *Cheirogaster bolivari* (Hernández-Pacheco, 1917) shows the advanced row of 4/8/4/8/4/8/4 with reduction of neural eight (JIMÉNEZ-FUENTES, 1992; JIMÉNEZ-FUENTES *et al.*, 1993). A reconstruction show figure 15.

GROESSENS-VAN DYCK & SCHLEICH (1985) listed some fragmentary single carapace plates under the name *Ergilemys* Ckhikvadze, 1972 from the Oligocene (Suevian) of Ronheim (South Germany) and figured a proximal pleural II remain. The sulci of central scutes are positioned more distal as in our specimen and the plate is lesser thick as in *Cheirogaster*.

References/material: Right proximate pleural IV remain from Espenhain SE: PMUL ES 1356/A.02.06.03 (plate 12, figure 1-2); femor from the same locality and horizon (plate 12, figures 3-4).

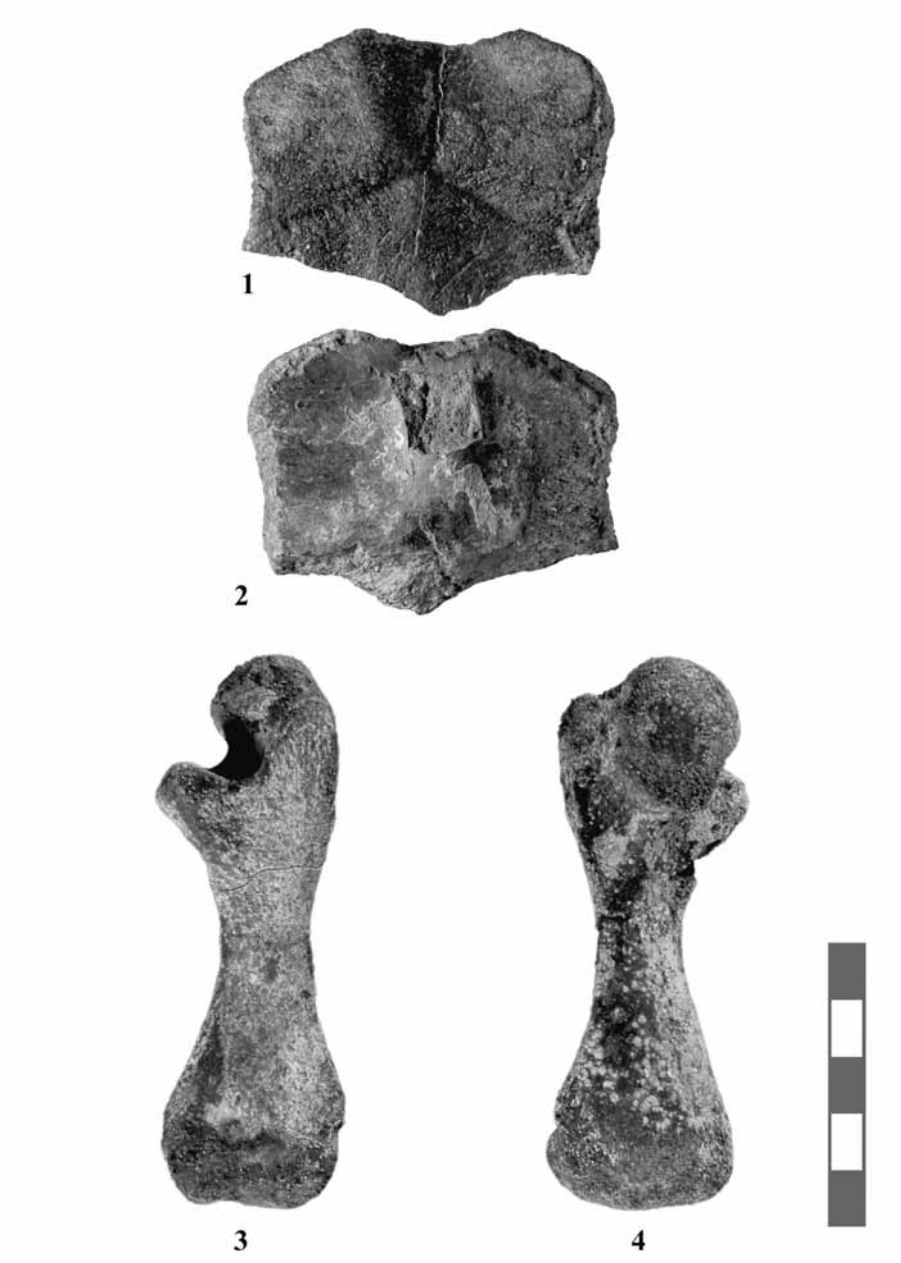

Plate 12. Cheirogaster *sp., Rupelian of Espenhain SE: figure 1 = remain of proximal pleural IV in dorsal view, figure 2 = same specimen in visceral view; figure 3 = PMUL ES 1371, femor, Rupelian of Espenhain SE, dorsal view, figure 4 = same specimen in lateral view; photographs by Dirk Urban, Erfurt. Scale bar 5 cm.*

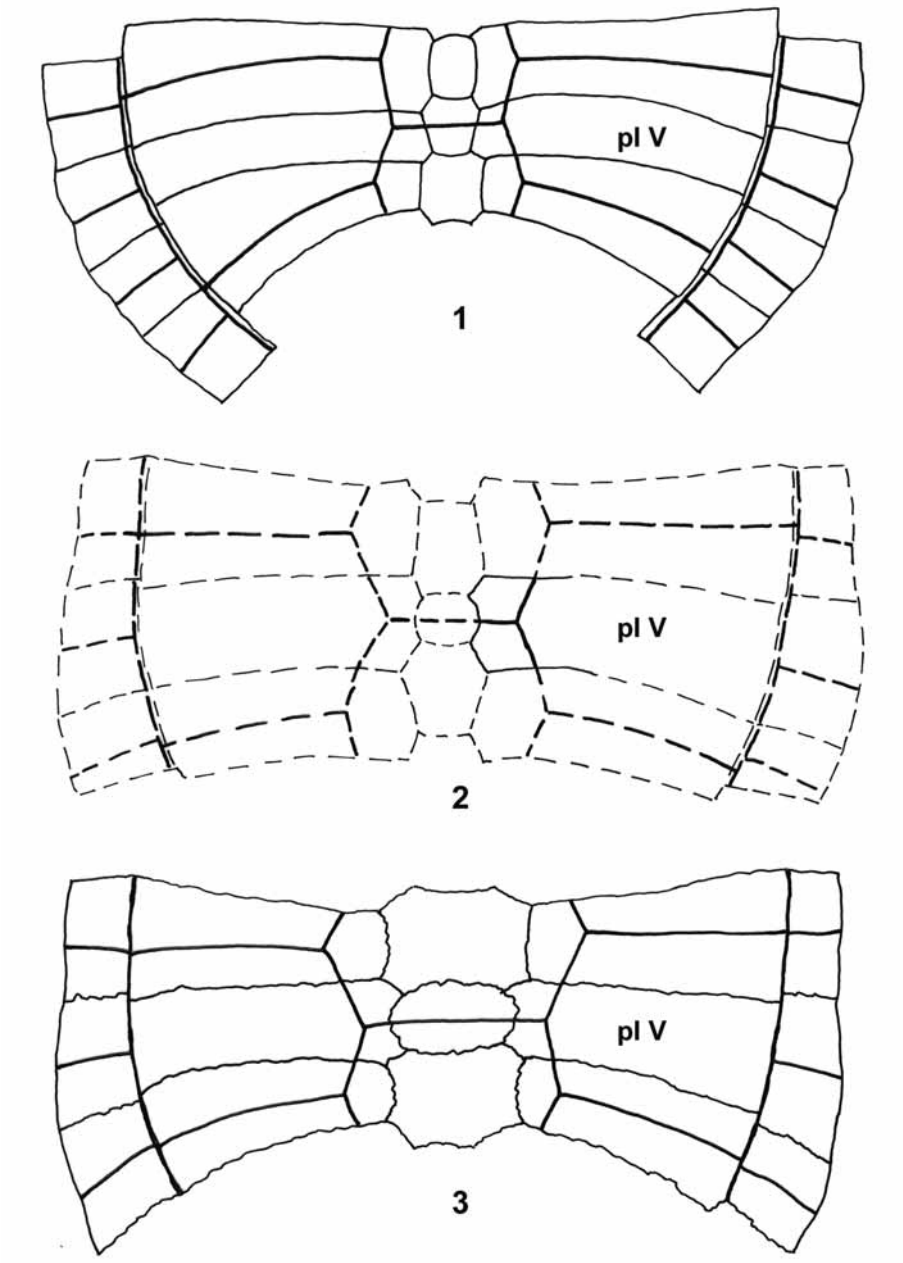

Figure 14. Schematic reconstructions of the posterior part of the carapaces of Hadrianus eocaenus *(Hummel, 1935) from the Eocene of the Geiseltal (figure 1), of* Cheirogaster bolivari *(Hernández-Pacheco, 1917) from the Miocene of Spain (figure 3), and of* Cheirogaster *sp. (figure 2), based on the proximal pleural V remain from the Oligocene of Espenhain in correlation with the adjoining pleurals and neurals. Original.*

Gen. et sp. indet.

Superfamily Chelydroidea Gray, 1831

Superfamily Testudinoidea Fitzinger, 1826

Synonyms:

Distal pleural remain, Emydidae Gray, 1851, emend. Wermut & Mertens 1955, Gen. et sp. indet., KARL, 1989: 233;

– Proximate pleural remain, Testudinidae Gray, 1822, emend. Auffenberg, 1974, Gen. et sp. indet., KARL, 1989: 233;

– Hyoplastron remain, Testudinidae Gray, 1822, emend. Auffenberg, 1974, Gen. et sp. indet., KARL, 1989a: 233-234, fig. 9, pl. VI, fig. 10a-b;

– Plate remain, coll. Adlung, Freiberg, Testudinidae Gray, 1822, emend. Auffenberg, 1974, Gen. et sp. indet., KARL, 1989a: pl. XXXII, fig. 9a-b;

– *Chelydropsis* cf. *decheni* (H. v. Meyer, 1852), KARL, 1990a: 479, fig. 1b, fig. 2;

– *Chelydropsis* cf. *decheni* (H. v. Meyer, 1852), Testudinidae et Emydidae indet., KARL, 1994: 333.

Remarks: A few indistinct remains of supposed Chelydroidea or Testudinoidea are only listed here, because the preservation does not permit a sure determination. The most important terrestrial emydid turtle taxa for the German Oligocene is the genus *Ptychogaster* Pomel, 1847. GROESSENS-VAN DYCK & SCHLEICH (1988) gave differential diagnosises for it taxa. An other important genus of the European Oligocene is *Clemmydopsis* Boda, 1927. *Clemmydopsis turnauensis* (H. v. Meyer, 1847) [syn. *Testudo riedli* Hoernes, 1892] is known from the Chattian/Oligocene from Trbovlje/Trifail in Slovenia formerly Styria also, it is the same locality of *Trionyx triunguis* Forskål, 1775 [syn. *Trionyx stadleri* Teppner, 1913], (GROSS, 2002; KARL, 1994/95). See REINACH (1900) also.

References/ material: PMUL ES 1378 nuchal remain, PMUL ES without number ?hyoplastron with secondary granulation. MMA without numbers: Emydidae indet. pleural remain, Testudinidae indet. hyoplastron dex. according KARL (1989); Chelydridae indet. KARL (1989, 1990).

Legion Archosauromorpha Huene, 1946

Supercohort Crurotarsi Sereno & Arcucci, 1990

Cohort Crocodylotarsi Benton & Clark, 1988

Magnorder Suchia Krebs, 1974

Superorder Crocodylomorpha Walker, 1968

Order Eusuchia emend. Huxley, 1875

Suborder Eusuchia Huxley, 1875

Infraorder Brevirostres (sensu Buffetaut, 1985)

Family Leidyosuchidae Rauhe & Rossmann, 1995

Genus *Diplocynodon* Pomel, 1847

Diplocynodon sp.

Synonyms:

– Crocodylia, MÜLLER, 1983: pl. XXVII, figs. 11a-c, 12;

– *Diplocynodon* sp., KARL, 1991b: 483-488, pls. 1-2;

– *Diplocynodon* sp., KARL, 1994: 337, from Böhlen, according to Pietzsch, 1964, Karl, 1990b;

– *Diplocynodon* sp., KARL, 1994: 337, from Espenhain, according to MÜLLER, 1983, KARL, 1990b.

Known distribution: First appearance in the Middle Eocene of both, Europe and North America. Although no subsequent occurrence has been reported from the Western Hemisphere it seems to have persisted in the Old World until the Middle Pliocene. *Diplocynodon* is the most common genus in European sites during the Oligocene. The main species here are *Dyplocynodon marini* Bataller, 1941 from the Oligocene of Tarrega in Spain and *Diplocynodon hantoniensis* (Wood, 1846) from the Oligocene of Hordwell in England.

Description: According to STEEL (1973), *Diplocynodon* is distinguished primarily by the double caniniform teeth in the upper jaw. The bridges of surface of dermal plates are broader than the diameters of holes; this is a significant character of *Diplocynodon*. The specimen NML G2213 shows contrary relations. The caudal vertebra from MMA (without number) is procoelous, and it may be the first of the tail (KARL, 1990, 1991b).

Remarks: The lesser known crocodile remains of *Diplocynodon* are here only listed. *Diplocynodon hallense* Kuhn, 1939 was described from the Geiseltalian (Lutetian) of the Geiseltal Basin. The nuchal plate dex. ant. In the "Sternberger Gestein" from Breitenfeld near Leipzig (see below) could belong to another crocodile, possibly a pristichampsid. *Pristichampsus rollinattii* (Gray, 1831) [syn. *Weigeltisuchus geiseltaliensis* Kuhn, 1939] is known from the Geiseltal, and ROSSMANN (1998) listed two teeth-crowns from the Upper Eocene/Lower Oligocene from Rot-Malsch near Heidelberg. GRAMANN (1958) describes a fragmentary left dental with 13 alveoles as *Diplocynodon hantonensis* (Wood, 1846) from the lower Oligocene Melanienton from the quarry "Altenburg III" of Borken. *Helmstedtisuchus freyi* Schleich & Windolf, 1994 from the Upper Eocene of Helmstedt (same fauna as *Glarichelys knorri*, syn. *Chelyopsis raabei* Karl & Schleich, 1994) is not a crocodilian, but a scombrid teleostean (ROSSMANN & KLAPPERT, 2000).

The type specimen of *Diplocynodon haeckeli* described by SEIDLITZ (1917) and 1919, a snout remain is destroyed during the second world war.

According BERG (1966) it is not a member of the genus *Diplocynodon* because the main feature of that, the twice canins formed by the 3. and 4. teeth of the lower jaw are absent. The original figure shows characters like the genus *Asiatosuchus* Mook, 1940. In conclusion BERG (1966) called it *Asiatosuchus ? haeckeli* (Seidlitz, 1917). According SEIDLITZ (1917, 1919) the type locality was Oligocene of Sieglitz near Camburg (Saale) 20 km NE of Jena in Thuringia, now the horizon is corrected to the border between middle and upper Eocene.

References/material: MMA, nuchal plate, caudal vertebra I from Phosphorite nodule horizon of Espenhain, according to KARL (1990); NML G2213- nuchal plate dex. ant. (non *Diplocynodon*) in "Sternberger Gestein" from Breitenfeld near Leipzig, according to KARL (1990).

PALAEOECOLOGICAL ASPECTS

Within the Weisselster Basin, there occur different ecological types of turtles: index genera for Paleogene litoral sediments as *Glarichelys* [syn. *Chelyopsis*]; *Psephophorus* as marine element; *Trionyx* as fluviatile and brackish element; and Testudinoidea as rare terrestrial/fluviatile elements. The important remain of *Cheirogaster* may origin from a giant land tortoise species of an island. An extremely pelagic representative of the marine tortoises within the materials newly described here is *Allopleuron*, a genus which was already known from the Upper Cretaceous of Western Europe and England as well as from the Paleocene of North America. Hence, the Oligocene materials described here is the stratigraphically youngest record and receives a special importance.

An another European softshelled turtles group of the Pelaeogene is represented with the genus *Allaeochelys* Noulet, 1867. GRAMANN (1956) listed fragmentary material from the early to middle Oligocene "Melanienton" of Borken (Lower Hassia) as it synonym *Anosteira crassesculpta* Harrassowitz, 1922, origin described for the Geiseltalian (Lutetian, middle Eocene) of Messel hole. KARL, GRÖNING & BRAUCKMANN (2006) describes an actual occurrence from the late Oligocene (Chattian: early "Eochattian" = whole sequence Rupelian-Chattian) of a clay pit in the Elbe-bank near Steutz, approximately 12 km WNW Dessau, Sachsen-Anhalt. It is the most neighbouring site of the Weisselster Basin. *Allaeochelys* was a high aquatic free swimming fluviatile element like *Carettochelys* Ramsay, 1887.

GROESSENS-VAN DYCK & SCHLEICH (1988) described further material of several Oligocene sites of the Mainz Basin and gave the follow taxa list: *Chelydropsis* Peters, 1868, *Trionyx* Geoffroy, 1809, "*Ocadia*" Gray, 1873, *Ptychogaster laurae* (Förster & Becker, 1886), *Ptychogaster laharpei* Portis, 1856, *Ptychogaster ronheimensis* Groessens-Van Dyck & Schleich, 1985, *Palaeochelys* Meyer, 1847, *Ergilemys* Ckhikhvadze, 1972, *Geochelone* Fitzinger, 1835, *Testudo* Linnaeus, 1758. Remains of such forms may be influenced in marine areas by rivers.

Crocodiles like *Diplocynodon* are a limno-fluviatil element and may be influenced in marine areas by rivers also, some populations with adaption to brackish areas was possible.

Abbreviations: BAF = Paläontologische Sammlung der Technischen University Freiberg/Sachsen (Bergakademie); BMNH = British Museum (Natural History) London; GFEF = Geologische Landesuntersuchung GmbH (formerly Geologische Forschung und Erkundung Freiberg/Sachsen); MMA = Museum Mauritianum Altenburg; NML = Naturkundemuseum Leipzig; PIMUZ = Palaeontologisches Institut der Universität Zürich; PMUL = Paläontologisches Museum der Universität Leipzig; SLMJ = Styrian Provincial Museum Joanneum Graz; SMFM = Forschungsinstitut und Museum Senckenberg Frankfurt am Main; SMNS = Staatliches Museum für Naturkunde Stuttgart.

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