

NEW SHELL REMAINS OF *PELTOCHELYS DUCHASTELLI* (DOLLO, 1884) FROM WESTERN AND MIDDLE EUROPE AND THE RISE OF TRIONYCHIDS (TESTUDINES: TRIONYCHOIDEA)

[Nuevos restos de caparazones de Peltochelys duchastelli (Dollo, 1884) de Europa Occidental y Central e incremento de los Trionícidos (Testudines: Trionychoidea)]

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ABSTRACT: Turtle remains, first described by GRABBE (1883) as *Tretosternon punctatum* Owen, 1842 from the early Cretaceous of Northwest Germany, are redescribed in detail. The material belonging to the species *Peltochelys duchastelli* Dollo, 1884 consists of some natural molds of carapace remains with a fine scar like surface, these remains are enclosed in the historic material which has been collected by Heinrich Friedrich Wilhelm Grabbe during the investigations for his doctoral thesis in the late 19th Century. The fossils are stored in the collections of the Geoscience Centre of Georg-August-University Göttingen, Germany. New material from Germany and Portugal is described, and the material from the

Guimarota mine is revised. The material which is described here gives evidence of soft shelled turtle evolution.

Key words: Upper Jurassic, Portugal, Lower Cretaceous, Belgium, Germany, *Peltochelys duchastelli* Dollo, 1884, new material, stratigraphical and palaeobiogeographical distribution.

RESUMEN: Se describen en detalle restos de tortugas citadas por primera vez por GRABBE (1883) como *Tretosternon punctatum* Owen, 1842 en el Cretácico temprano del noroeste de Alemania. El material pertenece a la especie *Peltochelys duchastelli* Dollo (1884) y se compone de unos moldes naturales de restos de caparazón con una superficie con finas marcas. Estos restos se incluyen en el material histórico recogido por Heinrich Friedrich Wilhelm Grabbe durante las investigaciones para su tesis doctoral en el siglo XIX. Los fósiles se guardan en las colecciones del Centro de Geociencias de la Universidad Georg-August de Göttingen (Alemania). Se describen nuevos restos de Alemania y Portugal, revisándose el material de la mina Guimarota. Lo que se describe aquí evidencia la evolución de los Trionícidos.

Palabras clave: Jurásico Superior, Portugal, Cretácico Inferior, Bélgica, Alemania, *Peltochelys duchastelli* Dollo, 1884, nuevo material, distribución estratigráfica y paleobiogeográfica.

INTRODUCTION

Peltochelys duchastelli was hitherto only known from the Wealden of Bernissart in Belgium (LAPPARENT DE BROIN, 2001; MEYLAN, 1988). The stratigraphical position of the Bernissart Wealden facies is Middle Barremian to earliest Aptian (Sainte-Barbe Formation, Mons Basin, Belgium) (YANS *et al.*, 2005). GRABBE (1883) described the actually rediscovered carapace remains as a member of *Tretosternon punctatum* OWEN, 1842 (*Tretosternon Bakewelli* Mantell), see also BENECKE (1884). Later, KOKEN (1887), ZITTEL (1889), and KUHN (1964, 1974) listed it as *Tretosternon Bakewelli* Mantell from the “Wälderthon des Bückeberg” without mentioning GRABBE (1883) or BENECKE (1884) as the original sources. The original material described by Grabbe was thought to be lost, and his dissertation has been fairly unknown. Now, the authors have recognized these shell remains, collected by Heinrich Friedrich Wilhelm Grabbe, from the end of the 19th century, in the paleontological collections of the Geoscience Centre of the Georg-August-University in Göttingen. There, the complete documentation of his dissertation is stored.

SYSTEMATIC PALAEOONTOLOGY

Order Testudines Linnaeus, 1758

Infraorder Cryptodira Cope, 1868

Superfamilie Trionychoidea Gray, 1825

(syn. Trionychoidea Fitzinger, 1826)

(includes Peltochelyidae, Carettochelyidae, Trionychidae)

Family Peltochelyidae Seeley, 1880

Genus *Peltochelys* Dollo, 1884

TAXONOMICAL NOTES: In the older literature a close relationship between *Tretosternon* Owen, 1842 and *Peltochelys* Dollo, 1884 was proposed. A detailed synonymy of *Peltochelys* Dollo, 1884 and *Helochelydra* Nopcsa, 1928 to *Tretosternon* Owen, 1842 is given by MŁYNARSKI (1976: 60). KUHN (1964) listed *Peltochelys* twice, as a member of the Dermatemydidae Gray, 1870 (KUHN, 1964: 54) and as a member of the Anosteirinae Lydekker, 1889 (KUHN, 1964: 183). According to MILNER (2004), OWEN (1842) initially described three Purbeck turtle taxa (*Platemys bullockii*, *Chelone obovata*, and *Tretosternon punctatum*) from four specimens (*T. punctatum* had two syntypes). Furthermore, all remains were located in private collections, none of them was figured or identified with a catalogue number, but they all were described in some detail. Of these four specimens, the holotype of *Pleurosternon* ('*Platemys*') *bullockii* survives with a continuous history of recognition and presents no taxonomic problems. The other three types were not referred subsequently by Richard Owen and were stated by LYDEKKER (1889) as to be lost, a conclusion followed by all later workers. Purbeck-Wealden turtles with a characteristic pustulate ornament on the carapace, generally called *Tretosternon*. The genus includes the Purbeck species *T. punctatum* and the Wealden species *T. bakewelli*, whereas *Tretosternon punctatum* is based only on unfigured, supposed to be lost types, which lack the generally accepted characters of the genus. KUHN (1964) moved the early Cretaceous German material to *Tretosternon bakewelli* (Mantell, 1827) based on the stratigraphic differentiation. Now, according to MILNER (2004) it seems the best to continue to treat *T. punctatum* as a nomen dubium with a lost lectotype. The replacement of the generic name for this material has been determined by LAPPARENT DE BROIN & MURELAGA (1999) who showed that the next published synonym that unequivocally applies here is *Helochelydra* Nopcsa, 1928, created for an Isle of Wight Wealden '*Tretosternon*' specimen. An unfortunate feature of Nopcsa's paper was that he created the new genus *Helochelydra* without naming a species comprised in. This is an unacceptable taxonomic practice, but can be valid for genera

SYSTEM	SERIES	STAGE	AGE (MYA)	EUROPE	ASIA	N-AMERICA	N-AFRICA	AUSTRALIA/ NEW GUINEA
Quaternary	Pleistocene/ Recent		2.588-0					<i>Carettochelys insculpta</i>
Neogene	Pliocene	Piacenzian	3.6-2.588					
		Zanclean	5.332-3.6					
	Miocene	Messinian	7.246-5.332					<i>Carettochelys sp.</i>
		Tortonian	11.608-7.246					
		Serravallian	13.82-11.608					
		Langhian	15.97-13.82					
		Burdigalian	20.43-15.97	<i>carettochelyine turtle</i>			carettochelyine turtle	<i>Carettochelys sp.</i>
Aquitanian	23.03-20.43							
Palaeogene	Oligocene	Chattian	28.4-23.03	<i>Allaeochelys parayrei</i>				
		Rupelian	33.9-28.4	<i>Allaeochelys parayrei</i>				
	Eocene	Priabonian	37.2-33.9	<i>Allaeochelys anglica</i> <i>Allaeochelys delbeidi</i>		<i>Anosteira manchuriana</i> <i>Anosteira sbantungensis</i> <i>Anosteira mongoliensis</i> <i>Anosteira maomingensis</i>	<i>Pseudanosteira pulchra</i> <i>Anosteira ornata</i> <i>Anosteira radulina</i>	
		Bartonian	40.4-37.2	<i>Allaeochelys jimenezi</i>		<i>Anosteira lignanica</i> <i>Burmemyx magnifica</i>		
		Lutetian	48.6-40.4	<i>Allaeochelys casasecai</i> <i>Allaeochelys parayrei</i> (<i>gracilis</i> + <i>crassesculpta</i>)				
		Ypresian	55.8-48.6					
	Palaeocene	Thanetian	58.7-55.8					
		Seelandian	61.1-58.7					
		Danian	65.5-61.1					

SYSTEM	SERIES	STAGE	AGE (MYA)	EUROPE	ASIA	N-AMERICA	N-AFRICA	AUSTRALIA/ NEW GUINEA
Cretaceous	Upper Cretaceous	Maastrichtian	70.6-65.5		<i>Anosteira shuwalovi</i>			
		Campanian	83.5-70.6					
		Santonian	85.8-83.5		<i>Kizylkumemys sp</i>			
		Coniacian	88.6-85.8					
		Turonian	93.6-88.6					
		Cenomanian	99.6-93.6		<i>Kizylkumemys sp</i> <i>Kizylkumemys sbultzi</i>			
	Lower Cretaceous	Albian	112-99.6	<i>Peltochelys duchastelli</i>				
		Aptian	125-112	<i>Sandownia barrisi</i>	<i>Kizylkumemys kboratensis</i>			
		Barremian	130-125	<i>Peltochelys duchastelli</i>				
		Hauterivian	133.9-130					
		Valanginian	140.2-133.9					
Berriasian		145.5-140.2	<i>Peltochelys duchastelli</i>					
Jurassic	Upper Jurassic	Tithonian	150.8-145.5	<i>Peltochelys duchastelli</i>	<i>Kizylkumemys sp.</i>			
		Kimmeridgian	155.6-150.8					
		Oxfordian	161.2-155.6					

Figure 1. Stratigraphical distribution of *Peltochelys duchastelli*, compiled by DE BROIN (1977, 1987), JOYCE et al. (2004), KARL et al. (2006), MEYLAN et al. (2000), SYROMYATNIKOVA & DANILOV (2009), TONG et al. (2009, 2010).

named before 1931¹. LAPPARENT DE BROIN & MURELAGA (1999) created the species name *nopcsai* for Nopcsa's *Helochelydra* material, and proposed that this generic name replaces *Tretosternon* for some of the British specimen with pustulate shells (MILNER, 2004).

CHARACTERS: Only known by shell, ten pairs of peripherals and paired ventral nuchal processes are present, intergular and one pair of gulars and a complete set of inframarginals present, big and broad plastral lobes present, shell surface sculptured with fine and, punctiform pits. The surface of the present pleural remains described here has a fine scar similar to punctuate sculptur (see plates). It is not pustular like in *Helochelydra nopcsai* Lapparent de Broin & Murelaga (1999).

Peltochelys duchastelli Dollo, 1884

BELGIUM

MATERIAL: Most parts of shell, IRSNB Ct. R. 16, lectotype, according DOLLO (1884) are IRSNB Ct. R. 17 and IRSNB Ct. R. 18 juvenile specimen of *Peltochelys duchastelli*.

LOCALITY: Coal mine of 19th century near Bernissart, Mons basin, Belgium.

HORIZON: Wealden facies, upper Barremian to lower Aptian, lower Cretaceous.

REMARKS: Only the original material is known from Belgium. It was described by DOLLO (1884, 1909) and reviewed by MEYLAN (1989) and PÉREZ-GARCÍA (2011), figures see there. According PÉREZ-GARCÍA (2011) are IRSNB Ct. R. 17 and IRSNB Ct. R. 18 a *Chelonii* indet.

¹ Article 69 of the ICZN code (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1999), German edition: INTERNATIONALE KOMMISSION FÜR ZOOLOGISCHE NOMENKLATUR (2000): *Internationale Regeln für die Zoologische Nomenklatur*, 2000: 116-118.

New shell remains of *Peltochelys duchastelli* (Dollo, 1884) from Western and Middle Europe and the rise of Trionychids (Testudines: Trionychoidea)



Plate 1. *Peltochelys duchastelli* Dollo, 1884 from the Guimarota mine in Portugal from GASSNER (2000): 1: hyoplastral remain (N.º T9, *Carettochelyidae?* indet. after BRÄM, 1973); 2: neural; 3: left xiphiplastron (N.º T8, *Carettochelyidae?* indet. after BRÄM, 1973); 4: ?scapula remain (may be a fish bone also) without scale (N.º T3, *Plesiochelyidae* indet. after BRÄM, 1973); 5: *Peltochelys duchastelli* Dollo, 1884 from Krebsbagen near Stadthagen in NW-Germany. Grabbe-collection. Photo Brigitte Stefan, TLDA. Scale bar = 5 cm. Figure 1 to 4 with permission of the "Dr. Friedrich Pfeil Verlag, Munich".

GERMANY

MATERIAL: GZG (Geoscience Centre of the University of Göttingen, Museum) n.º GZG.V. 010.404 (plate 1, fig. 5), natural mould with remains of the left pleurals I-II No, legit Heinrich Friedrich Wilhelm Grabbe. In KARL & TICHY (2004) and KARL, STAESCHE, TICHY, LEHMANN & PEITZ (2007) the present material was not yet enclosed because it was rediscovered recently.

LOCALITY: Krebsshagen, Maschinenschacht, Schaumburg-Lippe, Lower Saxony, NW-Germany according GRABBE (1883).

HORIZON: Old definition “Mittlerer Wealden” according GRABBE (1883), new definition Berriasian, Lower Cretaceous (ELSTNER & MUTTERLOSE, 1996). The Berriasian material from Northwest Germany is older than the Belgian type material. Other material from Northwest Germany from the Aptian (late Lower Cretaceous) near Nehden/Sauerland was referred to *Peltochelys duchastelli* by NORMAN *et al.* (1987), now lost. It is an approximately equivalent to the Wealden Clay unit of the Wealden Formation of SE-England and the “Bernissartian” of SW-Belgium (horizon of *Iguanodon*).

REMARKS: The pleural plates are very thin (4 mm thickness at the peripheral end with about 40 mm breadth, l/b-index = 10). General shape and position of a scute-sulcus is related to the right pleurals IV and V of *Peltochelys duchastelli*.

SYNONYMY OF THE GERMAN MATERIAL

- *Tretosternon punctatum* Owen (*Tretosternon Bakewelli* Mantell); GRABBE (1883: 48).
- *Tretosternon punctatum* Owen; KOKEN (1887: 314)
- *T. Bakewelli* Mantell; ZITTEL (1889: 534)
- *Tretosternon bakewelli* (Mantell, 1827); (KUHN 1964: 57)
- *Tretosternon punctatum* Owen after KOKEN (1887) and KUHN (1974: 25)
- *Tretosternon punctatum* Owen 1842; KARL, STAESCHE, TICHY, LEHMANN & PEITZ (2007: 51)

MATERIAL: Coll. Norbert Meyer (Stadthagen) n.º DZ 3, 1988 (plate 2).

LOCALITY: Road construction of the northwest beltway of Bückeberg (52º15'45.42" N, 9º01'45.06"E, 65 m), Lower Saxony, NW-Germany.

HORIZON: Bückeberg-Member. Berriasian, Wealden facies (western Lower Saxony Cretaceous basin), Lower Cretaceous.

New shell remains of *Peltochelys duchastelli* (Dollo, 1884) from Western and Middle Europe and the rise of Trionychids (Testudines: Trionychoidea)

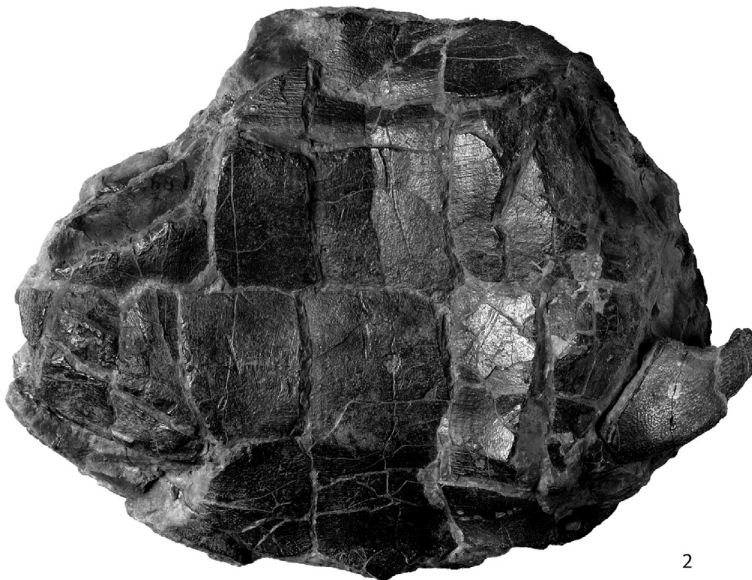
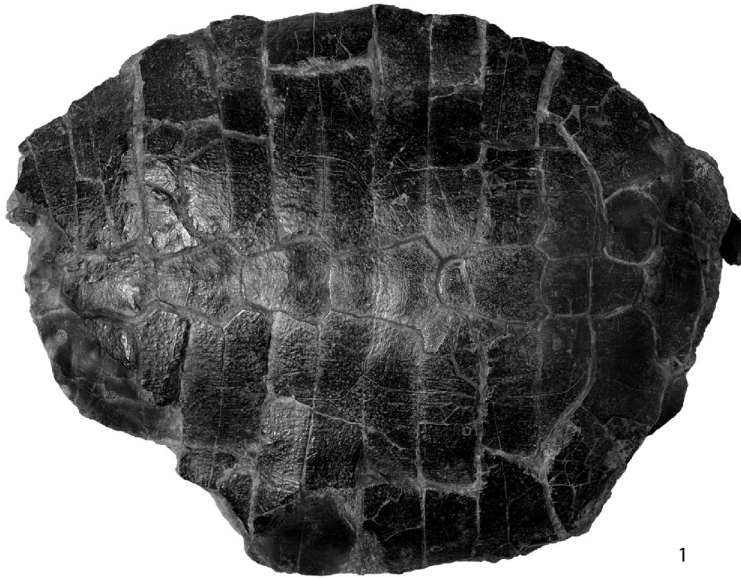


Plate 2. Peltochelys duchastelli Dollo, 1884 from north of Bückeberg in NW-Germany:
1: carapace in dorsal view, 2: plastron in ventral view; anterior part at right.
Photo Brigitte Stefan, TLDA. Scale bar = 5 cm.

MATERIAL: Authors collection (HVK), leg. et don. Kurt Wiedenroth (Garbsen) (plates 3-4).

LOCALITY: Bock's pit, Duingen (NW-embankment under the yellow sandlayers), Lower Saxony, NW-Germany.

HORIZON: Bückeberg-Member. Berriasian, Wealden facies (western Lower Saxony Cretaceous basin), Lower Cretaceous.

PORTUGAL

MATERIAL: The remains of turtles from Guimarota have been misunderstood by GASSNER (2000). Remains of pleurosternid turtles are not known from Guimarota. There is only one *Platycheilus* remain in his figure 1, all other shell remains are referred to *Peltochelys*, see plate 1, figures 1-4 here. BRÄM (1973) had already named some of the material with the correct group Carettochelyidae.

LOCALITY: Guimarota mine, Portugal.

HORIZON: Guimarota layer, Alcobacã Formation, Kimmeridgian, Upper Jurassic.

MATERIAL: GZG (Geoscience Centre of the University of Göttingen, Museum) GZG.V Working n.º 02-07, 09, 10-16, 20, 24, 37, 38, 47, collected by Jesper Milan during field trips in the summers of 2000-2004. All fragments here figured are related to the Guimarota material, see plate 5.

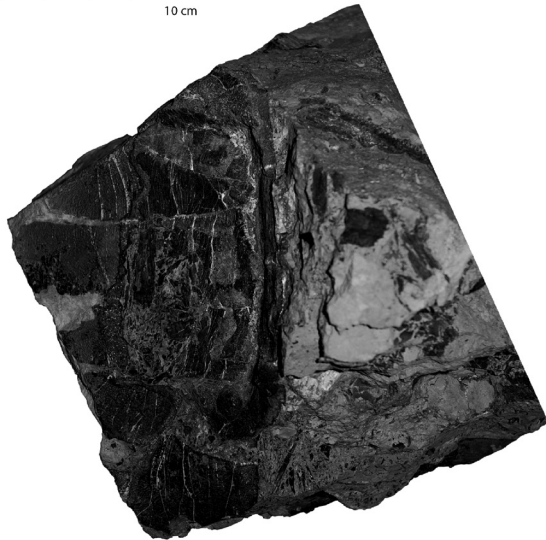
LOCALITY: Lourinhã approximately 70 km north of Lisboa, Portugal.

HORIZON: Lourinhã Formation, Late Kimmeridgian to Early Tithonian, Upper Jurassic.

New shell remains of *Peltochelys duchastelli* (Dollo, 1884) from Western and Middle Europe and the rise of Trionychids (Testudines: Trionychoidea)



1



2

Plate 3. Peltochelys duchastelli Dollo, 1884 from Duingen in NW-Germany. 1: Carapace with dorsal imprints at the sediment, includes remains of the nuchal, right peripherals I-III, preneural, neurals i-V and pleurals I-V. 2: counterpart of the left side of figure 1 with remains of pleurals I-V and adjacent peripherals. Photo H.-V. Karl, TLDA. Scale bar = 5 cm.

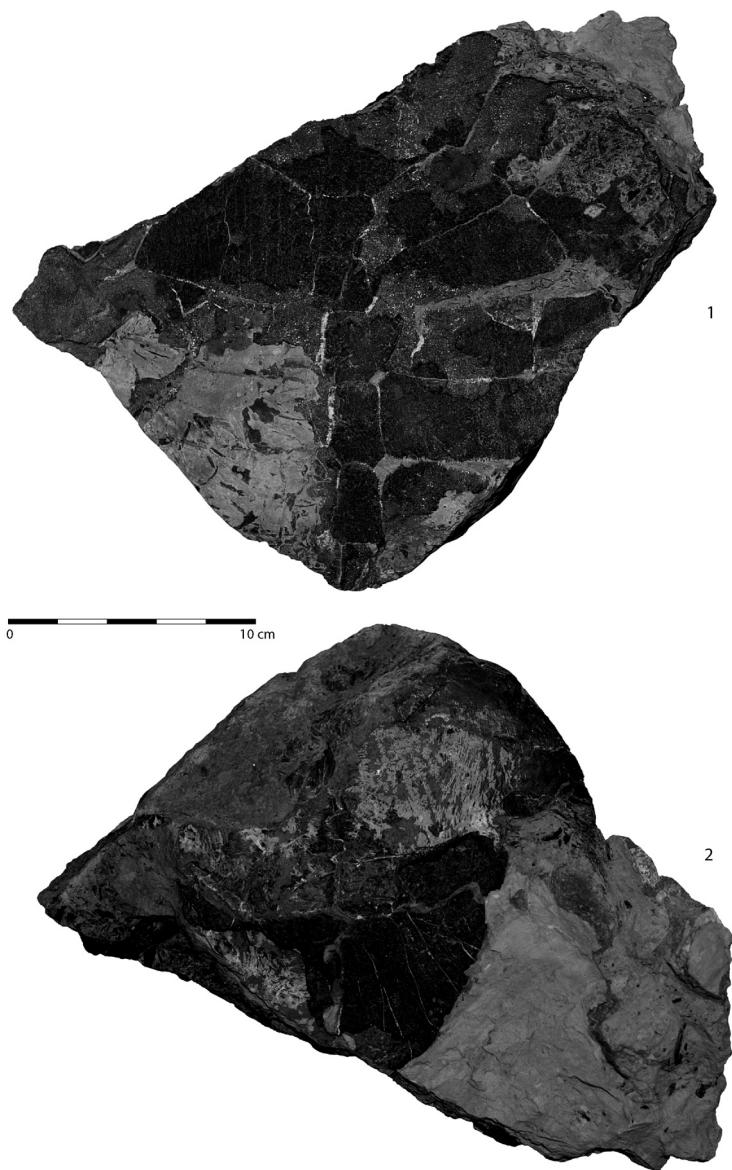


Plate 4. *Peltochelys duchastelli* Dollo, 1884 from Duingen in NW-Germany. 1: Specimen C: anterior half carapace in ventral view with imprints of visceral surface with bone remains, 2: backside of same specimen: posterior half of plastron in ventral view with imprints of visceral surface with bone remains of left hypoplastron and both xiphiplastra.

Photo H.-V. Karl, TLDA. Scale bar = 5 cm.

New shell remains of *Peltochelys duchastelli* (Dollo, 1884) from Western and Middle Europe and the rise of Trionychids (Testudines: Trionychoidea)

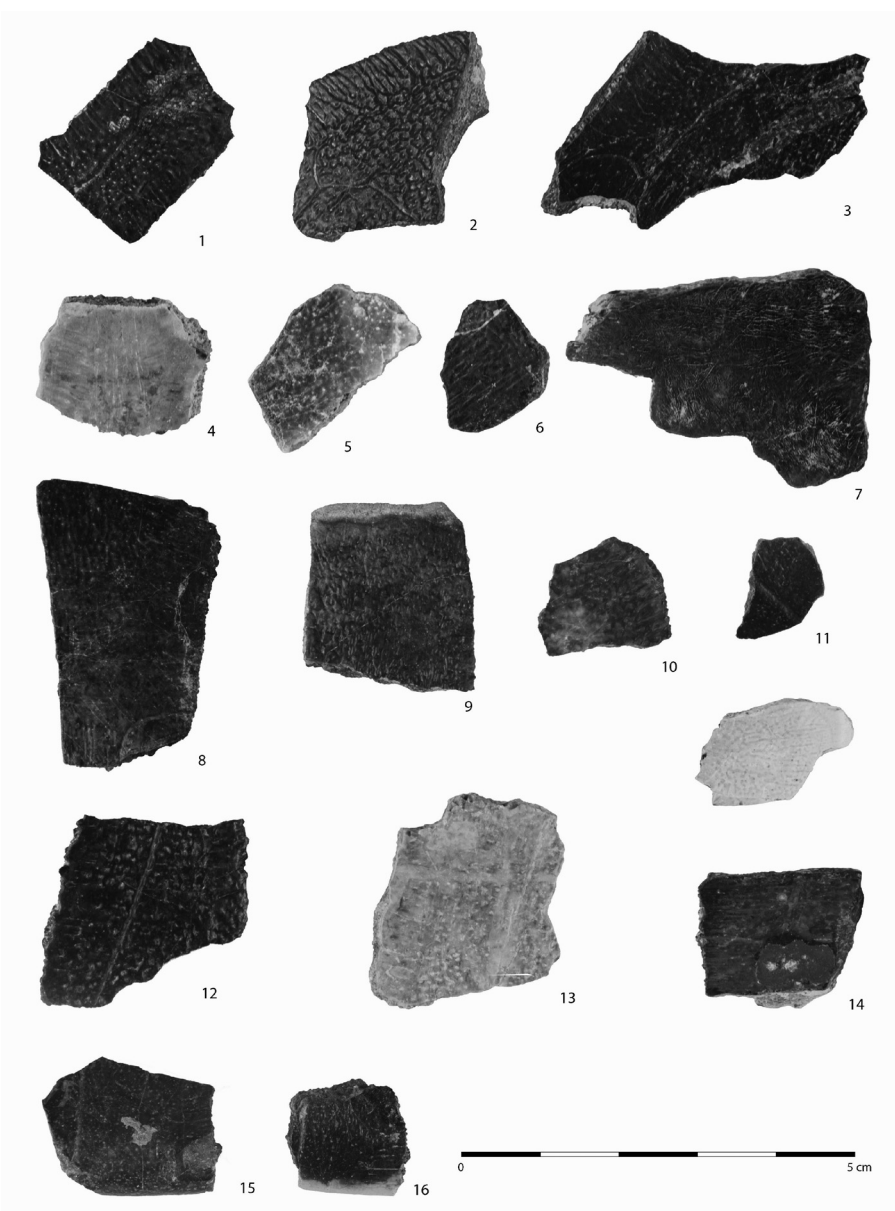


Plate 5. *Peltochelys duchastelli* Dollo, 1884 from Lourinhã in Portugal: 3+7 = pleurals I, 1-2, 4-6, 8-14 = pleural remains, 15+16 = peripheral remains. Photo Heike Künzel, TLDA. Scale bar = 5 cm.

PALAEOBIOGEOGRAPHY OF THE TRIONYCHIDS IN EUROPE

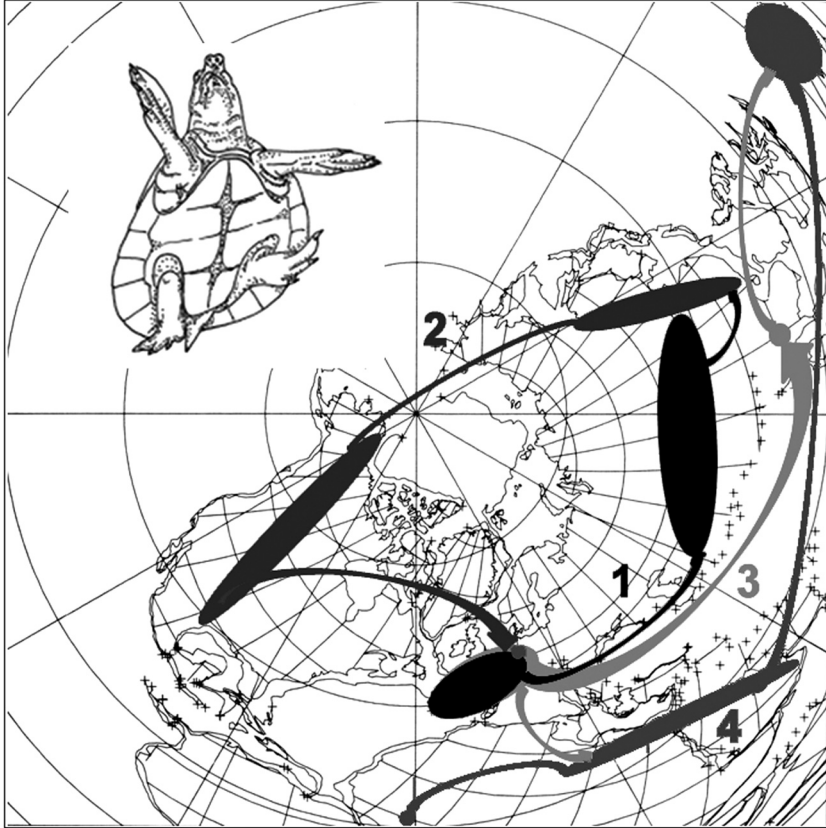


Figure 2. Palaeozoogeographical distribution of *Peltochelys duchastelli* in relation to the carettochelyids, compiled by DE BROIN (1987), JOYCE et al. (2004), and KARL et al. (2006). Legend: 1: Upper Jurassic and Lower Cretaceous *Peltochelyidae* (*Peltochelys*, *Kizylkumemys*, *Sandownia*); 2: Upper Cretaceous to Eocene *Anosteirinae* (*Anosteira*, *Pseudanosteira*); 3: Eo-Oligocene *Carettochelyinae* (*Allaeochelys*, *Burmemys*); 4: Miocene and Recent *Carettochelyinae* (*Carettochelys*).

The *Peltochelyidae* is the sister taxon of the *Carettochelyidae* and the *Trionychidae*. The family *Carettochelyidae* includes the subfamilies *Carettochelyinae* Boulenger 1887, includes only the recent genus *Carettochelys* Ramsay, 1886, furthermore the subfamily †*Anosteirinae* Lydekker, 1889, includes the extinct genera †*Anosteira* Leidy, 1871, †*Kyzylkumemys* Nesov, 1977 and *Pseudanosteira* Clark 1932. DE BROIN (1977) considers *Pseudanosteira* to be synonymous with *Anosteira*. However, the unique neural pattern suggests that it is a separate genus, as pointed out by MEYLAN (1988). KARL et al. (2006) summarized the stratigraphic and geographic occurrence of *Allaeochelys* after

LAPPARENT DE BROIN (2001). The genus with its single species *Allaeochelys parayrei* Noulet, 1867 ranged from the Early Eocene (MP 7) to the late Middle Eocene (Bartonian; MP15) in France, Belgium, England, Germany and Spain. JOYCE *et al.* (2004) described a related single peripheral plate from the Middle Miocene (MN 5) of the Hambach pit West of Cologne, Germany. The *Allaeochelys* specimen from the Oligocene described by KARL *et al.* (2006) is the first one documented at all. It connects biostratigraphically the records of the Eocene and Miocene in Central Europe (see numbers 3 and 4 within Fig. 2). Comparable materials are currently described from the Middle Eocene (MP 13-14) of Casaseca de Campeán (Corrales B) in Spain as *Allaeochelys jimenezi* Alonso Santiago & Alonso Andrés, 2005. Before that, JIMÉNEZ FUENTES (1971) described *Allaeochelys casasecai* from Spain.

DISCUSSION

According MEYLAN (1988) *Peltochelys* is the sister taxon of the Trionychia and shows a paired ventral nuchal process and 11 peripherals per side. Other primitive features are punctuate sculpturing that covers both carapace and plastron, a strongly sinuous midline sulcus on the plastron, all characteristics for the group *Adocus*, *Basilemys*, *Peltochelys*, carettochelyids and trionychids. Further characters are primitive for the Cryptodira like a complete set of epidermal scutes on carapace and plastron, two metaneurals and a complete neural row from the nuchal to the metaneural. JOYCE (2007) and STERLI (2010) listed "*Peltochelys durlstonensis* Dollo 1884", as a mixed name from *Peltochelys duchastelli* Dollo, 1884 and *Mesochelys durlstonensis* Evans & Kemp, 1975 (Walter Joyce pers. comm.).

His results are (all from JOYCE, 2007): Articulation sites between the eighth cervical vertebra and the nuchal plate have been reported for *Carettochelys insculpta* and *Peltochelys duchastelli* (Meylan, 1987). The presence of only ten pairs of peripherals is a synapomorphy for kinosternids and a synapomorphy of the clade formed by Trionychia and *Peltochelys*. Within Trionychoidea a median contact of the posterior costals was acquired independently four times: as a separate autapomorphy to *Dermatemys mawii* and *Adocus beatus* and as separate synapomorphies with the clade formed by *Kinosternon flavescens* and *Sternotherus odoratus* as well as with the clade formed by *Peltochelys* and Trionychia.

The anterior plastral lobe of *Proganochelys quenstedti*, *Kayentachelys aprix*, and most primitive pancryptodires has a set of gular scales that cover the entoplastron or parts of the epiplastra, or both. In contrast, numerous derived turtles, including *Pleurosternon bullockii*, *Peltochelys* and all known panpleurodires, only have one centrally positioned gular. A medial fusion of the gulars is an independently acquired autapomorphy for *Pleurosternon bullockii* and *Peltochelys*. Extragulars are lost in all living cryptodires, but still

occur in some taxa thought to be basal representatives of Cryptodira, such as *Adocus beatus* and *Peltochelys*. Within the context of Peter Meylan's study, *Adocus beatus*, *Basilemys variolosa*, *Zangerlia neimongolensis* and *Peltochelys* are placed along the phylogenetic stem of Trionychia. The characters that unite all known pantrionychians include reacquisition of extragulars and acquisition of anteriorly convex articulation between cervicals IV through VII. *Peltochelys* is united with the Trionychia based on two characters: the reduction of the number of peripherals from 11 to 10 pair and the medial contact of the posterior costals. This taxon diverged from all remaining pantrionychians no later than the Early Cretaceous. In contrast, according to this analysis and others, the only clade of extant Cryptodira currently hypothesized to have a lower Cretaceous representative is Pantrionychia with *Peltochelys* (JOYCE, 2007). Articulation sites between the eighth cervical vertebra and the nuchal have been reported for *Carettochelys insculpta* and *Peltochelys duchastelli* (Meylan, 1987).

Although *Peltochelys* still has quite a few original features, it has the trionychids and carettochelyids and a common feature that is likely to be interpreted as synapomorphies: the number of pairs of peripherals to ten decreased, while almost all other turtles have eleven pairs. In addition, paired ventral process of nuchal is present as in *Peltochelys*, otherwise only with the prior Carettochelyidae. Original features of *Peltochelys* on shell are a intergular and one pair of gulars, a complete set of inframarginals, big and broad plastral lobes and a sculptured with fine, punctiform pits shell surface, much like in Adocidae (MEYLAN, 1988; MEYLAN & GAFFNEY, 1989). After MEYLAN & GAFFNEY (1989) *Peltochelys* is the oldest evidence of a representative of Trionychoidea outside of Asia and argues for a Laurasian and not for an Asian origin of Trionychoidea (HIRAYAMA *et al.*, 2000). The new material supports this view and extends the stratigraphic and geographic distribution of the genus *Peltochelys* considerably. It is quite possible that the skull of *Sandownia barrisi* is related to the shells of *Peltochelys duchastelli*.

The environment of Kimmeridgian Lusitanian basin was interpreted to be lagoonal, with freshwater influx, which was periodically flooded by salt water (HELMDACH, 1971; SCHUDACK, 2000). Palynological investigations (VAN ERVE & MOHR, 1988) indicate a wooded swamp region, comparable with recent tropical mangrove forests (GLOY, 2000; MARTIN, 2000). The conditions of the Lower Saxony Cretaceous basin were more influenced by marine in the sense of a lagoon region.

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Pfeil, Munich” for the permission to use the illustrations from the Guimarota monography on plate 1, figures 1-4.

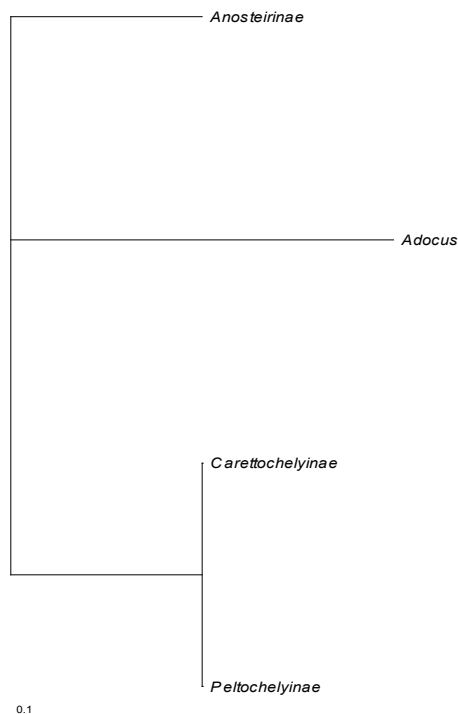


Figure 3. Simplified dendrogram of the carettochelyid soft-shelled turtles made with PARS and TREEVIEW. Used characters are 1: hard shelled (0) or soft shelled (1); 2: pleural and peripheral sulci present (0) or absent (1); 3: plastral sulci present (0) or absent (1); 4: keel elements absent (0) or present (1).

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