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NEW MATERIALS OF THE GIANT SEA TURTLE *ALLOPLEURON* (TESTUDINES: CHELONIOIDEA) FROM THE MARINE LATE CRETACEOUS OF CENTRAL EUROPE AND THE PALAEOGENE OF KAZAKHSTAN

[Nuevos ejemplares de la tortuga gigante de mar* Allopleuron *(Testudines: Chelonioidea) del Cretácico Superior marino de Europa central y del Paleógeno de Kazajistán]

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ABSTRACT: Current examinations in German collections show that several bone remains from the Late Cretaceous of northern Germany could be allocated to the highly pelagic turtle *Allopleuron* Baur, 1888 as *Allopleuron* cf. *hofmanni* (Gray, 1831). Previously *Allopleuron* was reported from the Late Cretaceous in the Netherlands and Belgium as well as from Palaeogene in North America and Germany (KARL, 2007). The latter, from the Rupelian (Early Oligocene) in Central Germany, is stratigraphically the youngest record of the genus. Additionally, a mounted skeleton from the Lutetian (early Middle Eocene, Palaeogene) in Kazakhstan is described as *Allopleuron qazaqstanense* n. sp.

Key words: Late Cretaceous, Northern Germany, Palaeogene, Kazakhstan, marine chelonioid turtle, *Allopleuron hofmanni*, *Allopleuron qazaqstanense* n. sp., palaeozoogeography.

RESUMEN: Exámenes actualizados en colecciones alemanas muestran que algunos restos óseos del Cretácico Superior del norte de Alemania podrían ser asignados a la tortuga pelágica *Allopleuron Baur*, 1888, como *Allopleuron* cf. *hofmanni* (Gray, 1831). Anteriormente se conocía *Allopleuron* en el Cretácico de Holanda y Bélgica, así como en el Paleógeno de América del Norte y Alemania (KARL, 2007). Este último, del Rupeliense (Oligoceno inferior) del centro de Alemania, es el registro estratigráfico más joven del género. Además, un esqueleto montado del Luteciense (Eoceno medio) en Kazajistán, se describe como *Allopleuron qazaqstanense* n. sp.

Palabras clave: Cretácico Superior, norte de Alemania, Paleógeno, Kazajistán, tortuga marina quelonioide, *Allopleuron hofmanni*, *Allopleuron qazaqstanense* n. sp., paleozoogeografía.

INTRODUCTION

As a result of current examinations of different fossil collections several bone remains from the Late Cretaceous of northern Germany could be more precisely allocated to the highly pelagic turtle *Allopleuron* Baur, 1888. Previously they were only determined as "marine reptiles". Up to now *Allopleuron* was reported from Late Cretaceous deposits in the Netherlands and Belgium as well as from Palaeogene sites in North America and Germany (KARL, 2007).

The most precise age and palaeoecological data of the materials from northern Germany are known for the specimens of the Misburg Formation in the region of Hanover.

MISBURG FORMATION

The base of the Misburg Formation as defined by ERNST (1963) is situated in the Lower Campanian *Offaster pilula* biozone, the top is located in the *Belemnitella minor/Nostoceras polyplocum* biozone (late Upper Campanian). Geochemistry, cyclicity, and sedimentology of the Misburg Formation are described in detail by NIEBUHR (2005, 2006, 2007; NIEBUHR *et al.*, 1997). It consists of about 18 cycles and covers a time-span of nearly 7.5 my between 82 and 74.5 my (OGG *et al.*, 2004). About four long cycles are allocated to the Lower Campanian, 12 to 13 cycles are of early Upper Campanian age, and a single long cycle belongs to the late Upper Campanian. The highest water level was present in the lowermost Upper Campanian, after the *Belemnitella mucronata* transgression (latest Lower Campanian). The sedimentation rates

decrease after the following maximum water level and finish completely towards the *Nostoceras polyplocum* regression and the transition into the Ahlten Formation. The lithological change coincides with a distinct change from the greyish colours of the Misburg Formation towards the yellowish-beige colours of the Ahlten Formation (NIEBUHR *et al*., 1997).

The Misburg Formation yields numerous invertebrate fossils as for example Hexactinellida, Bivalvia, Ammonoidea, Belemnitida, Brachiopoda, Echinoidea, as well as micro-and nannofossils like coccolites, calcispheres, Foraminiferida, Ostracoda, Bryozoa, and microflora. Vertebrates are barely known. This is the reason why the *Allopleuron*-bearing rock is of special importance.

The hemipelagic sediments of an open epicontinental sea with a water depth of 70-100 m are in concordance with the occurrence of marine turtles like *Allopleuron hofmanni* (Gray, 1831) in the Misburg Formation.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758

Infraorder Cryptodira Cope, 1868

Superfamily Chelonioidea Baur, 1893

Family Cheloniidae Gray, 1825

Subfamily Allopleuroninae Weems, 1988

According to WEEMS (1988) the Allopleuroninae can be defined as large, extremely thin-shelled, strongly fontanellized sea turtles with strongly reduced, anteroposteriorly elongate plastral elements, a deeply excavated nuchal element, but without dermochelyid epithecal shell.

Genus *Allopleuron* Baur, 1888

TYPE SPECIES: *Allopleuron hofmanni* (Gray, 1831), Upper Cretaceous: Maastrichtian, Pietersberg near Maastricht, South Limburg, Netherlands.

CHARACTERS: LYDEKKER (1889) induced to refer to this species OWEN'S (1851) material of *Chelone camperi* because of their size and shape, and in particular their carinate structure. The carapace is long and narrow, with deeply emarginate nuchal; the neurals are comparatively short and wide, with type 6B of hexagonals (KARL & TICHY, 2005), and with a strongly knoblike keel. The pleurals are long antero-posteriorly, extending only a short distance downwards to the slender and well distinct ribs. The peripherals are long, the posterior ones have a free entire border. The skull has a short and wide palate and a broad mandible with short and flat symphysis, but without distinct projection at the posterior border of the alveolar surface. The typical humerus morphology is already characterized by HIRAYAMA (1995).

1

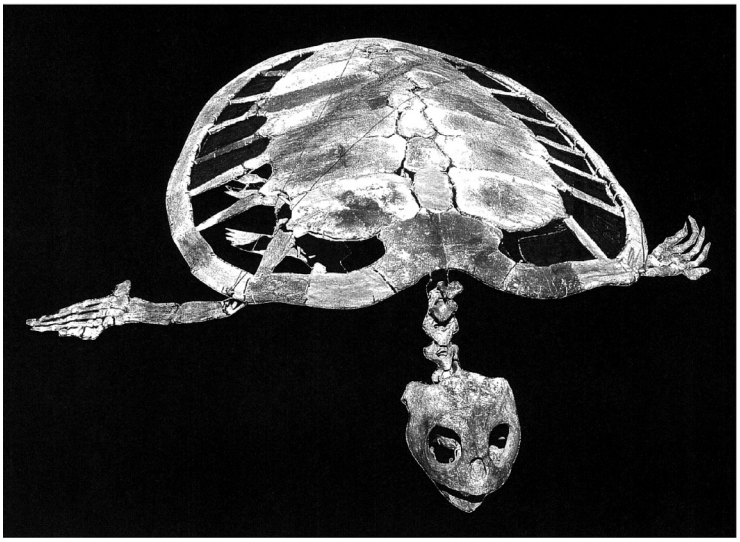

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Plate 1.1: Allopleuron hofmanni *(Gray, 1831), Upper Cretaceous*: *Maastrichtian, St. Pietersberg, Maastricht, South Limburg, Netherlands, Maastricht specimen NHMM 000001, exhibition, Natuurhistorisch Museum Maastricht, described by* WINKLER *(1869: 43-49), see also* MULDER *(1996: fig. 3), width of the carapace = 109 cm. Copyright Centraal Archief DSM Heerlen; 2:* Allopleuron qazaqstanense *n. sp., Middle Eocene*: *Lutetian, Kazakhstan, mounted and restored skeleton, exhibition, RhinoPolis Museum, Gannat, France. Photo and mounting by Andreas Haenel, Minden.*

The systematic position of the genus was discussed several times, for example by GAFFNEY & MEYLAN (1988), HIRAYAMA (1995), KARL (2002, 2007), KUHN (1964), LAPPARENT DE BROIN (2001), MLYNARSKI (1976) and MULDER (2003). Certain remains of sea turtles from the Campanian of Polunino 2 (Russia) are similar to *Allopleuron* by (i) the lack of a prefrontal-postorbital contact, (ii) the presence of an interdigitating contact between costals and neurals, (iii) the loss of a suprapygal-pygal contact, (iv) the reduction of horn sulci, and (v) the possible development of the secondary bony palate as indicated by the rather long dentary symphysis (AVERIANOV & YERKOV, 2004).

SYNONYMS: See KUHN (1964), MULDER (2003), and KARL (2007).

FURTHER SPECIES:

(i) *Allopleuron insulare* (Cope, 1872), Palaeocene, Virginia (USA) and Eocene, New Jersey (USA);

(ii) *A. lipsiense* Karl, 2007, Early Oligocene (Rupelian), Weißelster Basin, Saxony (Germany);

(iii) *A. qazaqstanense* n. sp., Eocene (Lutetian), Kazakhstan.

Bibliography: Redescribed original materials from the Upper Cretaceous (Maastrichtian) of the Pietersberg near Maastricht, South Limburg, Netherlands, see MULDER (2003).

ADDITIONAL MATERIAL OF *ALLOPLEURON HOFMANNI* FROM THE TYPE REGION: Fragment of a scapula on a detritic marlaceous limestone block (plate 2, figure 1).

LOCALITY: ENCI-Maastricht, South Limburg, Netherlands.

AGE: Upper Cretaceous: Maastrichtian.

REMARKS: The new scapula from the type region of *Allopleuron hofmanni* was bought by Martin Röper, Solnhofen, Germany (1978) from Dr. F. Krantz, Rheinisches Mineralien-Kontor KG, Bonn, Germany.

***Allopleuron* cf. *hofmanni* (Gray, 1831)**

NEW LATE CRETACEOUS MATERIALS FROM NORTHERN GERMANY:

(I) HILDESHEIM COLLECTION, RMH = Roemer- und Pelizaeus-Museum, Hildesheim, Lower Saxony, Germany, without catalogue number: (i) proximate fragment of scapula, labelled: 1986, "MK"; (ii) distal fragment of coracoid, originally labelled: "*Cimoliosaurus*", U. Sen. [= "Upper Senon"], Granul. Kr. [= "Granulaten-Kreide"], 1903 (plate 2, figures 2-4).

LOCALITY: Braunschweig-Broitzem (52° 14' N, 10° 29' E), possibly the same locality from where BEURLEN (1928) described "*Hoplitocarcinus joh.-böhmi* n. sp." [= *Homolopsis joh-boehmi* (Beurlen, 1928)]: at that time the brickyard quarry H. Bautler & Co. "Untersenon (Granulatenschichten)".

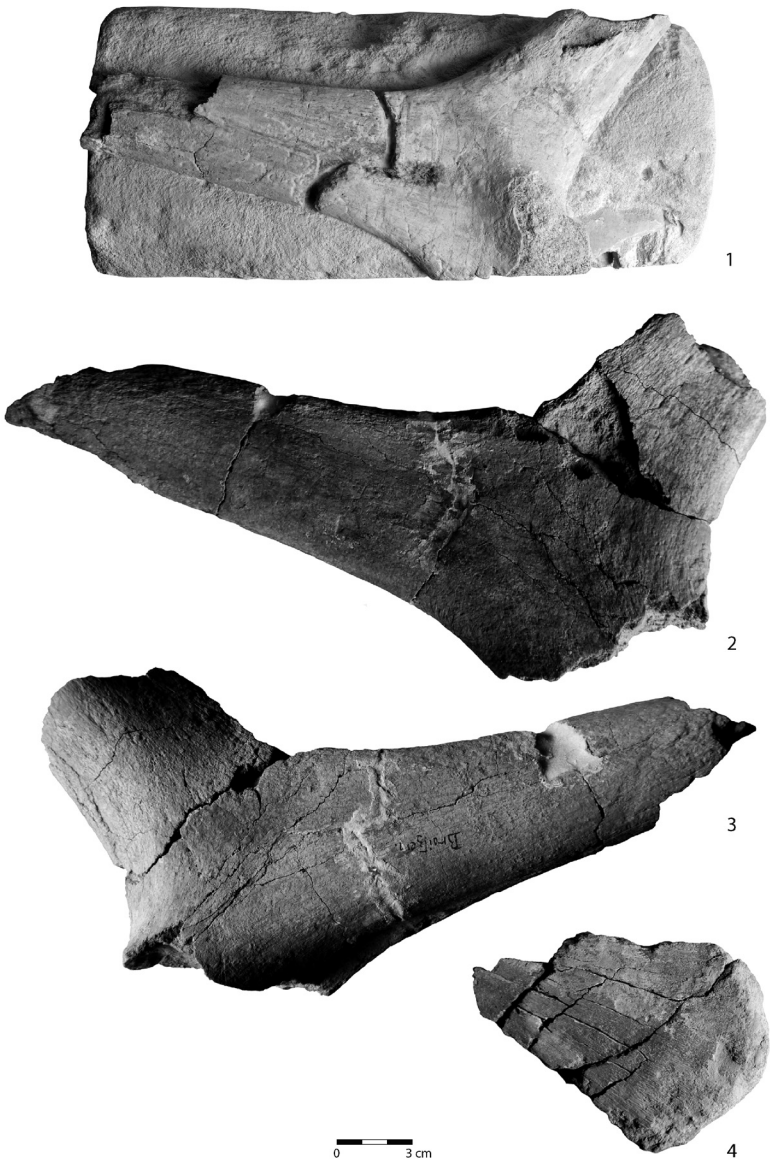

Plate 2. 1: Allopleuron hofmanni *(Gray, 1831), Upper Cretaceous*: *Maastrichtian, St. Pietersberg, Maastricht, Major Müller Museum, Solnhofen, Bavaria, Germany, without n.º, proximate fragment of scapula; 2-3:* Allopleuron *cf.* hofmanni *(Gray, 1831), Upper Cretaceous*: *Turonian, Braunschweig-Broitzem, Roemer-und Pelizaeus-Museum Hildesheim, without number, 2-3 = proximate fragment of scapula 4 = distal fragment of coracoid; photographs of 2-3: Dr Jürgen Vespermann, Hildesheim, with Panasonic Lumix G3.*

AGE: Oerlinghausen Formation ("Lamarcki-Pläner" of the older literature), Turonian, Litholex ID 2008063, former "Untersenon", Upper Cretaceous.

REMARKS: *Cimoliasaurus* Leidy, 1851 (Plesiosauria, Elasmosauridae, alternative spelling *Cimoliosaurus*, occurs in the Cretaceous in Canada (Northwest Territories), United States (Alabama, Maryland, Montana, New Jersey and Texas), Great Britain, Switzerland, Russia, Australia, and New Zealand. The characters of the present material are identical with those of the specimens from the type locality of *Allopleuron hofmanni* (Gray, 1831), also see MULDER (2003: plate 41).

(II) FRERICHS COLLECTION: Fragment of pleural (plate 3, figure 2), collection of Udo Frerichs, Langenhagen, Lower Saxony, Germany.

LOCALITY: Quarry "Heidelberg Nord" (former "Teutonia Nord") of "Heidelberg Zement" in Hannover-Misburg, Lower Saxony, Germany.

AGE: *minor-polyplocum* biozone, early Upper Campanian, Upper Cretaceous.

REMARKS: The fossil is associated on the same limestone block with several fragmentary bones of mosasaurs and probably plesiosaurs.

(III) SCHOLZ COLLECTION: Radius, ulna, four carpals, metacarpal I, phalanx 2/IV (plate 3, figure 1), collection of Hans-Peter Scholz, Wolfsburg-Fallersleben, Lower Saxony, Germany.

LOCALITY: Sehnde-Höver, SE Hanover, Lower Saxony, Germany.

AGE: Lower Campanian, Upper Cretaceous.

REMARKS: The fossil was previously regarded as sea turtle, marine reptile or even terrestrial vertebrate (FRERICHS, 2006a). A humerus of *Clidastes* was reported from the same locality (FRERICHS, 2006b). These single bones completely fit within a hand of *Allopleuron* (see MULDER, 2003: plate 45, figure 3). In sea turtles these bones show sexual dimorphism and morphological changes during the ontogeny (WYNEKEN, 2001).

Allopleuron qazaqstanense **n. sp.**

SYNONYMS: None, the specimen was only figured in ANONYMUS (2001).

DIAGNOSIS: A new species of *Allopleuron* with the following characters: No keel elements present. Very large peripheral fontanelles in the carapace; free costae not longer than pleural plate; ridge of free costae absent; lateral peripherals not as strong 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 (MONOTYPIC): Mounted skeleton in the excavation of RhinoPolis Museum Gannat, France (plate 1, figure 2).

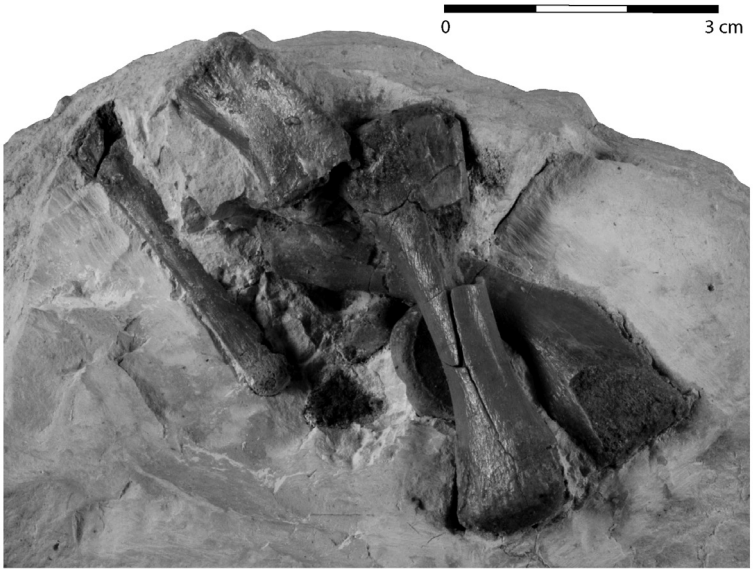

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Plate 3. Allopleuron *cf*. hofmanni *(Gray, 1831). 1: Upper Cretaceous*: *early Upper Campanian, Hannover-Misburg, Frerichs collection, Langenhagen, distal fragment of pleural; 2: Upper Cretaceous*: *Lower Campanian, Sehnde-Höver, Scholz collection, Wolfsburg-Fallersleben, radius, ulna, metacarpal 1, phalanx 2/IV*.

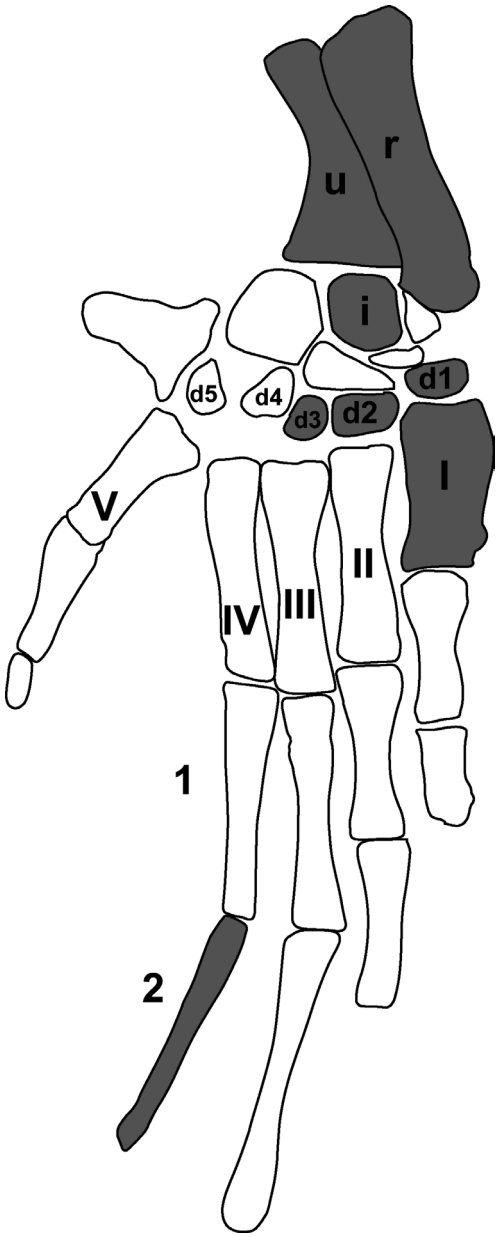

Figure 1. Manus of Allopleuron hofmanni *(adapted from MULDER, 2003) with red marked bone elements preserved from Sehnde-Höver, SE Hanover, Lower Saxony, Germany. Compare with plate 3, figure 2; r = radius, u = ulna, I = intermedium, d1-5 = distal carpals 1-5, I-V = metacarpals 1-5.*

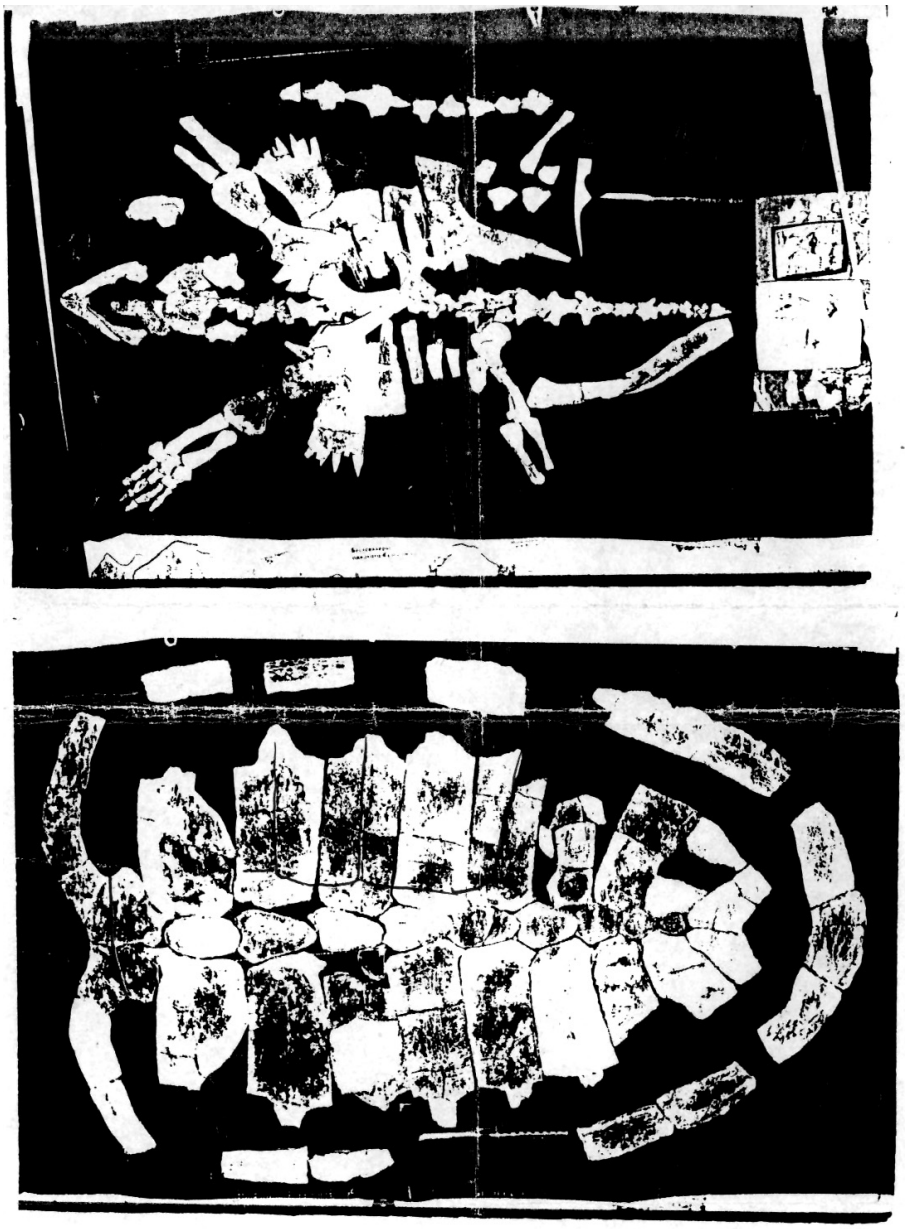

Figure 2. Allopleuron qazaqstanense *n. sp., Middle Eocene*: *Lutetian, Kazakhstan, sketch of the preserved parts of the skeleton (provided by Andreas Haenel, Minden) before preparation and restoration.*

PRESERVATION: Most parts of carapace, internal skeleton, and some skull remains are present (figure 1). Parts of skull, shell and the extremities are reconstructed. Length of carapace = 190 cm. Pygal and some peripherals are lost. Nuchal, neurals and nearly all pleurals are preserved.

TYPE LOCALITY: Kazakhstan, no detailed locality indicated.

AGE: Lutetian (40.4-48.6 my), Middle Eocene.

ETYMOLOGY: *qazaqstanensis* (m), *-ensis* (f), *-ense* (n), adj., from *Qazaqstan* = Kazakhstan (official name: the Republic of Kazakhstan), transcontinental country in Eastern Europe and Central Asia.

CHARACTER ANALYSIS IN *ALLOPLEURON*: In accordance with the conditions in *Allopleuron insulare* the character analysis is restricted to a few special characters. These are:

(1) presence or absence of knoblike keels [present = 0, absent = 1];

(2) relative length of anterior peripherals [long = 0, short = 1];

(3) degree of reduction of the first peripheral, contact of peripheral II and nuchal [absent = 0, present = 1];

(4) type of hexagonal neurals [6A = 0, 6B = 1];

(5) ridge of free costal [present = 0, absent = 1];

(6) contact peripheral/pleural [present = 0, absent = 1 (figure 1)].

The character differentiation with DOLMOVE (Interactive Dollo and Polymorphism Parsimony by Joseph FELSENSTEIN, 1986a) shows a simple tree: (*Allopleuron lipsiense*, (*Allopleuron qazaqstanense*, (*Allopleuron insulare*, *Allopleuron hofmanni*))). The differentiation with PARS (Discrete character parsimony algorithm, version 3.6a3 by Joseph FELSENSTEIN, 1986b) corresponds with DOLMOVE, but shows a larger distance between *Allopleuron lipsiense* + *A. qazaqstanense* n. sp. and *A.* + *A. hofmanni*.

Thus there are two most parsimonious trees:

I: ((*Allopleuron lipsiense*: 1.50, *A. qazaqstanense*: 1.50): 1.00, *A. insulare*: 1.50, *A. hofmanni*: 0.50) [0.5000];

II: (*Allopleuron lipsiense*: 1.50, (*A. qazaqstanense*: 1.50, *A. insulare*: 1.50): 1.00, *A. hofmanni*: 0.50) [0.5000].

Both, DOLMOVE and PARS, confirm a clear specific independence of *Allopleuron qazaqstanense* n. sp.:

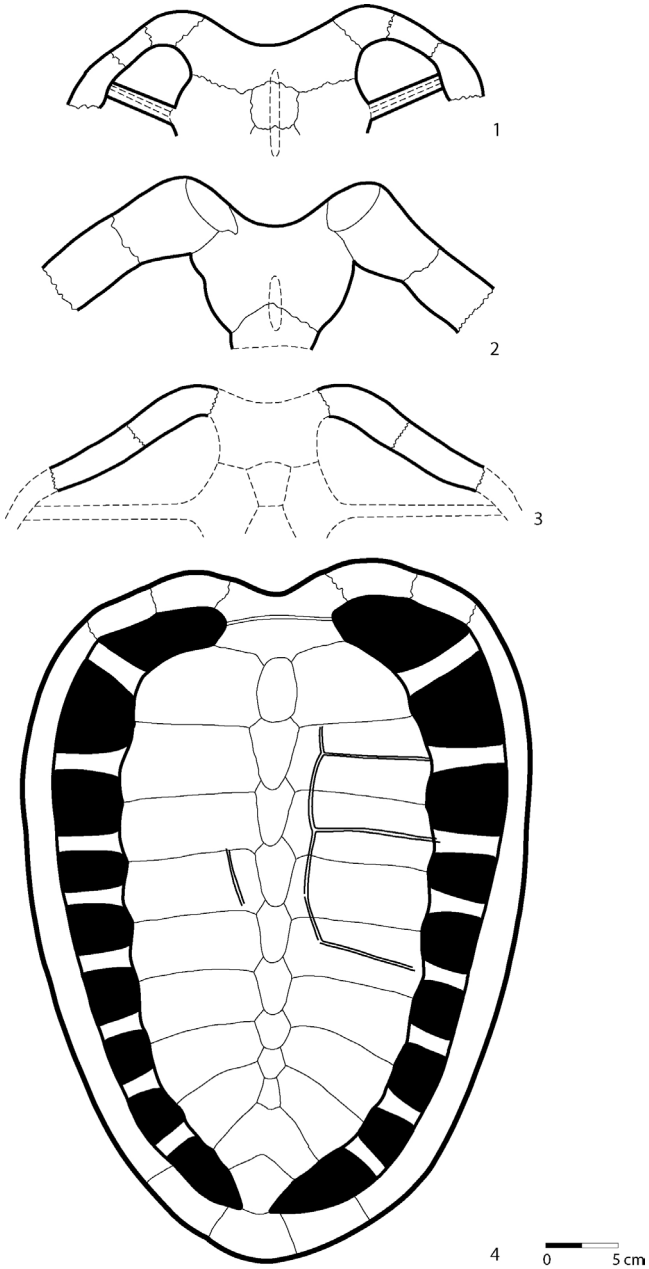

Figure 3. 1-3: Ink sketches of the anterior carapace region; 1: Allopleuron hofmanni*; 2:* A. insulare*; 3:* A. lipsiense*; 4: carapace reconstruction of* Allopleuron qazaqstanense *n. sp., based upon the preserved material (by H.-V. KARL and Heike KÜNZEL, TLDA).*

Tree 1 requires a total of 6.000 (figure 3a)

BETWEEN	AND	LENGTH
1	2	1.00
2	*Allopleuron lipsiense*	1.50
2	*Allopleuron qazaqstanense* n. sp.	1.50
1	*Allopleuron insulare*	1.50
1	*Allopleuron hofmanni*	0.50

Tree 2 also requires a total of 6.000 (figure 3b)

BETWEEN	AND	LENGTH
1	*Allopleuron lipsiense*	1.50
1	2	1.00
2	*Allopleuron qazaqstanense* n. sp.	1.50
2	*Allopleuron insulare*	1.50
1	*Allopleuron hofmanni*	0.50

DISCUSSION

The genus *Allopleuron* covers hitherto a stratigraphical range from the Upper Cretaceous (Cenomanian) to the Palaeogene (Lower Oligocene: Rupelian). It was widespread on the southern continental shelf in the whole Laurasian-Holarctic region which was possibly the breeding area of the species of this highly pelagic sea turtle genus.

The geographical and stratigraphical distribution of *Allopleuron hofmanni* was previously restricted to the Maastrichtian type area in the southeastern part of the Netherlands and northeastern Belgium. In the present paper we add three stratigraphically older Upper Cretaceous localities in Lower Saxony, northern Germany: (i) Braunschweig-Broitzem (Turonian), (ii) Sehnde-Höver (Lower Campanian), and (iii) Hannover-Misburg (early Upper Campanian). Other fossils previously named as *Allopleuron* or *A. hofmanni* from Upper Cretaceous and early Palaeogene deposits in North and West Europe have to be removed:

(i) As shown by KARL & LINDOW (2011), the Copenhagen (Denmark) material is not comparable with the genus and species.

(ii) The Kent (Great Britain) material was previously determined as "*Chelone camperi* Gray, 1831" and later regarded as a junior synonym of *A. hofmanni* by OWEN (1851). LYDEKKER (1889) transferred it to *Puppigerus* Cope, 1870 and thus named it *P. camperi*. Because of this confusion Eric Mulder proposed to avoid the name "*Chelone camperi*" (pers. inf.).

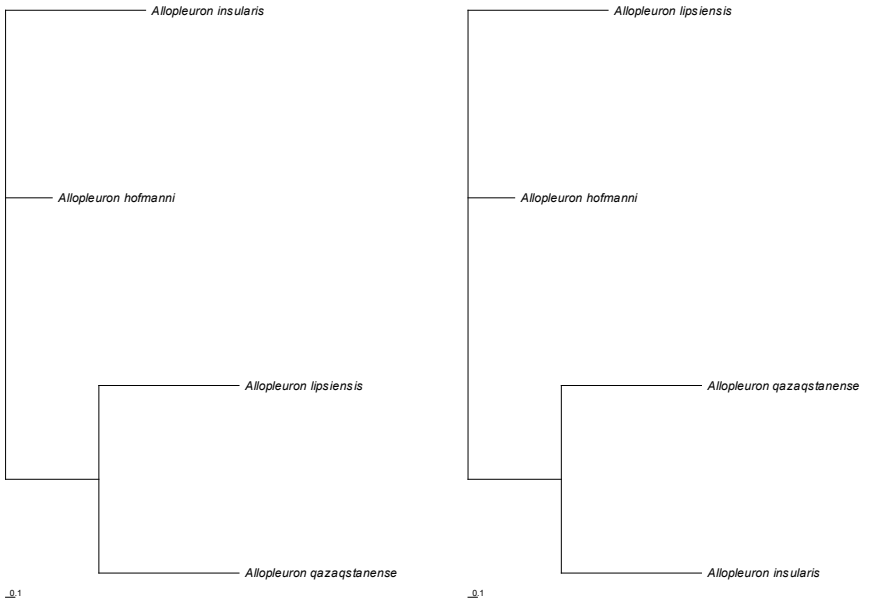

Figure 4a-b. Two most parsimonious trees of the species of Allopleuron *found by PARS, Discrete character parsimony algorithm, version 3.6a3 by Joseph* FELSENSTEIN *(1986b), prepared by using TreeView©Roderic Page.* Allopleuron hofmanni *as outgroup.*

In the Palaeocene/Eocene times *Allopleuron* obtained a certain evolutionary peak with the two species *A. insulare* and *A. qazaqstanense* n. sp. The youngest species is *A. lipsiense* Karl, 2007 from the Early Oligocene (Rupelian) in Germany.

Like Eocene whales and Recent *Dermochelys*, *Allopleuron* had surely a cosmopolitan marine distribution, but was possibly not yet adapted to gigantothermy in the Upper Cretaceous (ALBRIGHT *et al.*, 2003):

The extant leatherback tortoise *Dermochelys coriacea* has a rather constant body temperature of about 25 °C to 26 °C. In cold water of 7.5 °C the animals can hold their body temperature of 25,5 °C for 24 hours. This species is also able for heat exchange to prevent overheating, and with its extensive subcutaneous fat it is well isolated. This permits it to migrate from tropical seas (where it breeds) into temperate areas (where it feeds on jellyfish). These special adaptations enables such large reptiles to maintain a constant and relatively high body temperature (= gigantothermy) and high metabolic rates. Such characters are necessary for large animals which used to move through different climate zones.

Fossil remains of *Dermochelys* are not known from older deposits than Pliocene/early Pleistocene in the USA (Lee Creek Mine, Beaufort County, North Carolina), but are only documented by two dermal ossicles (USNM 358306, USNM

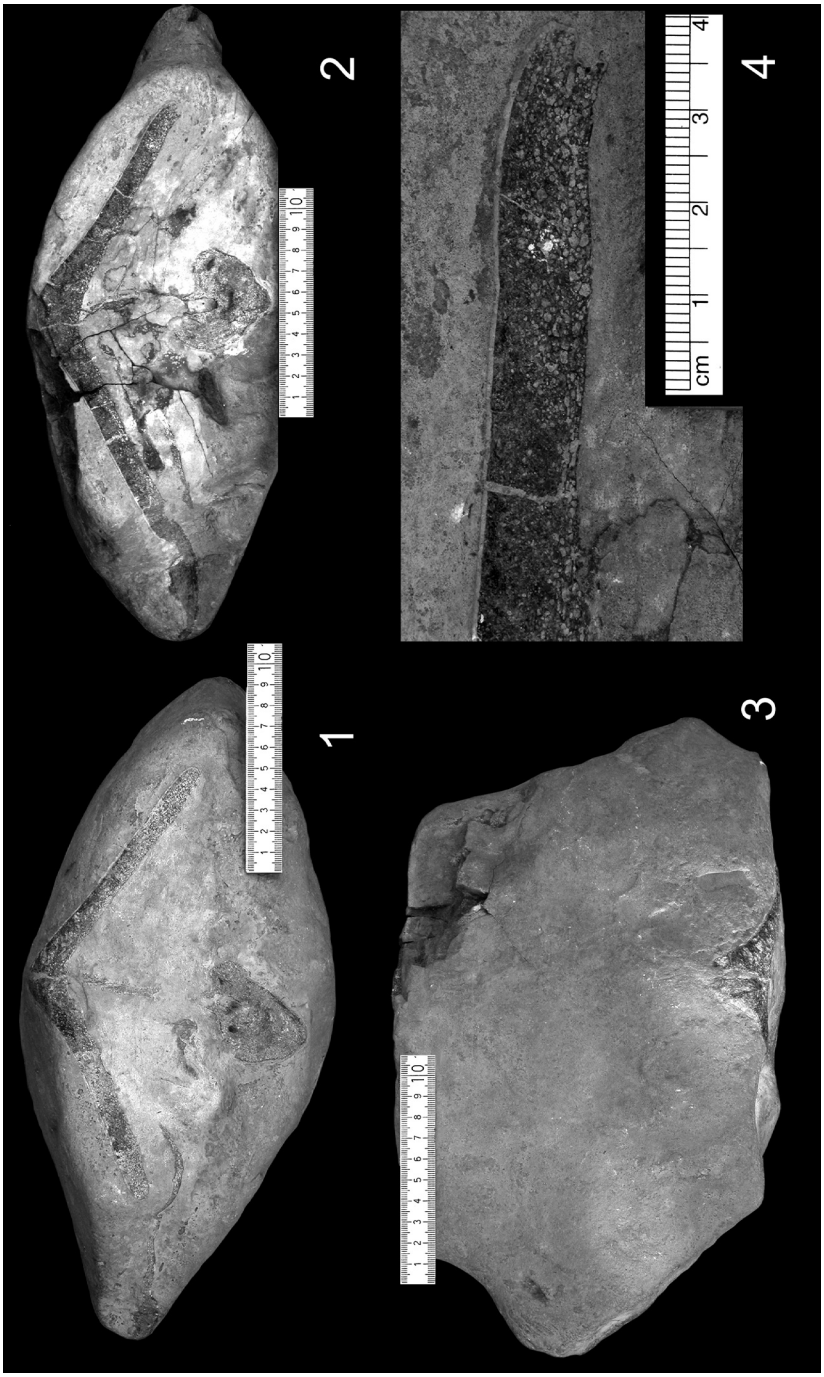

Plate 4. Testudines fam. indet., fragment of carapace in phosphorite nodule, Early Eocene (Moler Member, "Zementstein" of Greifswalder Oie type), Greifswalder Oie E Rügen, Mecklenburg-Vorpommern, Baltic Sea, Greifswald collection. Photograph: Dr Jörg Ansorge, Greifswald.

3583308). The evolution of the Dermochelyidae (= leatherback tortoises) with their homothermy adaptations may be therefore connected with the beginning of cooler temperatures in the Pliocene or already in the late Miocene. At this time another leatherback genus, *Psephophorus*, still lived in the region of Denmark in the North Sea, but was most probably restricted to a few individuals.

The reason for the disappearance of *Allopleuron* during the Oligocene may be the lack of such homothermy adaptations as mentioned above.

DOUBTFUL SPECIMENS, PARTIALLY REMOVED FROM *ALLOPLEURON*

I: GREIFSWALD COLLECTION

Fragment of carapace, phosphorite nodule; Early Eocene (Moler Member, "Zementstein", Greifswalder Oie type); Greifswalder Oie E Rügen, Mecklenburg-Vorpommern, Baltic Sea, Germany; collection of Greifswald University:

OBST & ANSORGE (2010) regarded the fossil in question as a remnant of a tortoise. Because of the strongly carinate shape of the carapace and the short side areas a placement within *Allopleuron* cannot be excluded, but is less probable due to the following characters: (i) distribution of the Substantia compacta, and (ii) the lack of sutures of the bone plates in those areas as usual in turtles. Furthermore the vertebrae and the ribs are not connected with the carapace (plate 4). Maybe the fossil belongs to the Dermochelyidae. This family is documented by *Eosphargis breineri* Nielsen, 1959 from equivalent strata in Denmark (NIELSEN, 1959, 1963).

II: FRITZ VAN DER HOCHT COLLECTION, KERPEN (RHINELAND; GERMANY)

Fragment of carapace (plate 5, figure 1), phosphorite nodule (24 x 17 x 7 cm); Late Oligocene (Chattian, Grafenberg-Schichten); gravel pit of Rheinische Kieswerke A. Rottmann, Duisburg-Rheinhausen, North Rhine-Westphalia, Germany:

Before preparation the nodule had a very hard sandy iron surface, including several steinkerne and moulds of Late Oligocene molluscs and echinids. The fracture shows parts of a carapace with a thickness up to 15 mm. Here a placement within *Allopleuron* is possible, too, because of the relation of relatively week plates compared with the size of the animal. The other known Palaeogene tortoises in Central Europe (*Tasbacka*, *Rupelchelys*, and *Glarichelys*) differ distinctly in this character. The neurals are not carinate like in the Upper Cretaceous *Allopleuron hofmanni* but flat like in the Rupelian *A. lipsiense*. For a definite determination a more detailed preparation would be necessary. For comparison of the bone histology of the specimen (pl. 5, fig. 2) with *Rupelchelys breitkreutzi* Scheyer, 2007 see SCHEYER (2007).

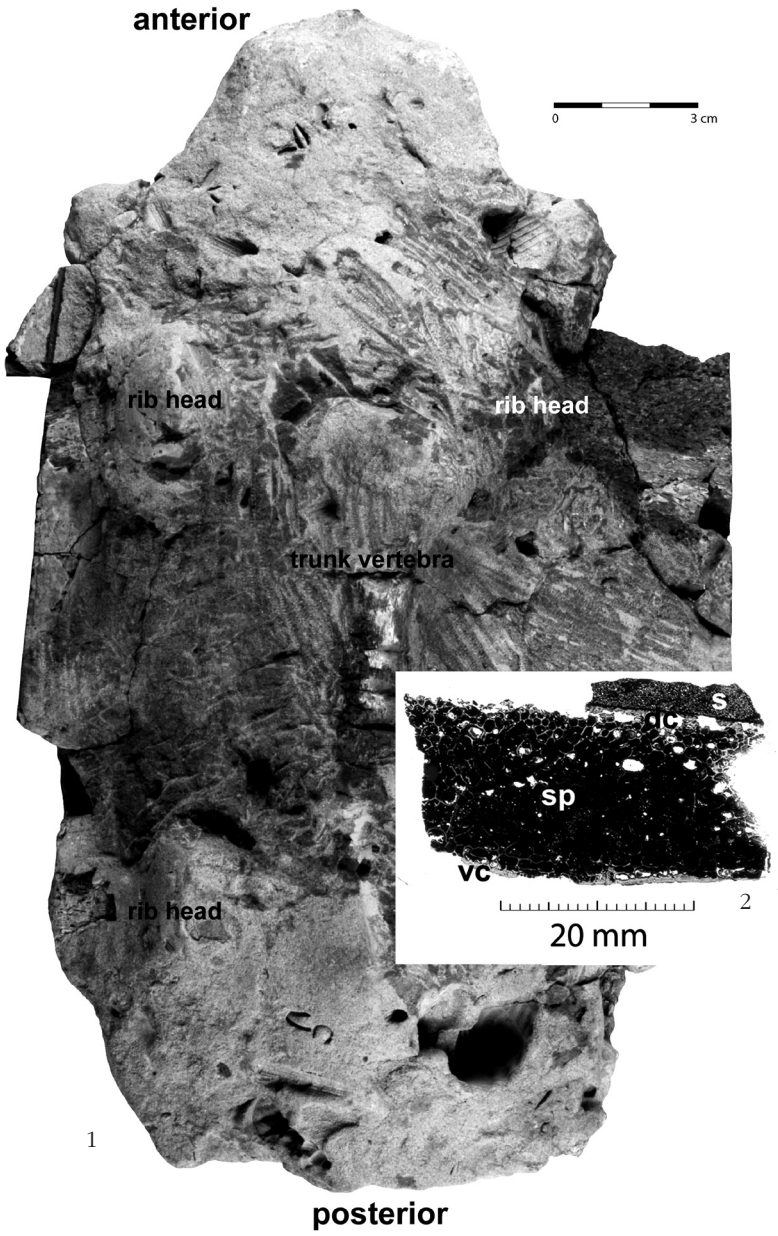

Plate 5. Allopleuron*? sp., fragment of carapace in phosphorite nodule, Late Oligocene: Chattian (Grafenberg-Schichten), gravel pit of Rheinische Kieswerke A. Rottmann, Duisburg-Rheinhausen, van der Hocht collection, Kerpen, Rhineland, 1: visceral view; 2: parasagittal thin section of pleural.*

System	Series	Stage	Age (mya)	Europe	N-America	Locality	Reference
Palaeogene	Oligocene	Chattian	28.4-23.03				
		Rupelian	33.9-28.4	*Allopleuron lipsiensis*		Espenhain and Böhlen near Leipzig, Germany	1
	Eocene	Priabonian	37.2-33.9				
		Bartonian	40.4-37.2				
		Lutetian	48.6-40.4	*Allopleuron qazaqstanense*		Kazakhstan, transcontinental country in Eastern Europe and Central Asia	11
		Ypresian	55.8-48.6		*Allopleuron insularis*	Monmouth county, New Jersey, USA	2
	Palaeocene	Thanetian	58.7-55.8			Stafford county, Virginia, USA	3
		Seelandian	61.1-58.7				
		Danian	65.5-61.1				
Cretaceous	Upper Cretaceous	Maastrichtian	70.6-65.5	*Allopleuron hofmanni*		Maastricht, Netherlands Brabant, Belgium	4
		Campanian	83.5-70.6	*Allopleuron* cf. *hofmanni* *Allopleuron* sp.		Hanover-Misburg, Germany Polunino 2, Volgograd region, Russia	5 6
		Santonian	85.8-83.5	*Allopleuron hofmanni*		Near Vitoria, Alava Province, Spanish Basque country, Spain	7
		Coniacian	88.6-85.8				
		Turonian	93.6-88.6	*Allopleuron* cf. *hofmanni* *Allopleuron hofmanni*		Braunschweig-Broitzem, Germany Montrichard, Loire et Cher, Loire Valley, France	8 9
		Cenomanian	99.6-93.6	*Allopleuron hofmanni*		Petreval district, Seine-Maritime, Normandy, France	10
	Lower Cretaceous	Albian	112-99.6				
		Aptian	125-112				
		Barremian	130-125				
		Hauterivian	133.9-130				
		Valanginian	140.2-133.9				
		Berriasian	145.5-140.2				

Figure 5. Stratigraphical distribution of Allopleuron*, based upon* Karl *(2007),* Moody *(1993) and the new results.*

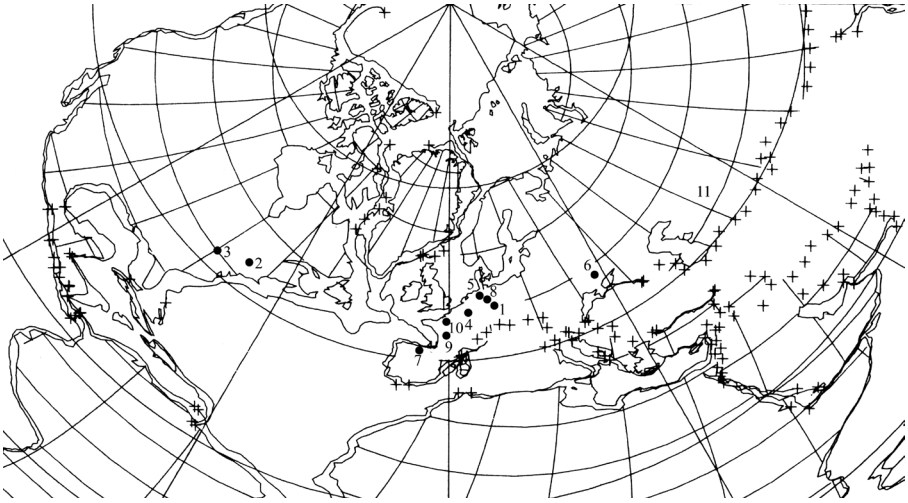

Plate 6. Map of the distribution of Allopleuron*, based upon* SMITH, HURLEY & BRIDEN *(1982).*

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