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New carettochelyine turtle occurrence from the Oligocene in Germany and its palaeozoogeographic importance

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Abstract: A new specimen of a Paleogene carettochelyine turtle from a locality in Germany is described and determined as *Allaeochelys parayrei* NOULET, 1867. It was discovered in Late Oligocene (Chattian) sediments of the Elbe-bank near Dessau. The new record enlarges the palaeozoogeographic distribution of this species.

Key words: Chelonii, Trionychia, Carettochelyinae, *Allaeochelys parayrei* NOULET, 1867, systematics, palaeozoogeography.

Resumen: Se describe un nuevo hallazgo de una tortuga caretoquelínida de una localidad en Alemania. El fósil, determinado como *Allaeochelys parayrei* NOULET, 1967, se descubrió en sedimentos del Oligoceno tardío (Chatiano) de la ribera del río Elbe cerca de la ciudad de Dessau. El nuevo registro amplía la distribución paleozoogeográfica de esta especie.

Palabras clave: Chelonii, Trionychia, Carettochelyinae, *Allaeochelys parayrei* NOULET, 1867, sistemática, paleozoogeografía.

Kurzfassung: Ein neuer Fund einer carettochelyinen Schildkröte aus dem Paläogen (Alt-Tertiär) von einer Fundstelle in Deutschland wird beschrieben und bestimmt als *Allaeochelys parayrei* NOULET, 1867. Der Fund stammt aus Schichten des Ober-Oligozän (Chattium) des Hohen Elbe-Ufers bei Dessau. Der neue Nachweis vergrößert die paläozoogeographische Verbreitung dieser Art.

Schlüsselwörter: Chelonii, Trionychia, Carettochelyinae, *Allaeochelys parayrei* NOULET, 1867, Systematik, Paläozoographie.

1 Introduction

Soft-shelled turtles (Trionychoidea) are known from Paleogene deposits in Germany for a long time (KARL, 1998). They have been reported for example from the Eocene of the famous Messel maar near Darmstadt (KELLER & SCHAAL, 1988) as well as from the Eckfeld maar in the Eifel Mountains (GRÖNING & BRAUCKMANN, 1996) and from the "Geiseltal" near Halle (HAUBOLD, 1983).

Among the most important and/or abundant genera are *Trionyx* GEOFFROY SAINT-HILAIRE, 1809, *Rafetoides* KARL, 1998 and *Allaeochelys* NOULET, 1867.

The first two mentioned genera are typical soft-shelled turtles (Trionychidae BELL, 1828) with strongly reduced carapaces. The most ancient member of the Trionychidae is the recently described *Sandow-*

nia harrisi MEYLAN et al., 2002 from the Lower Cretaceous of the Isle of Wight, England. During the Tertiary they were spread out over nearly all continents whereas Recent trionychids are restricted to warmer regions and are no more present in Europe. The animals are largely aquatic; they leave the water only when the females deposit their eggs.

Allaeochelys of the family Carettochelyidae BOULENGER, 1887 belongs to an extinct group of soft-shelled turtles which existed from the Paleogene to the Neogene in North America, Europe and Asia. The carapace of this group is evidently less reduced than within the Trionychidae. Next living relative is *Carettochelys insculpta* RAMSEY, 1886 of New Guinea and a rather small area in the Northern Territory in Australia, where the latter occurrence was discovered not before 1969. This species lives mainly in large rivers and lagoons.

Up to now, the definition of species in Paleogene soft-shelled turtles is not quite clear.

According to WALKER & MOODY (1985), *Eurycephalochelys* is a valid genus from the Lower Eocene of England. The characters of its skull differ clearly from those of *Rafetoides* and *Trionyx*.

A detailed palaeozoogeographic analysis of the related trionychine taxa was published by KARL (1999).

Further genera related to the Anosteirinae are *Pseudanosteira* LEIDY, 1931 from the Eocene (Uintan; fig. 2 - centre) and *Kizylkumemys* NESSOV, 1977 from the Late Cretaceous (Cenomanian) of Central Asia (Karakalpakia). 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).

Kizylkumemys NESSOV, 1977 is the most ancient definite genus of the Carettochelyidae. It is characterized by narrow plastral lobes and a distinctly marked ridge on the carapace. Like juvenile individuals of the Recent *Carettochelys insculpta* RAMSAY, 1886, the Anosteirinae (*Kizylkumemys*, *Anosteira*, *Pseudanosteira*) share one or more spines on the dorsal ridge which originate from bony neurals. Furthermore, the furrows of the scutes are retained in the adults; but they reach only a length of approximately 15 to 20 cm. Within the Carettochelyinae BOULENGER, 1887 with the genera *Carettochelys*, *Allaeochelys*, *Burmemyx* HUTCHISON et al. 2004 and *Chorlakkichelys* DE BROIN, 1987, the scutes of the adults are completely reduced; they are growing to a remarkable carapace length up to 50 cm (DANILOV, 2005).

2 Terminology

The Carettochelyidae include the Carettochelyinae (with the genera *Allaeochelys* and *Carettochelys*) as well as their adelphotaxon *Anosteira*. This means: Carettochelyidae = (*Anosteira* (fig. 2 - top, fig. 3) + (Carettochelyinae = (*Allaeochelys* + *Carettochelys* (fig. 2 - bottom))))). The Carettochelyinae are characterized by the extensive reduction of their dermal plates which can occasionally be still present in atavistic individuals. A detailed differential diagnosis of the Carettochelyinae was already supplied by HARRASSOWITZ (1922a). Fig. 4 in the present article shows a schematic reconstruction of the carapace and plastron of *Allaeochelys parayrei*. The morphology of the complete shell of the Carettochelyidae corresponds with the modern

turtles. Even if the dermal plates are reduced and the shell is covered by the corium, the bony elements are only weakly reduced. Thus all elements of the shell exclusively the posterior neuralia (behind NV = Neurale V) are regularly present.

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

Carapace scutes: cervical = ce, centrals = c 1 – c 5, laterals = l 1 – l 4, caudal = ca.

Plastron plates: epiplastrals = epi, entoplastron = ento, hyoplastrals = hyo, hypoplastrals = hypo, xiphiplastrals = xiphi.

Plastron scutes: gulars = gu, humeral = hu, pectorals = pec, abdominals = ab, femorals = fe, annals = an (Fig. 1).

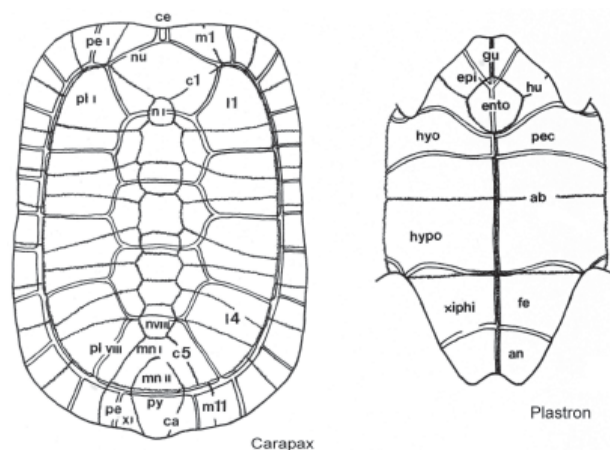


Fig. 1: Schematic position of plates and scutes of the testudinid turtle shell, modified from STAESCHE (1961). Abbreviations: see chapter “Terminology”.

3 Systematic Palaeontology

Order Chelonii BRONGNIART, 1800 (LATREILLE, 1800)

Suborder Cryptodira COPE, 1868

Superfamily Trionychoidea FITZINGER, 1826

Family Carettochelyidae BOULENGER, 1887

Subfamily Carettochelyinae BOULENGER, 1887

Genus *Allaeochelys* NOULET, 1867

Type species: *Allaeochelys parayrei* NOULET, 1867 (original designation); originally described

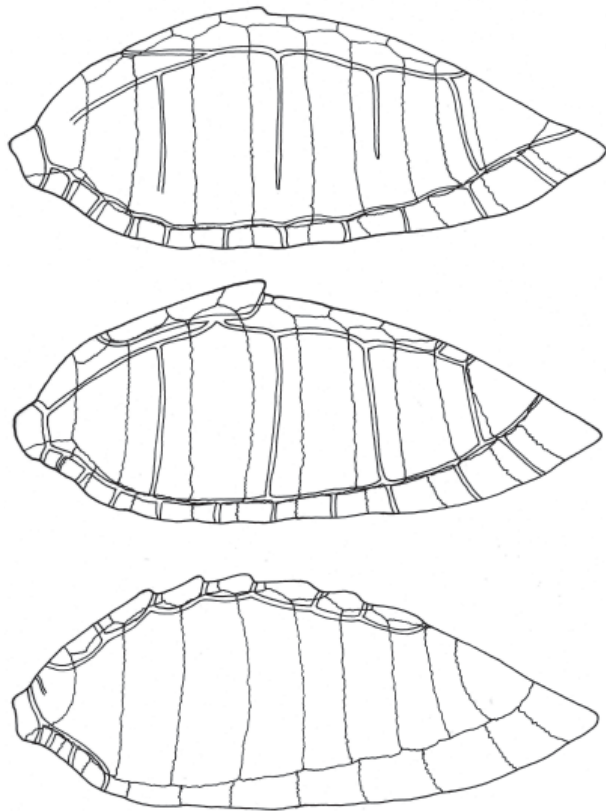


Fig. 2: Schematic position of plates and scutes of the carettochelyid shell in lateral view (from left), after MLYNARSKI (1969). Top: *Anosteira* LEIDY, 1871; centre: *Pseudanosteira* CLARK, 1931; bottom *Carettochelys* RAMSAY, 1886. Note the development of horny scutes.

from the Eocene of southern France (NOULET 1867).

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

Remarks: Neither the genus name *Allaeochelys* nor the author NOULET (1867) are listed within the “Fossilium Catalogus” on “Trionychia fossilia” by HUMMEL (1932).

Allaeochelys parayrei NOULET, 1867
Fig. 4, Pl. 1

Diagnosis: See MLYNARSKI (1976: 74).

New material: Specimen MNVD 24091 (see pl. 1), deposited in the geological magazine of the Museum für Naturkunde und Vorgeschichte Dessau: internal mould of carapace with poor remains of the shell, mostly peripherals. The structure of them, the drop-like shape as well as the sharply carinate median dorsal line are the main characters for the spe-

cific determination.

Locality: Clay pit in the Elbe-bank near Steutz, approximately 12 km WNW Dessau, Sachsen-Anhalt.

Horizon: Late Oligocene (Chattian: early “Eochattian”). The age determination of the whole sequence (Rupelian – Chattian) is based mainly on otolites which also indicate a shallow-marine environment (somewhat distant from the coastal line) for the “Eochattian” part of the section (A. MÜLLER, 2000). The biostratigraphical age of the underlying Rupelian part of the section (“Septarien-Ton”) is also confirmed by foraminifers (HAUSMANN 1964, 1965).

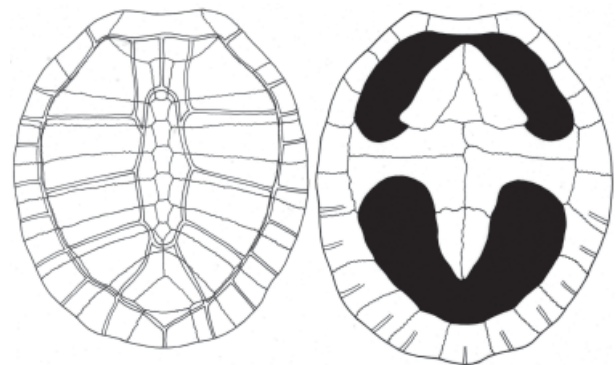


Fig. 3: Schematic position of plates and scutes of *Anosteira ornata* LEIDY, 1871, after MLYNARSKI, 1969.

Morphology

Measurements: Total preserved length of carapace = approximately 40 cm; maximal breadth = approximately 26,5 cm; height = approximately 11,5 cm.

Brief description: Shape of carapax oval, drop-like, vaulted; median dorsal line sharply carinate.

Discussion: The ornament of the shell varies both individually and ontogenetically. There are differences between carapace and plastron, median and peripheral regions of the shell as well as in juvenile and adult stages. Generally, the ornament is finer in smaller and younger individuals than in adults. These differences were used for distinguishing two separated putative species from the Messel Formation (Middle Eocene: Early Lutetian: Geiseltalian) of the Messel maar near Darmstadt (Hesse, southern Germany): *Anosteira gracilis* HARRASSOWITZ, 1922

and *A. crassesculpta* HARRASSOWITZ, 1922. HARRASSOWITZ (1922a: 201-202) defined the two species as follows:

Anosteira gracilis: ornament fine, mostly with 5-6 vermicular elevations (= short irregular ridges) per 10 mm; costale 1 without anterior process; phalanges more elongate, phalanges 1 and 2 of second finger fused.

Anosteira crassesculpta: ornament coarser; mostly with 3-4 vermicular elevations (= short irregular ridges) per 10 mm; strong tendency towards tuberculation, in particular within the median region of the plastron; limbs more robust, phalanges somewhat shorter and more robust, phalanges 1 and 2 of second finger not fused.

KELLER & SCHAAL (1988) already expressed that it is far from clear if these few differences are sufficient for separating the two species. As pointed out above, the differences between both “species” are putative; we regard them as conspecific. As far as can be judged from the few preserved remains of plates of the shell, the Dessau specimen from the Late Oligocene does neither show clear differences from the Middle Eocene Messel materials nor from the type species of the Eocene of southern France. Therefore we prefer to determine the *Allaeochelys* remains of all three regions as *A. parayrei* until better characters for a specific differentiation are known. This is already suggested by DE LAPPARENT DE BROIN (2001).

Remarks: Remains of carettochelyid turtles were hitherto known in Germany from the Middle Eocene (= Lutetian) of the Messel maar NE of Darmstadt and were originally described as *Anosteira crassesculpta* HARRASSOWITZ, 1922 and *Anosteira gracilis* HARRASSOWITZ, 1922. According to GROESSENS VAN DYCK (1978), the European material belongs to the genus *Allaeochelys* NOULET, 1867. There are hitherto no clear characters known for a specific differentiation between the western and central European representatives of this genus. The morphology of all Trionychidae is very variable. This means that further and more completely preserved materials are necessary for a decision of the taxonomic composition of *Allaeochelys*. The closest relatives are the North American and Chinese representatives of *Anosteira* LEIDY, 1871 from Cretaceous and Palaeogene deposits (KARL, 2002).

Allaeochelys parayrei was previously known

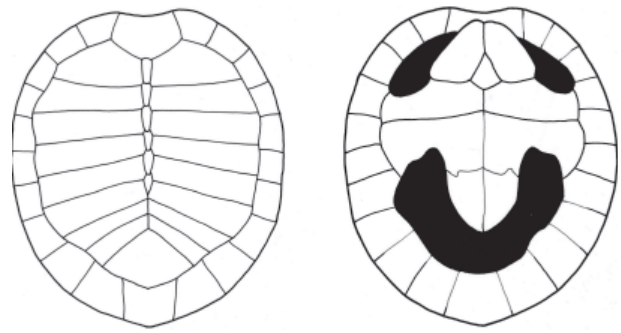


Fig. 4: Schematic position of plates and scutes of *Allaeochelys parayrei* NOULET, 1867, Scale bar = 2 cm (new reconstruction, original).

from the Early Eocene to the late Middle Eocene (Bartonian) in France, Spain, England, Belgium and Germany (DE LAPPARENT DE BROIN, 2001). The new specimen from Dessau is the stratigraphically youngest record of *Allaeochelys*. Compared with *Allaeochelys* from Messel (which reaches a maximum length of about 25-30 cm), the Dessau specimen is unusually large. A further locality of *Allaeochelys* in Germany is Bad Adelholzen (Siegsdorf area in Bavaria; early Middle Eocene: Lutetian; DARGA et al. 1999, KARL, 2002).

HARRASSOWITZ (1922b) proposed an evolutionary line (founded on “evolutionary mechanics”) from *Allaeochelys/Anosteira* via *Carettochelys* to *Trionyx*. It is based upon a supposed continuous prolongation of the cervical vertebrae in connection with a stronger curvature of the articulation facets. He also assumed a continuously opisthocoelic morphology of the trionychid cervical vertebrae which he used to separate the Trionychia from the Cryptodira. This opinion was emphatically contradicted by the former Greifswald palaeontologist Otto JAEKEL and did not become generally accepted.

Stratigraphic and geographic occurrence of *Allaeochelys*: According to DE 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 W of Cologne, Germany. The *Allaeochelys* specimen described in the present article is the first one documented from the Oligocene at all. It connects biostratigraphically the records of the Eocene and Miocene in Central Europe (see numbers 3-5 within Fig. 5). Comparable materials are currently described from the Middle Eocene (MP 13-14) of Casaseca de Campeán (Cor-

rales B) in Spain as *Allaeochelys jimenezi* SANTIAGO & ANDRÉS, 2005.

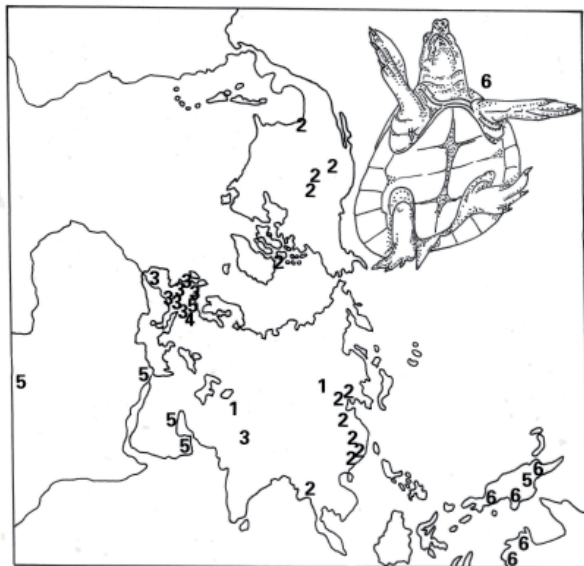


Fig 5: World map illustrating the currently known distribution of carretochelyid turtles from the Cretaceous to present, updated from a compilation by JOYCE et al. (2004). Legend: 1 - Cretaceous Anosteirinae; 2 - Eocene Anosteirinae; 3 - Eocene Carettochelyinae; 4 - Oligocene Carettochelyinae (*Allaeochelys* described in the present article); 5 - Miocene Carettochelyinae; 6 - Recent Carettochelyinae.

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Plate 1: *Allaeochelys parayrei* NOULET, 1867, MNVD 24091; Late Oligocene (Chattian: early „Eochattian“), clay pit in the Elbe-bank near Steutz, approximately 12 km WNW Dessau, Sachsen-Anhalt, Germany. Top: = lateral view (from left); centre: = lateral view (from right); bottom = ventral view.

Plate 1

