ISSN: 0211-8327 Studia Palaeocheloniologica IV: pp. 73-86

FIRST RECORD OF *CHITRACEPHALUS DUMONII* (TESTUDINES: PLEURODIRA; EARLY CRETACEOUS) IN CENTRAL EUROPE AND THE RISE OF MATAMATA-LIKE TURTLES

[Primer registro de* Chitracephalus dumonii/= *?*Salasemys pulcherrima *(Testudines: Pleurodira) (Cretácico Inferior) en Europa Central. Ampliación del conocimiento de las tortugas similares a las Matamata]

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(FECHA DE RECEPCIÓN: 2011-12-29)
BIBLID [0211-8327 (2012) Vol. espec. 9; 73-86]

ABSTRACT: Here we describe the first record of the turtle *Chitracephalus dumonii* Dollo, 1884 (syn. ?*Salasemys pulcherrima* Fuentes Vidarte *et al.*, 2003) from Early Cretaceous (Berriasian) deposits in northwestern Germany. Several carapace remains have been found within the material collected by H. F. W. Grabbe in the the early 1880s, deposited in the Geoscience Centre of the Göttingen University, which show typical morphological characters of this species. It represents the stratigraphically oldest representative of *Chitracephalus* (syn. *?Salasemys*). The supposed phylogenetic relationship of this species in the relation to the Late Jurassic *Platycephalus oberndorferi* WAGNER, 1853 (Platychelidae) and the modern *Chelus fimbriatus* Schneider, 1783 (Chelidae) is discussed.

Key words: *Chitracephalus dumonii/?Salasemys pulcherrima*, turtles, Pleurodira, Early Cretaceous, northwestern Germany, phylogenetic relationship.

RESUMEN: Se presenta el primer registro de la tortuga *Chitracephalus dumonii* Dollo, 1884 (syn. ?*Salasemys pulcherrima* Fuentes Vidarte *et al.*, 2003) en el Cretácico Inferior (Berriasiense), en el noroeste de Alemania. Se muestran varios restos de caparazón con caracteres típicos de esta especie en el material recogido por H. F. W. Grabbe a finales del siglo XIX, que están depositados en el Centro de Geociencias de la Universidad de Göttingen. Son los más antiguos representantes de *Chitracephalus* (syn. *?Salasemys*). Se discute la supuesta relación filogenética desde la especie del Jurásico Tardío *Platycephalus oberndorferi* Wagner, 1853 (Platychelidae) y la reciente *Chelus fimbriatus* Schneider, 1783 (Chelidae).

Palabras clave: *Chitracephalus dumonii/?Salasemys pulcherrima*, turtles, Pleurodira, Cretácico Inferior, noroeste de Alemania, relaciones filogenéticas.

INTRODUCTION

FUENTES VIDARTE *et al.* (2003) described a nearly complete specimen of their new turtle taxon *Salasemys pulcherrima* (Testudines). It was collected from the Early Cretaceous "Tenadas del Jabalí" site in Salas de los Infantes, Burgos (Spain; figure 1, point 6). The original authors regarded it as a primitive turtle belonging to the Eucryptodira group. Its carapace is oval and flat, almost square in shape, with a well developed deep nuchal notch and a complex ornamentation formed by strong, protruding ribs. The plastron is small, of cruciform-type, and with two clearly-defined fontanelles between the hyoplastra and the hypoplastra as well as between the hypoplastra and the xiphiplastra. As shown in the present contribution, *Salasemys pulcherrima* seems to be a younger synonym of *Chitracephalus dumonii* Dollo, 1884 which was at first described from Early Cretaceous (Middle Barremian to Earliest Aptien) strata YANS *et al.* (2005) at Bernissart in Belgium.

Recently, the authors discovered certain turtle remains in the HEINRICH FRIEDRICH WILHELM GRABBE collection (Geoscience Centre, Göttingen) which are supposed to be conspecific with the Spanish and Belgium materials. GRABBE collected the specimens for his doctoral thesis (1883) from Berriasian ("Middle Wealden") deposits at the northern slope of the Bückeberge near Wendthagen in the principality Schaumburg-Lippe, Lower Saxony (northwestern Germany).

A comparative discussion of the characters of the Late Jurassic *Platychelys oberndorferi* Wagner, 1853, the Early Cretaceous *Chitracephalus dumonii* and the Recent *Chelus fimbriatus* Schneider, 1783 (Matamata) demonstrates the close phylogenetic relationship between these three species which are here regarded as different stages of an evolutionary line leading towards the Recent Matamata turtles. This is the reason why brief descriptions of *Platychelys oberndorferi* and *Chelus fimbriatus* are included in the present paper, too.

The present article is an extended version of a contribution to the Gaffney-Turtle-Symposium in Drumheller, Canada, October 17th & 18th, KARL & REICH (2009).

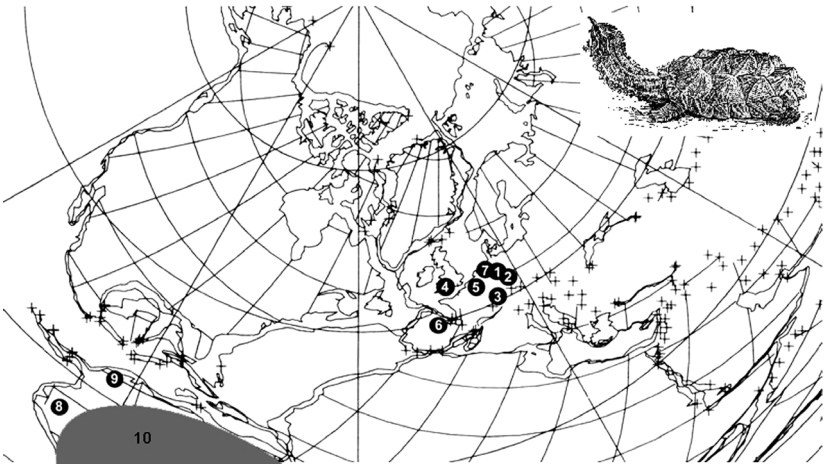

Figure 1. Map of the distribution of Platychelys, Chitracephalus (both: Mesozoic, Europe), and Chelus (Neogene and Recent, South America), based upon Smith, Hurley & Briden (1982). Platychelys: 1: Kelheim, Southern Franconian Alb, Bavaria, South Germany; 2: Eichstätt, southern Franconian Alb, Bavaria, South Germany; 3: Solothurn, Switzerland; 4: Swanage, Durlston Bay, Dorset, southern England, UK; Chitracephalus/Salasemys: 5: Bernissart, Belgium; 6: Tenadas del Jabalí site in Salas de los Infantes, Burgos, Spain; 7: Körssen N Wendthagen (S Stadthagen), principality Schaumburg-Lippe, Lower Saxony, north-western Germany; Chelus: 8: Upper Magdalena River Valley, Colombia; 9: Urumaco, north-western Falcón, Venezuela; 10: Recent areal of Matamata.

SYSTEMATIC PALEONTOLOGY

Order Testudines Linnaeus, 1758

Gigaorder Casichelydia Gaffney, 1975

Megaorder Pleurodira Gaffney, 1975

Infraorder Pleurodira Cope, 1868

Family Platychelyidae Bräm, 1965

Genus *Platychelys* Wagner, 1853

TYPE SPECIES: *Platychelys oberndorferi* Wagner, 1853

SYNONYMS: See KUHN (1964) and BRÄM (1965)

***Platychelys oberndorferi* Wagner, 1853**

SYNONYMS: See KUHN (1964) and BRÄM (1965)

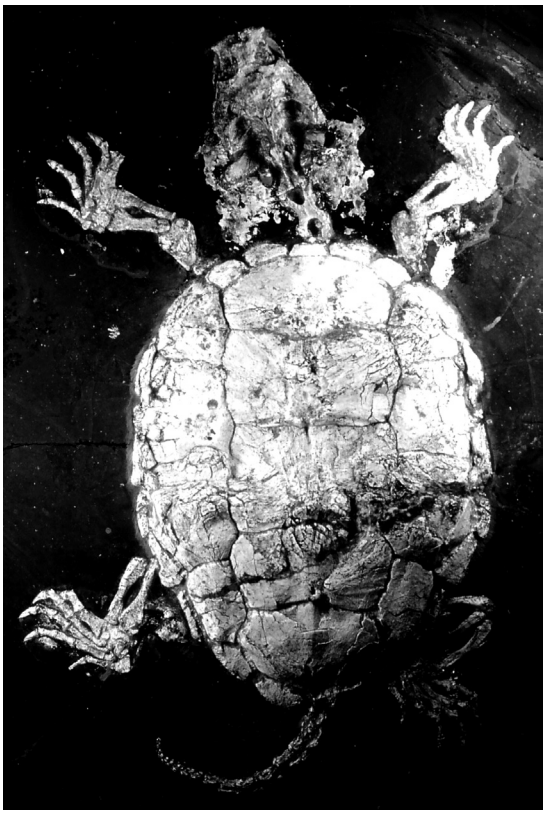

Plate 1. Platychelys oberndorferi *Wagner, 1853, Late Jurassic*: *Tithonian (Solnhofen Limestone), Eichstätt, Bavaria, complete skeleton in dorsal view, IGPS Nr. 650, coll. Stefan Schäfer (Puchheim); ultraviolet-light photograph by Helmut Tischlinger (Stammham). Note the strong hyoid bones behind the skull. Whithout scale.*

ADDITIONAL SYNONYMY

1889 ?*Platychelys anglica* n. sp. Lydekker: 217-218, fig. 48

1964 ?*Platychelys anglica* Lydekker, 1889. KUHN: 13

2004 ?*Helochelydra anglica* (Lyddekker) comb. nov. MILNER: 1458-1460, fig. 11

NEW MATERIAL: Complete skeleton in dorsal view, IGPS Nr. 650, coll. Stefan Schäfer, Puchheim, Bavaria (plate 1).

LOCALITY: Abandoned quarry in "lithographic limestone" (= Solnhofen Limestone) at Eichstätt, Southern Franconian Alb, Bavaria, South Germany.

HORIZON: Late Jurassic: Tithonian.

STRATIGRAPHICAL AND GEOGRAPHICAL OCCURRENCE: (i) Late Jurassic: Kimmeridgian, Solothurn (Switzerland); (ii) Late Jurassic: Tithonian, Eichstätt and Kelheim (type locality), Southern Franconian Alb, Bavaria (South Germany); (iii) Late Jurassic/Early Cretaceous transitional beds: "Purbeck Limestone Group", Swanage, Durlston Bay, Dorset (southern England, UK) (under *Helochelydra anglica*).

CHARACTERS: Skull compact, upper jaw with distinct labial ridges; temporal region slightly indented; orbitae dorsorostrad; middle ear processus with tympanic opening in posterior direction; angle of ears > 180°; horns of Os hyoides (cbI and cbII) extremely enlarged (plate 4, figure 3); extremities strong, not specialized, five fingers and five toes strongly developed; carapace distinctly sculptured, each side with three separate supramarginals; total width of centrals diminishing in posterior direction, C1 being the broadest and C5 the narrowest one (as shown in BRÄM, 1965); tail of moderate length, 18 vertebrae visible (see plate 1).

Genus *Chitracephalus* Dollo, 1884

TYPE SPECIES: *Chitracephalus dumonii* Dollo, 1884

SYNONYMS: See KUHN (1964)

***Chitracephalus dumonii* Dollo, 1884**

SYNONYMS:

1884 *Chitracephalus dumonii* n. g. n. sp. Dollo: 70-71, pl. 1 (complete skeleton).

1909 *Chitracephalus dumonii*. Dollo: 101.

1911 *Chitracephalus dumonii*. Wegner: 106.

1964 *Chitracephalus dumonii*. Kuhn: 35-36

2003 *?Salasemys pulcherrima* nv. g. nv. sp. Fuentes Vidarte *et al.*: 109

2009 *?Salasemys pulcherrima* KARL & REICH: 90

CHARACTERS: Skull extremely narrow, elongated and flat upper jaw without distinct labial ridges; temporal region slightly indented; orbitae dorsorostrad; middle ear processus with tympanic opening in lateral direction; angle of ears = about 180° (plate 4, figure 1); horns of Os hyoides (cbI and cbII) extremely enlarged (plate 4, figure 2); extremities tender, not specialized, with five fingers and five toes; carapace distinctly sculptured, without supramarginalia; total width of centrals diminishing in posterior direction, C1 being the broadest and C5 the narrowest one (see DOLLO, 1884; FUENTES VIDARTE *et al.*, 2003); tail short, about 10 vertebrae visible (see plates 2-4).

NEW MATERIAL: (i) Pleural fragment n.º GZG.V.010.401 (plate 2, fig. 1); (ii) pleural fragment n.º GZG.V.010.402 (plate 2, fig. 2); (iii) pleural fragment

n.º GZG.V.010.004 (plate 3, fig. 1a-c); (iv) peripheral fragment n.º GZG.V. 010.403 (plate 2, fig. 3a-b); (v) scapula n.º GZG.V.010.003 (plate 3, fig. 2). All specimens: leg. Heinrich Friedrich Wilhelm Grabbe, Geoscience Centre, Georg August University, Göttingen, Germany.

LOCALITY: Engine shaft (Maschinenschacht) on Körssen N Wendthagen (S Stadthagen), northern slope of the Bückeberge, principality Schaumburg-Lippe, Lower Saxony, north-western Germany (figure 1, point 2).

AGE: Early Cretaceous: Berriasian (ELSTNER & MUTTERLOSE, 1996; HISS *et al.*, 2005; "Middle Wealden" in the older literature, as for example GRABBE, 1883), argillaceous sandstone below "Hauptflöz" (bulk bed), rich in fossil plants.

REMARKS: Like in the type specimen of *Salasemys pulcherrima* Fuentes Vidarte *et al.*, 2003 the carapace plates are flat, with parts of a well developed and complex sculpture by strong, protruding ribs similar to the structure of a spider-web (see plate 2 and 3, fig. 1a-c).

Family Chelidae Gray, 1873

Genus *Chelus* Duméril, 1806

TYPE SPECIES: *Testudo fimbriata* Schneider, 1783, Recent, northern and central South America (Venezuela, Guayanas, northern and central Brazil, northern Bolivia, eastern Peru, Ecuador, eastern Colombia).

SYNONYMS: See FRITZ & HAVAŠ (2007).

FURTHER SPECIES: Two fossil species have been assigned to *Chelus* by shell characters:

(i) ***Chelus colombianus* Wood, 1976**, Villavieja Formation (Late Tertiary, Neogene: Upper Miocene), upper Magdalena River Valley, Colombia;

(ii) ***Chelus lewisi* Wood, 1976**, Urumaco Formation (Late Tertiary, Neogene: Upper Miocene, Huayquerian), several localities in the vicinity of Urumaco, north-western Falcón, Venezuela.

***Chelus fimbriatus* (Schneider, 1783)**

CHARACTERS: Skull compact; upper jaw without labial ridges; temporal region slightly indented, tripartite by shifting of middle ear processus; orbitae dorsorostrad; middle ear processus with tympanic opening in anterior direction; angle of ears < 180°; horns of Os hyoides (cbI and cbII) strongly enlarged (plate 4, figure 4); extremities strong, not specialized, with five fingers and five toes; carapace distinctly sculptured, without supramarginalia; total width of centrals diminishing in posterior direction, C1 being the broadest and C5 the narrowest one (see GAFFNEY, 1977; PRITCHARD & TREBBAU, 1984; SEDDON *et al.*, 1997; SÁNCHEZ-VILLAGRA *et al.*, 1995); tail short (see plate 4).

System	Series	Stage	Age (mya)	Platychelyidae	Chelidae
Quaternary	Holocene Pleistone	Rezent Upper Middle Lower	2.588-Rezent		*Chelus fimbriatus*
Neogene	Pliocene	Piacenzian	3.6-2.588		
		Zanclean	5.332-3.6		
	Miocene	Messinian	7.246-5.332		*Chelus colombianus* *Chelus lewisi*
		Tortonian	11.608-7.246		
		Serravallian	13.82-11.608		
		Langhian	15.97-13.82		
		Burdigalian	20.43-15.97		
		Aquitanian	23.03-20.43		
Palaeogene	Oligocene	Chattian	28.4-23.03		
		Rupelian	33.9-28.4		
	Eocene	Priabonian	37.2-33.9		
		Bartonian	40.4-37.2		
		Lutetian	48.6-40.4		
		Ypresian	55.8-48.6		
	Palaeocene	Thanetian	58.7-55.8		
		Seelandian	61.1-58.7		
		Danian	65.5-61.1		
Cretaceous	Upper Cretaceous	Maastrichtian	70.6-65.5		
		Campanian	83.5-70.6		
		Santonian	85.8-83.5		
		Coniacian	88.6-85.8		
		Turonian	93.6-88.6		
		Cenomanian	99.6-93.6		
	Lower Cretaceous	Albian	112-99.6		
		Aptian	125-112		
		Barremian	130-125	*Chitracephalus dumonii* from Belgium	
		Hauterivian	133.9-130	*?Salasemys pulcherrima* from Spain[1]	
		Valanginian	140.2-133.9		
		Berriasian	145.5-140.2	*Chitracephalus dumonii*	
Jurassic	Upper Jurassic	Tithonian	150.8-145.5	*Platychelys oberndorferi*	
		Kimmeridgian	155.6-150.8		
		Oxfordian	161.2-155.6		
	Middle Jurassic	Callovian	164.7-161.2		
		Bathonian	167.7-164.7		
		Bajocian	171.6-167.7		
		Aalenian	175.6-171.6		
	Lower Jurassic	Toarcian	183-175.6		
		Pliensbachian	189.6-183		
		Sinemurian	196.5-189.6		
		Hettangian	199.6-196.5		

Figure 2. Stratigraphic distribution of Platychelys, Chitracephalus *and* Chelus.

[1] Probably a junior synonym of *Chitracephalus dumonii*.

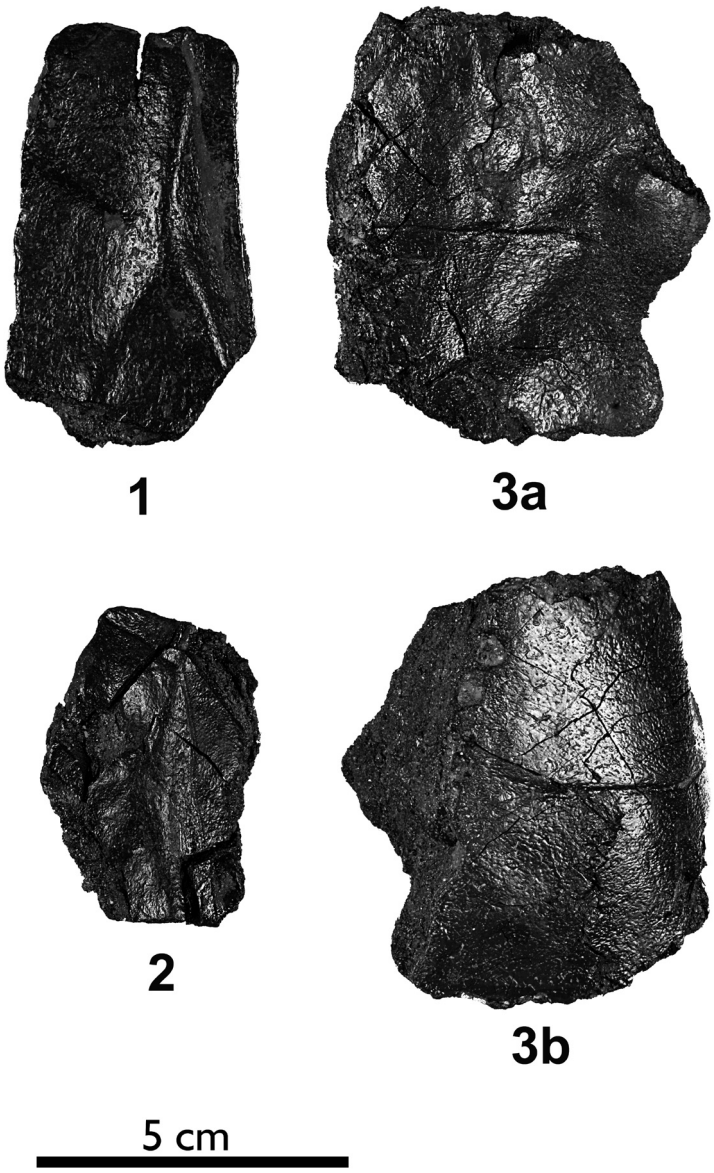

Plate 2. Chitracephalus dumonii *Dollo, 1884, Early Cretaceous*: *Berriasian ("Middle Wealden"), Wendthagen, Schaumburg-Lippe, Lower Saxony, north-western Germany, Grabbe collection, Geoscience Centre, Göttingen; figure 1: pleural n.º GZG.V.010.401; figure 2: pleural n.º GZG.V.010.402; figure 3: peripheral n.º GZG.V.010.403, a = dorsal, b = ventral; photograph by Gerhard Hundertmark (G öttingen), plate by Alexander Gebler (Göttingen) according KARL & REICH (2009).*

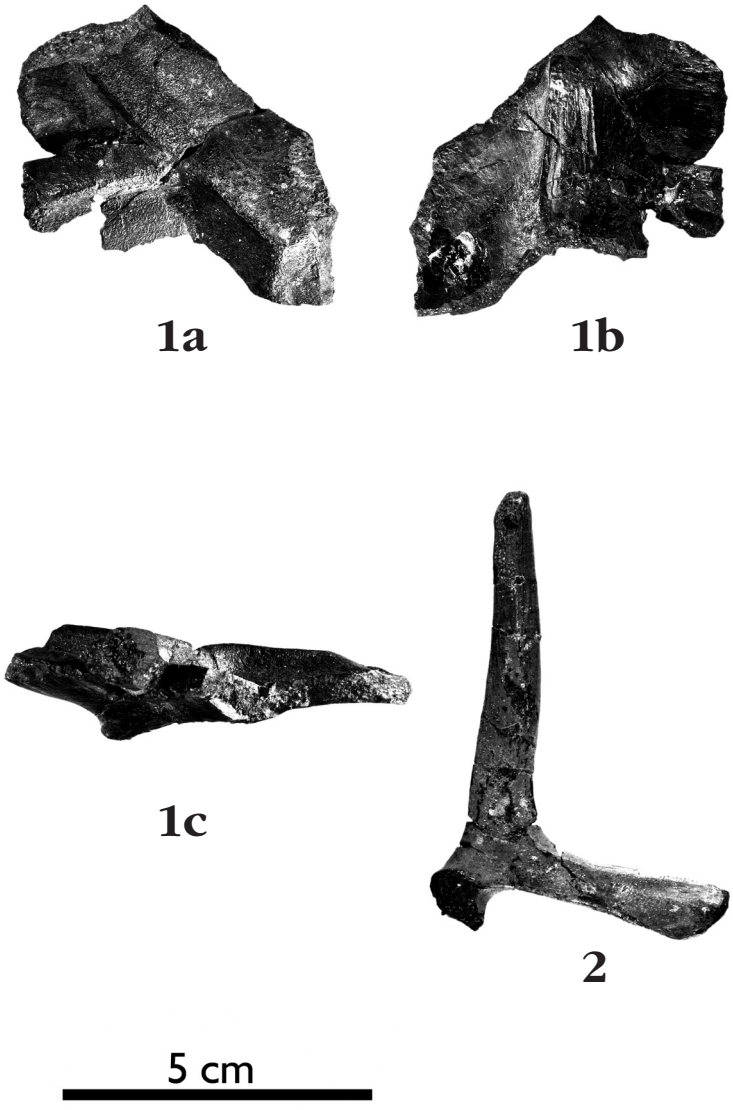

Plate 3. Chitracephalus dumonii *Dollo, 1884, Early Cretaceous*: *Berriasian ("Middle Wealden"), Wendthagen, Schaumburg-Lippe, Lower Saxony, north-western Germany, Grabbe collection Geoscience Centre, Göttingen; figure 1: pleural n.º GZG.V.010.004, a = dorsal view, b = visceral view, c = cross section at fracture; figure 2: scapula n.º GZG.V.010.003; photograph by Mike Reich (Göttingen), plate by Dirk Urban (Erfurt). according KARL & REICH (2009).*

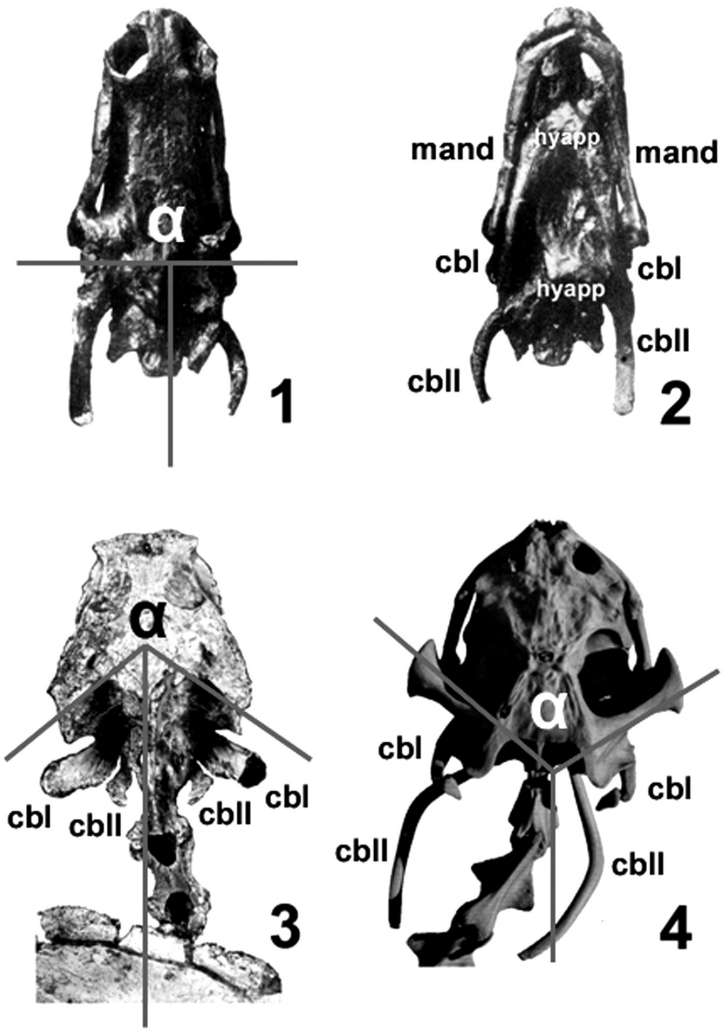

Plate 4. Figure 1: Chitracephalus dumonii *Dollo, 1884, Early Cretaceous*: *Middle Barremian to Earliest Aptien, Bernissart (Belgium), skull in dorsal view (from* DOLLO, *1884*: *fig. 2); figure 2:* Chitracephalus dumonii *Dollo, 1884, Early Cretaceous*: *Middle Barremian to Earliest Aptien, Bernissart (Belgium), skull in palatal view (from* DOLLO, *1884*: *fig. 1); figure 3*: Platychelys oberndorferi *Wagner, 1853, Late Jurassic*: *Tithonian (Solnhofen Limestone), Eichstätt (Bavaria), specimen IGPS Nr. 650 (see plate 1), nuchal region, neck, skull; figure 4:* Chelus fimbriatus *(Schneider, 1783), Recent Matamata turtle (CT image), head and neck skeleton (from ©DigiMorph, <http://digimorph.org/>, image processing Ted Macrini and Jessie Maisano, with permission by Timothy Rowe of DigiMorph.org). Abbreviations*: α = *angle of middle bas processus, mand = mandibula (lower jaw), hyapp = hyoid apparatus, cbI = cornu branchiale I, cbII = cornu branchiale II. Plate by Enrico Paust (TLDA). Without scale.*

DISCUSSION

Up to now, five species of turtles are known from the Early Cretaceous of north-western Germany: *Pleurosternon bullocki* (Owen, 1842), *Hylaeochelys menkei* (F. A. Roemer, 1836), *Peltochelys duchastelii* Dollo, 1884 and *Chitracephalus dumonii* Dollo, 1884 (? syn. *Salasemys pulcherrima* Fuentes Vidarte *et al*., 2003; see KARL & TICHY, 2005; KARL *et al*., 2007).

S. pulcherrima was originally reported from the Early Cretaceous (Late Hauterivian/Aptian) of Salas de los Infantes, Burgos, Spain. The newly rediscovered German material is of Berriasian age and thus several million years older than the Spanish specimen (see figure 2). Nevertheless the general morphology of the carapace of the latter closely resembles *Chitracephalus dumonii* Dollo, 1884 from the Berriasian of Bernissart, Belgium (figure 1, point 3). Therefore it cannot be excluded that *Salasemys* is a junior synonym of *Chitracephalus*. A similar sculpture of a turtle shell as in the new material was previously unknown from any localities in Germany (GRABBE, 1883), France (DE LAPPARENT DE BROIN, 2001) and Great Britain (MILNER, 2004). On the other hand, NOPCSA (1934) and STROMER (1935) already presumed relations of *Chitracephalus* to the Pleurodira which would be important under palaeozoogeographic respect. If the Belgian *Chitracephalus* belongs to the Pleurodira: the family Chelidae as supposed by STROMER (1935: 12, under "Chelyidae"), this taxon really might have had its origin in the Laurasian region.

Based upon common morphological characters, we here suppose close relations between the three genera *Platychelys*, *Chitracephalos*, and *Chelus* which are regarded as different stages on a phylogenetic lineage.

Most ancient species of this group is *Platychelys oberndorferi* Wagner, 1853 from the Late Jurassic (Tithonian) "Solnhofen Limestone" in Bavaria which was originally only based upon fragments of the shell, but is now also known from a complete skeleton (see above). Its general morphology as well as the proportions of the carapace is strikingly similar to the Recent *Chelus fimbriatus* as follows: (i) The two visible vertebrae of the neck are clearly elongated and thus indicate a long neck; (ii) The legs are strongly developed and thus well developed for walking and adherence on the bottom of the water in a strong current; (iii) Additionally the phalanges are highly adapted to swimming (KARL & TICHY, 2006).

Second stage of this supposed lineage is the Early Cretaceous *Chitracephalus dumonii* in which shell and skull are flat and elongated. In the type specimen (DOLLO, 1884: fig. 4 = IRSNB R 12) the carapace shows the same typical radial structures as in *Salasemys pulcherrima*. The extremities are relatively weak and have short and unspecialized fingers and toes. The neck is relatively long, with the ability for lateral side-necking slightly indicated, as shown in DOLLO (1884: pl. 1, figs. 3-6). The lower jaw is arched and weak, without broadened and

specialized alveolar region. On the other hand, the hyomandibular apparatus is markedly well developed and is nearly as large as the total ventral side of the skull (DOLLO, 1884: pl. 1, fig. 1). The reductions in the skull are similar to those in the Chelidae, and the fronto-dorsad direction of the orbitae largely resembles *Chelus* (DOLLO, 1884: pl. 1, fig. 2). Furthermore there is a strong conformity of the plastrons of *Chitracephalus* (DOLLO, 1884: pl. 1, fig. 7 = IRSNB R 11) and *Salasemys*. In general, the complete complex of morphological characters is similar in both taxa which was already used for a comparative palaeobiological reconstruction (KARL *et al*., 2007): During the Early Cretaceous: *Chitracephalus/Salasemys* occupied the ecological niche of the Late Jurassic *Platychelys oberndorferi*. The specialization towards hunting in wait seems to have been in a very early stage as shown by the still lateral direction of the middle ear processus in *Chitracephalus*. In *Chelus* it is already directed distinctly frontolaterally.

LEMELL *et al*. (2010) studied the feeding apparatus of the Recent Matamata *Chelus fimbriatus* to elucidate the feeding mechanics of an aquatic feeding specialist that has never been investigated in detail before, regarding gross morphology. Here we repeat their results directly to give an approximate image for the presumed habits of the fossil relatives:

> The skull and hyoid apparatus as well as associated musculature were examined by computer tomography and dissection; the tongue was examined by scanning electron microscopy. The flat skull, the possibility to enormously depress the mandible combined with a cheek-like development, the large, ossified hyoid apparatus, and a well-distensible esophagus enable the turtle to produce an enormous suction force the prey is inhaled with. The jaw adductors are poorly developed in relation to other turtles and thus help keep the skull shape flat; nevertheless, they are able to generate high velocities and exhibit some new performance lines. The hyoid musculature is as well-developed as the hyoid apparatus itself, promoting the high depression velocity that is necessary for good feeding performance. The tongue is nearly reduced and lacks dorsal morphological differentiations. Taking all the morphological features into account, *Chelus fimbriatus* is an extremely well-adapted turtle making this species a very interesting object of investigation (LEMELL *et al*., 2002, 2010).

ACKNOWLEDGMENTS

We are grateful to Stefan Schäfer (Puchheim, Bavaria) for making his important material available to us, Helmut Tischlinger (Stammham, Bavaria) for the ultraviolet-light photographs, Gerhard Hundertmark (Göttingen) and Dirk Urban (Erfurt) for the photographs, and Alexander Gehler (Göttingen) for additional assistance.

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