Identification and Taphonomy of a Miocene Leatherback Turtle (Testudines: Dermochelyidae) from the Westerschelde, The Netherlands

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Master thesis

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Abstract

The Westerschelde Estuary in The Netherlands is rich in vertebrate fossil content. In a recent trawling campaign aimed to sample a vertebrate assemblage, over 5000 specimens have been retrieved, all currently in the possession of the Natuurhistorisch Museum Rotterdam. One specimen is a fragment of a dermochelyid sea-turtle carapace. The Westerschelde is hereby the second locality to confirm the presence of dermochelyids in the Miocene North Sea. The Westerschelde fragment is described and identified as *Psephophorus polygonus* Meyer, 1847. The various secondary marks present on the carapace fragment are suggestive of both predatory and scavenging origin. In order to estimate the size of the Westerschelde specimen, two *Dermochelys coriacea* specimens from The Royal Belgian Institute of Natural Sciences have been analysed. Based on the assumption that *Psephophorus* has 7 longitudinal ridges on its carapace similar to *D. coriacea*, the size of the complete carapace is estimated to have been 168 *126 cm. Based on the physical traits of the Westerschelde specimen, and a re-examination of *P. polygonus* specimens from the Naturhistorisches Museum Wien, it is argued that previously assigned characteristics are not discriminative taxonomic properties of dermochelyids in general and of *P. polygonus* in particular. An improved cladistic analysis on dermochelyids is performed based on previously defined-, and new taxonomic characters. With use of the cladistic analysis it is argued that *Psephophorus calvertensis* Palmer, 1909 as well as the Westerschelde specimen can be assigned to *Psephophorus polygonus*, which can thus be proven to be cosmopolitan, similar to the extant species *Dermochelys coriacea*.

Keywords: Chelonii; North-Sea Basin; phylogeny; *Psephophorus calvertensis*; *Psephophorus polygonus*; Testudines; Tortonian

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Introduction

The Westerschelde Estuary is known for its rich vertebrate fossil content. During a trawling expedition of the Natural History Museum of Rotterdam in 2014, over 5000 fossil mammalian remains have been collected (Post & Reumer, 2016). These remains are known to originate from a single locality and are therefore of high paleontological and paleoecological interest. The assemblage consists mostly of Cetacea. Furthermore, vertebrae of an extinct shark of genus *Carcharodon* and a dermochelyid sea-turtle carapace fragment are of interest (Veenhof, 2015 unpublished).

The family Dermochelyidae is currently represented by only one extant species, which is *Dermochelys coriacea* (Vandelli, 1761). However, the dermochelyids prove to have a complex evolutionary history (Wood et al., 1996). Over 7 extinct dermochelyid genera are currently described: from the Paleocene-Eocene: *Arabemys* (Tong et al., 1999); from the Eocene: *Cosmochelys* (Andrews, 1919), *Egyptemys* (Wood et al., 1996) and *Eosphargis* (Lydekker, 1889); from the Oligocene: *Cardiochelys* (Moody, 1993) and *Natemys* (Wood et al., 1996); and *Psephophorus* (Meyer, 1847) mainly from the Miocene.

The dermochelyid (or 'leatherback turtle') is the largest extant sea-turtle: it can grow up to 240 cm in length and can weigh over 600 kg (Pough et al., 2013). Unlike other sea-turtles, the leatherback turtle's carapace is made up of thousands of small bones (ossicles) and is embedded in a leathery skin. The carapace of the extant species possesses 7 ridges reaching from the front to the back of the turtle. Currently, the extant *Dermochelys* has a wider geographic distribution than any other ectothermal amniote (Pough et al., 2013). They are cold-water resistant, and can dive to depths up to 1000 meters (Pough et al., 2013).

The Miocene *Psephophorus* from Slovakia has first been described in 1846 without a name provided (Meyer, 1846), after which the name was assigned a year later (Meyer, 1847). Unfortunately, no drawing was ever published, so the neotype is only known to have consisted of approximately 70 ossicles and included a ridge. It was described in detail by Seeley (1880). Only one of the two slabs described by Seeley (1880) is lost. The other is currently deposited at the Naturhistorisches Museum Wien (NHMW 2011/0330/0001) and is currently considered the neotype of *Psephophorus polygonus* (Wood et al., 1996).

Only three recent studies have identified a specimen as *Psephophorus polygonus*: one from Italy (Chesi et al., 2007), one from Denmark (Karl et al., 2012) and one from Slovakia (Delfino et al. 2013). Delfino et al. (2013) described additional *P. polygonus* specimens from the same locality as the *P. polygonus* neotype. The genus *Psephophorus* is generally described as a wastebasket genus (Wood et al., 1996) due to the large number of diverse species that are attributed to it, e.g. *P. californiensis* (Gilmore, 1937), *P. calvertensis* (Palmer, 1909), *P. rupeliensis* (Van Beneden, 1883), and *P. scaldii* (Van Beneden, 1871). Taxonomic specifications to confidently determine whether these species all belong to the genus *Psephophorus* are lacking partly due to identifications being based on different parts of the skeleton, such as either bones or carapaces, which evidently cannot be compared.

In this study, a new well preserved fragment of a dermochelyid carapace from the Westerschelde is presented, of which a thorough investigation is done on what species it belongs to. Based on additional study of the *Psephophorus polygonus* neotype, an isolated ossicle from the same locality (Delfino et al., 2013), and two *Dermochelys coriacea* specimens, a new phylogeny of the Dermochelyidae in general, and of the genus *Psephophorus* in particular is proposed. The phylogenetic analysis is aimed to help determine which species the Westerschelde specimen belongs to. By the study of comparative material we try to gain more insights on the complex history of dermochelyid evolution. With an additional taphonomic analysis concerning secondary marks on the carapace, a more complete understanding of the ecology of the Miocene Westerschelde area can be created.

Abbreviations

RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium

NMR – Natuurhistorisch Museum Rotterdam, The Netherlands

NHMW – Naturhistorisches Museum Wien, Austria

Geological setting

The ‘Western Scheldt’, or in Dutch ‘Westerschelde’ Estuary is a geologically dynamic estuary in the south-west of the Netherlands (Figure 1). In this study, only the Dutch naming ‘Westerschelde’ will be used. The estuary is the only direct passage from the river Scheldt into the sea, and an important shipping route towards Antwerp, Belgium.

The base of the Westerschelde is the London-Brabant Massif which has been flooded from the Late Cretaceous onwards. On top of the massif lies a Late Cretaceous chalk, followed by clayey sand and sandstone (Du Four et al., 2006). A slight slope towards the NNE is present (Le Bot et al., 2003). The Paleogene and Neogene deposit thickness varies from 10 to 30 meters, whereas the Quaternary deposits are only up to 10 meters thick (Du Four et al., 2006).

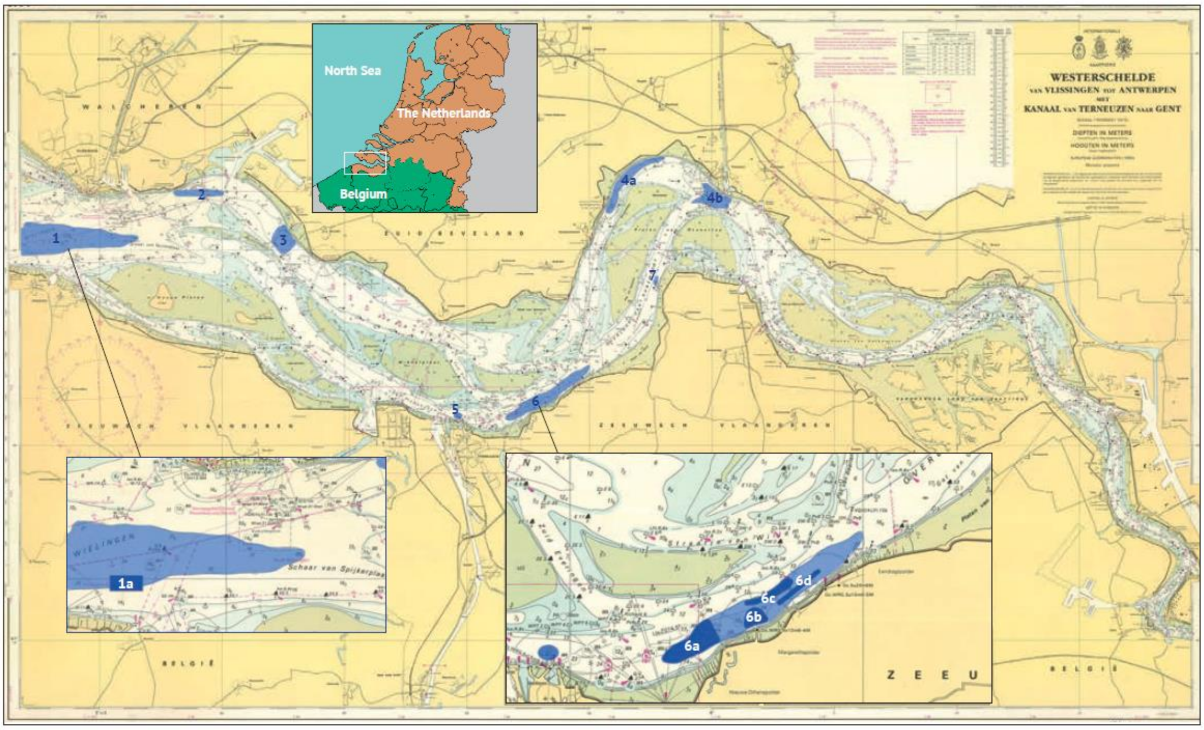

Figure 1. Map of the Westerschelde Estuary and its trawling localities. The specimen is retrieved from site 6d in 2014 (Image from Post & Reumer, 2016).

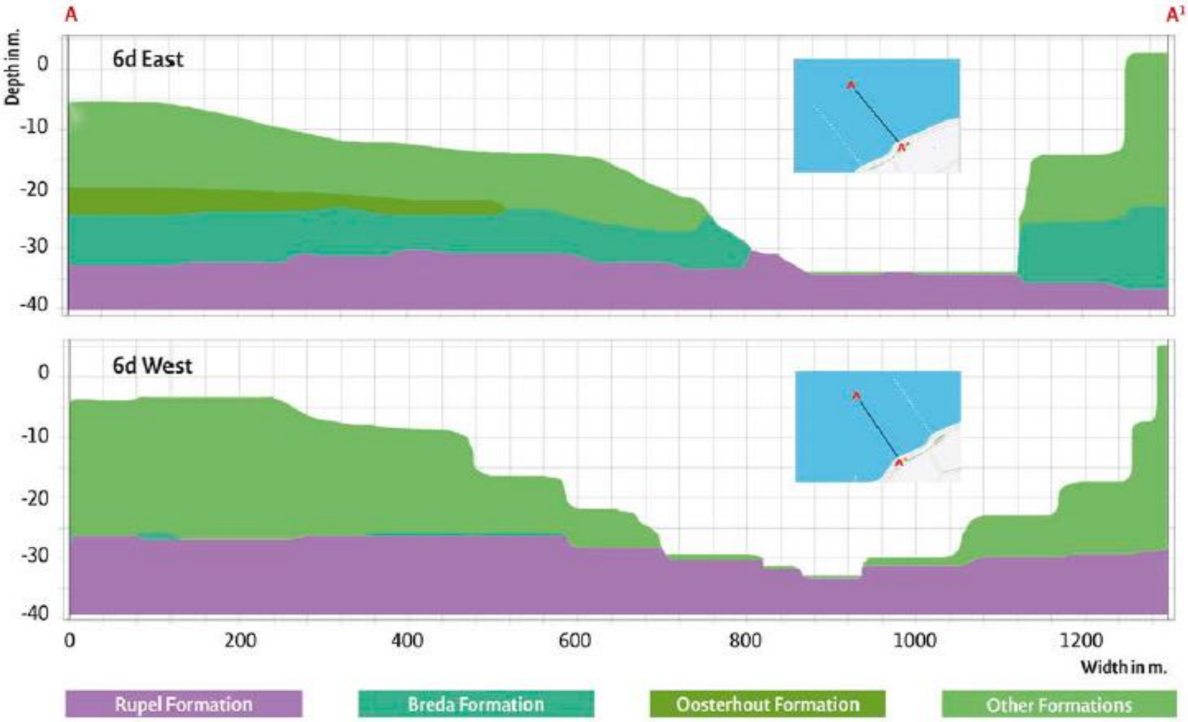

Figure 2. Profile of site 6d of the Westerschelde Estuary (Image from Post & Reumer, 2016).

The formations present in the Westerschelde Estuary (from bottom to top) are the Rupel Formation (Rupelian), the Breda Formation (Langhian-Zanclean), the Oosterhout Formation (Zanclean – Piacenzian), the Maassluis Formation (Gelasian), with Holocene deposits on top (Drees, 1986). As can be seen in Figure 2, the river Scheldt cuts deeply through these formations, eroding through the Breda Formation and exposing the Rupel Formation (Du Four et al., 2006; Post & Reumer, 2016). This indicates the exposure to be of Oligocene to Miocene age.

The material from the trawling expedition is from the Breda Formation, which consists of Langhian-Zanclean strata (Post & Reumer, 2016). The Breda Formation is a regional lithostratigraphical unit consisting mostly of marine, locally glauconitic sand- and claystones (Doppert et al., 1975). The formation mainly consists of (very) fine sand with grey-green to black-green glauconite, and contains carbonate (Westerhoff, 2003). Occasional pyrite, phosphorite, vivianite, and shark teeth as well as other fossilized, unidentified bones can be found (Westerhoff, 2003).

A detailed stratigraphical analysis of the Miocene of the North Sea Basin based on organic-walled dinoflagellate cysts has been done by Munsterman & Brinkhuis (2004). They defined fourteen informal dinocyst zones for the southern North Sea Miocene (SNSM) which includes an age-model (Munsterman & Brinkhuis, 2004). The age model has later been recalibrated to Ogg et al. (2016), enabling more accurate dating based on dinocyst assemblages. The Westerschelde specimen has been assigned to zone SNSM12 (Munsterman, 2017), which is associated with the Breda Formation and is aged early-middle Tortonian (Munsterman & Brinkhuis, 2004; Munsterman, 2017). Zone SNSM12 is defined by “The interval from the HO of *Cannosphaeropsis passio* to the HO of *Palaeocystodinium golzwense*” (Munsterman & Brinkhuis, 2004).

Materials and Methods

Materials

This study investigates a newly discovered dermochelyid carapace fragment: specimen NMR 9988-0661. The name ‘Westerschelde specimen’ will be used synonymously to NMR 9988-0661. Furthermore, the type specimen of *Psephophorus polygonus* NHMW 2011/0330/0001 has been re-studied, along with a distinctive isolated ossicle of *P. polygonus*, NHMW 2011/0151/0001. Additionally, two *Dermochelys coriacea* specimens have been studied: RBINS 268 from Cape of Good Hope, South Africa, and RBINS 15516 from Mariakerke (Oostende), Belgium.

Phylogeny

The fossil carapace NMR 9988-0661 has been retrieved and prepared by the Natural History Museum, Rotterdam. All measurements have been made by use of measuring tape. A detailed analysis of the dermochelyid phylogeny has been carried out based on the cladistic analysis of Wood et al. (1996), concerning 13 different genera within the family Dermochelyidae. Based on own observations and new insights, the following alterations have been made:

- When a character is not applicable to the specimen/species, a '-' has been indicated, whereas Wood et al. (1996) used the indicator 'absent'.
- *Psephophorus polygonus* characters 10 and 11 have been altered, stating it does have an expression of the ridge on the internal side (= 0), and that it does have tectiform ('roof-shaped') ridges (= 1). Furthermore, characters 14 and 15 have been filled out based on the argument that both dorsal and visceral flexure is present (14 = 0; 15 = 1).
- Alabama specimen character 13 has been altered to absent (0) because no undulating ridge crest is visible on its image in Wood et al. (1996).
- *Psephophorus calvertensis* characters 13 and 19 have been edited from '?' in Wood et al. (1996) to: containing an undulating ridge (= 1), and the ossicles do not vary greatly in size and shape (= 0).
- Character 16 'pointed in cross-section' has been specified in three factors, where absent = 0; the outgroup, Japan specimen and *Eosphargis* = 1 as they have scuti rather than ossicles, but the keel on the scuti is pointy; and present = 2.
- Character 17 'sunflower patterns' has been differentiated between big and elongated = 1 and small and circular = 2.
- Characters 20 to 22 from Wood et al. (1996) have been fused together as one character.
- Characters 21 to 24 have been added (see Cladistics).

All characteristics (1 to 24) have been evaluated for NMR 9988-0661 and it has been added to the matrix as 'Westerschelde specimen', to determine which species it belongs to (Table 1). Each characteristic is briefly described in Appendix 1. For full descriptions, see Wood et al. (1996) and the Cladistics section below. With this newly created classification, a new cladogram has been created using PAUP 4.0 beta (Swofford, 1998) which resulted into a consistency index of 0.9556, and a retention index of 0.9770.

Table 1. Data matrix of taxonomic characteristics of dermochelyids, numbers 1 to 20 from Wood et al. (1996) and newly added 21 to 24. The 13 groups are as in Wood et al. (1996), with addition of the new Westerschelde specimen and a second Dermochelys coriacea specimen. Newly added characters (21-24) are thoroughly described in the Cladistics section of Phylogeny.

Characters	**1-5**	**6-10**	**11-15**	**16-20**	**21-24**
Outgroup	00000	0002-	-----	1000-	-000
Japan sp.	00001	0002-	-----	1000-	-000
Eosphargis	00101	1102-	-----	1000-	-001
Natemys peruvianus	11111	??100	-0000	0111-	0012
‘Psephophorus’ rupeliensis	11111	1?100	-0000	0111-	0012
New Zealand sp.	11111	?1100	-0000	0000?	1021
Egyptemys oregonensis	11111	??111	01010	00011	1121
Egyptemys eocaenus	11111	?1111	01010	00011	1121
Cosmochelys dolloi	11111	?1111	01000	20012	1121
Alabama sp.	11111	??110	1?001	0201?	1121
Psephophorus polygonus	11111	??110	10101	02002	1123
Psephophorus calvertensis	11111	??110	1?101	02002	1123
Westerschelde sp.	1111?	??110	1?101	02002	1123
Dermochelys coriacea	11111	11110	10101	22013	2234
Dermochelys coriacea 2	11111	11110	10101	22013	2234

Size reconstruction

To reconstruct the approximate size of the Westerschelde specimen, two *Dermochelys coriacea* specimens were studied. The analysis focused on the distance between their ridges (Table 2). RBINS 268 consists of a complete *D. coriacea* carapace with a carapace curved length along the median ridge of 140.2 cm, and a maximum carapace curved width of 105.3 cm. RBINS 15516 is a leathery remainder of the carapace with a maximum curved length of 149.0 cm. RBINS 268 has been measured on straight distance between ridges to avoid bias of variability in ridge steepness and size; RBINS 15516 has been measured on curved distance between ridges due to large curvatures in the structure, which did not enable accurate straight distance measurement. The measurements were taken at the front and middle of the carapace, as shown in Figure 3. Angle variability between ridges has also been measured for RBINS 268.

Table 2. Measurements of the distance between the different ridges of Dermochelys coriacea specimens RBINS 268 and RBINS 15516.

Between ridges (cm)	**1 and 2**	**2 and 3**	**3 and 4**	**4 and 5**	**5 and 6**	**6 and 7**
RBINS 268 – front	17.5	15.2	16.7	16.1	16.8	16.8
RBINS 268 – middle	15.0	17.0	18.6	17.2	18.4	15.3
RBINS 15516 – front	-	20.0	17.0	16.7	18.9	17.1
RBINS 15516 – middle	-	16.8	18.2	17.9	16.7	14.3*

*= this part was highly curved

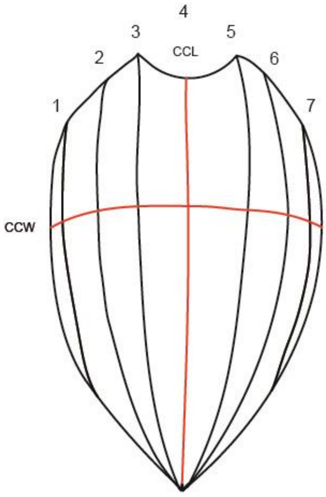

Figure 3. Schematic drawing of a *Dermochelys coriacea* carapace. The red lines indicate measurement locations: CCL = curved carapace length, CCW = curved carapace width. The ridge numbers are indicative for Table 2.

XRD-Analysis

X-Ray Powder Diffraction (XRD) has been performed on a loose ossicle broken off from of the Westerschelde specimen, as well as on sediment originating from the specimen. XRD-analysis was primarily used to determine the carbonate content in the carapace and the main mineral composition of the sediment. In preparation of the XRD-analysis, the ossicle was first surrounded by Araldite DBF to avoid potential destruction, prior to being sawn in half with use of a diamond saw. These non-weathered surfaces were then used for analysis. It was analysed through normal XRD-analysis which analysed the whole prepared surface, including some remaining sediment and Araldite DBF. To correct for the Araldite DBF, a separate analysis of just the Araldite DBF was also performed. The sediment was first grinded to an approximate size of 35 µm, and was then analysed as well.

Systematic palaeontology

Order TESTUDINES Linnaeus, 1758

(CHELONII Brongniart, 1800; Latreille, 1800)

Family DERMOCHELYIDAE Gray, 1825

Genus *Psephophorus* Meyer, 1847

Psephophorus polygonus Meyer, 1847

Neotype: NHMW 2011/0330/0001

Material studied: NMR 9988-0661

Locality: The carapace was recovered in area 6d of the Westerschelde Estuary, province of Zeeland, The Netherlands (Figure 1). It was retrieved in the NMR expedition 2014-3, December 17, 2014 tow no. 3 (Post & Reumer, 2016; Post et al., 2017).

Age: Late Miocene, early-middle Tortonian, 11.5-8.8 Ma (Munsterman, 2017).

Description of the Westerschelde specimen

Carapace - Because the specimen only consists of a carapace, the analysis and diagnosis is purely based on the morphology of the carapace and its ossicle arrangement. Specimen NMR 9988-0661 (Figure 4A) measures 34-43 by 51 cm. The well preserved carapace is made up of a mosaic of ossicles with varying sizes: the medial side average is 16.7 mm (n=22) and the lateral side average is 18.5 mm (n=22) resulting into an overall average of 17.6 mm. In the centre, one ridge is prominently visible. In cross-section, the ridge structure on the ventral side of the carapace is oriented in a rounded arch similar to the dorsal side of the carapace (Figure 4B). The ridge is not steep: it has an angle of approximately 15° on the external side and of 12° on the visceral side. The slope extends far onto the adjacent ossicles. The shape of the ridge is slightly tectiform with a rounded off top. The maximum distance from the ridge to the edges of the specimen is 21.5 cm on the lateral side and 20.7 cm on the medial side as in Figure 4A. The ridge ossicles are on average 24 mm long (n=11), but the shape of the ossicles varies from elongate to semi-circular, with maximum diameters of 31 and 14 mm,

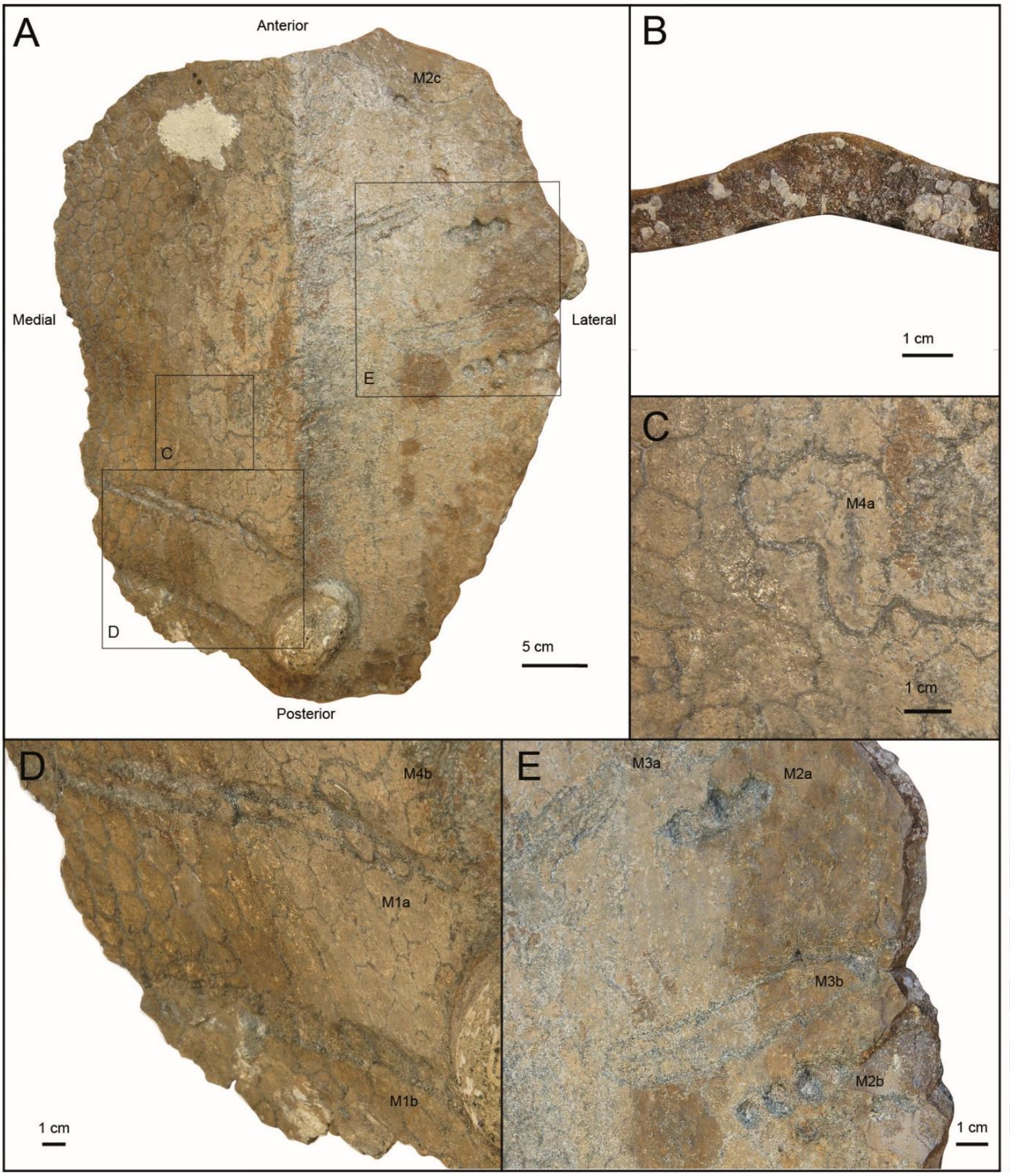

Figure 4. A: dorsal view of the Westerschelde specimen, a well preserved carapace fragment (NMR 9988-0661). B: anterior view of the ridge. C: a rounded 'sunflower' ossicle on the left and homogeneous curved mark (M4a) that penetrated the surface of the bone on the right. D: two parallel scratches (M1) which have penetrated the surface of the bone. E: quasi-parallel circular bite marks (M2) penetrating over halfway into the bone, and circular scratch structures (M3) penetrating into the surface of the bone.

respectively. There is one circular 'sunflower' ossicle visible, which is a larger (30 mm) ossicle with scalloped margins surrounded by other ossicles (Wood et al., 1996; Figure 4C).

The chemical composition of the carapace bone determined by XRD-analysis is listed in Figure 5A. It shows the presence of carbonate-fluorapatite and fluorapatite, as well as calcite and quartz.

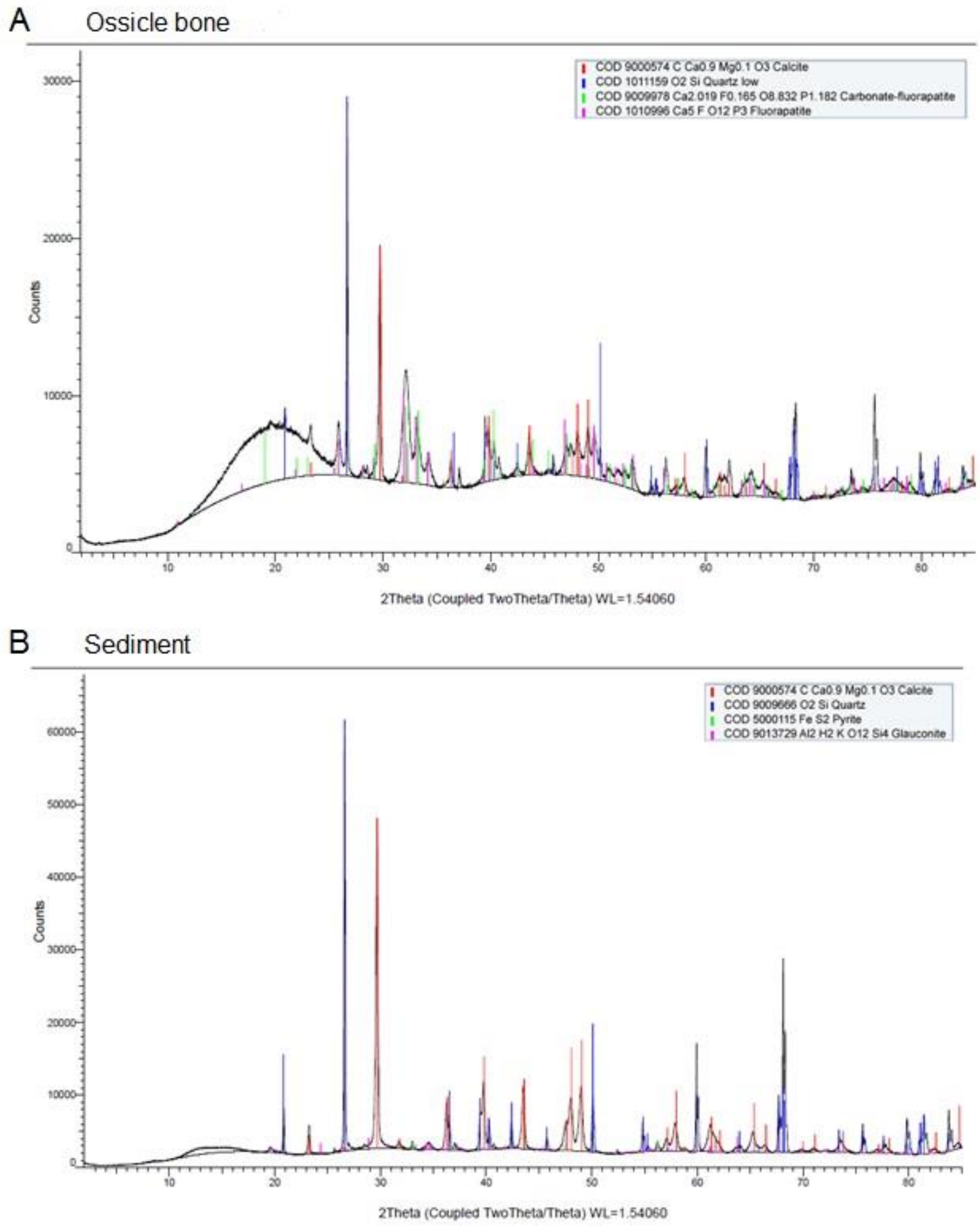

Figure 5. XRD-analysis of A: an ossicle bone fragment of NMR 9988-0661. B: the sediment removed from the carapace during preparation.

Taphonomy - There are several secondary marks on the carapace. Firstly, a pair of ‘scratches’ perpendicular to the ridge are present on the carapace (Figure 4D). These are named marks 1 (M1a, b). The top scratch ‘M1a’ consists of two different scratches scraping off the surface of the carapace, displacing some of the bone. The ossicle boundary structures are still visible. M1a is in total 19.5 cm long and the two depressions are 0.7 cm and 0.5 cm wide (top and bottom, respectively). The lower scratch ‘M1b’ is one big depression in which material has been removed rather than displaced. The ossicle boundaries are still visible, resulting into a ‘ladder’ pattern of deeper and less deep depressions where the ossicle boundary is cut through deeper than the ossicle surface. M1b is 16 cm long and 1.6 cm wide. The two scratches look different in character but are oriented parallel to each other.

Secondly, two bundles of deeper depressions are present, named marks 2 (M2a-c) (Figure 4E). The bundles consist of 3 to 4 aligned holes of on average 1 cm across, with a slightly pointy V-shaped structure. They penetrate over halfway into the bone. The two bundles are aligned quasi-parallel. There is a single ‘hole’ visible on the anterior side (‘M2c’, Figure 4A) with a shape similar to the aligned holes. Therefore, it is possibly of the same origin and so it will be considered part of M2 too.

Thirdly, elongated circular shapes are present on the carapace with a slight depression in the center following the elongation of the surrounding feature (Figure 4E). These shapes will be named marks 3 (M3a, b). The structures are 8.6 cm and 12.4 cm long (M3a and M3b, respectively). M3a and M3b are oriented (nearly) parallel to each other, and the distance between the two is comparable to the distances between the two M2 marks.

Lastly, there are thin depressions visible on the carapace of 2 mm thick (marks 4: M4a, b; Figure 4C, D). The homogeneous structures are mostly curved, and appear to follow the edges of ossicles. However, the structures also frequently cross through the ossicles. One mark also crosses through the M1a structure (Figure 4D).

Sediment - The dorsal side of the carapace has high quantities of sediment still attached to the specimen. The sediment consists of poorly sorted fine calcareous gray sandstone, with abundant larger glauconite pebbles of up to 5 mm. The XRD-analysis results of the sediment are shown in Figure 5B, indicating a high abundance of quartz as well as calcite. The presence of glauconite as well as pyrite is consistent with the content of the Breda Formation (Westerhoff, 2003; See Geol. Setting). Several shell fragments of up to 3 cm were found in the highly bioturbated sedimentary assemblage. The bioturbation is clear by the presence of a variety of burrows ranging from 1.5-5 mm in thickness.

Description of other specimens and comparison to the Westerschelde specimen

In order to get the best possible idea of to which taxonomic group the Westerschelde specimen belongs to, the *Psephophorus polygonus* neotype has been studied, as well as an isolated ossicle from the same locality (Delfino et al., 2013).

The Psephophorus polygonus type specimen - The type specimen of *Psephophorus polygonus*, NHMW 2011/0330/0001, is in fact a neotype as the original type specimen is (partly) lost. The specimen has been studied to compare it to the Westerschelde specimen. It is a carapace fragment of approximately 38 by 33 cm with some extra loose ossicles still attached to the sediment, and it contains a steep ridge in the middle. The type specimen originates from Devínska Nová Ves, Slovakia, and is dated Late Badenian (Delfino et al., 2013) or latest Langhian (Ursula Göhlich, pers. comm.). The ossicles of the neotype and those of the Westerschelde specimen are highly similar in shape; both carapaces are made up of a mosaic of irregular ossicles. An average ossicle size of 23 mm is recorded for the neotype (n=16), compared to17.6 mm for the Westerschelde specimen. The thickness of the neotype carapace is 6 mm, whereas that of Westerschelde specimen is 8 mm at the lowest. The neotype ridge has a distinct, steep angle that is located on the elongated anteroposterior ridges only, whereas the Westerschelde specimen shows a gradual height decrease along multiple adjacent ossicles. The ridge cross-section is not fully exposed, but it is still evident that the visceral surface is almost straight (Figure 6A). The neotype also contains two subtle, rounded versions of a ‘sunflower pattern’, similar to the ones found in the Westerschelde specimen.

The specimen NHMW 2011/0151/0001 – The ossicle NHMW 2011/0151/0001 previously described by Delfino et al. (2013), has been re-analysed for this study. It is an isolated ridge-ossicle retrieved from the same locality as the *Psephophorus polygonus* type specimen (Delfino et al., 2013). The overall ridge cross-section is highly curved, also on the visceral side (Figure 6B). Even though this appears exceptional for *P. polygonus* (Wood et al., 1996; Delfino et al., 2013), the overall aspect of the ossicle still appears similar to the *P. polygonus* type specimen. The structure differs from the Westerschelde specimen in its angle, which is significantly steeper (See discussion). Furthermore, the ridge of NHMW 2011/0151/0001 is located fully on one ossicle, whereas in the Westerschelde specimen ossicle thickness reduces gradually over the distance of adjacent ossicles.

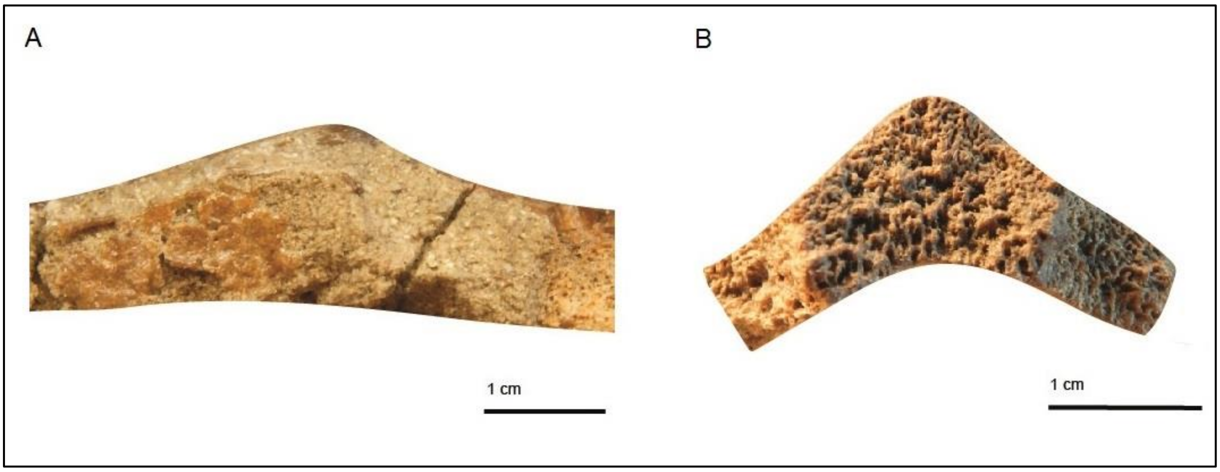

Figure 6. A: cross-section of the ridge of the *Psephophorus polygonus* neotype NHMW 2011/0330/0001. B: cross-section of the ridge of an isolated ridge ossicle NHMW 2011/0151/0001 (Delfino et al., 2013)

Phylogeny

Based on 22 characters, Wood et al. (1996) created a cladogram of dermochelyids. The phylogenetic representation of Wood et al. (1996) is basic, but due to the carapace-specific identifications, clear variations in carapace morphology are shown between different taxa. Although the basic variations between species are clearly shown, there is still a three-way branch of *Psephophorus calvertensis* (Palmer, 1909), *Dermochelys coriacea* (Vandelli, 1761) and the Alabama specimen, a slab from the Eocene of Alabama that still needs to be described (Wood et al., 1996). *Psephophorus polygonus* is positioned as the sister taxon of this complex system (Wood et al., 1996). The Westerschelde specimen is of Tortonian age (Munsterman, 2017), and based on Wood et al. (1996)'s characteristics, it corresponds best with *Psephophorus calvertensis*. The main characteristics are that the Westerschelde specimen also has a tectiform ('roof-shaped') ridge, and the ridge in cross-section is visible on both the dorsal- and ventral side of the carapace. Other variations of *Psephophorus* that are not included in the analysis by Wood et al. (1996) are: *Psephophorus scaldii* (Van Beneden, 1871), which is described on a humerus, and *Psephophorus californiensis* (Gilmore, 1937), which is described on a femur. Therefore, both could not be considered in Wood et al. (1996)'s analysis, nor in the current one.

On the other hand, the definition of *Psephophorus polygonus* (Meyer, 1847) is based on just one slab and recent literature has suggested that *P. polygonus* can also have tectiform ridges, curvatures on the ventral side (Delfino et al., 2013), and sunflower patterns (Karl et al., 2012). All of these characteristics agree with the Westerschelde specimen. This leaves us with the question whether *P. polygonus* is a more diverse taxon than previously suggested by Meyer (1847) and Wood et al. (1996), or whether it is just a wastebasket taxon.

So could the Westerschelde specimen also be *Psephophorus polygonus*? The only record of *Psephophorus calvertensis* is by Palmer (1909), from Maryland. No other similar specimen is reported after that. On the other hand, *Psephophorus polygonus* has several finds in Europe: Italy (Chesi et al., 2007), Denmark (Karl et al., 2012), and Slovakia (Meyer, 1846; Delfino et al., 2013). The Westerschelde Estuary's geographical location during the Miocene is at the southern part of the North Sea. During the Miocene, the sea spans across the entire Netherlands and continues all the way around Denmark. Several findings of *Psephophorus polygonus* specimens (Karl et al., 2012) in the Gram Formation, Denmark does not only imply a geographical agreement because it is from Europe, but moreover, it is from the same sea. The Westerschelde is therefore the second locality to confirm presence of dermochelyids in the North Sea. Additionally, a *Carcharocles megalodon* specimen (Bendix-Almgreen, 1983) has also been found in the Gram Formation, which is possibly similar to the 'giant shark' found in the Westerschelde assemblage (Post & Reumer, 2016). The Gram Formation is dated to Serravalian-Tortonian age (Piasecki, 2005), which is comparable to the Breda Formation being of Langhian-Zanclean age (Post & Reumer, 2016). The Tortonian age of the Westerschelde specimen supports the correspondence with the *P. polygonus* from Karl et al. (2012). Therefore, the presence of *P. polygonus* in the same waters strongly argues that the Westerschelde specimen is in fact *P. polygonus*.

The only clear phylogenetic differences between *Psephophorus calvertensis* and *Psephophorus polygonus* based on Wood et al. (1996)'s record are the ridge being expressed on the external surface of the carapace only, and its ridge either tectiform or arched shaped. It is stated that *Psephophorus polygonus* would not have a visceral expression of the ridge, and no tectiform or arched ridge shape, whereas *Psephophorus calvertensis* has both characters (Wood et al., 1996). However, in a more recent study, Delfino et al. (2013) argues that *Psephophorus polygonus* does have tectiform ridges and also contains a curved ventral side on the ridge. A tectiform ridge shape does not have to indicate the ridge to be pointy; as long as the shape slopes down like a roof, it counts as 'tectiform'. This would mean that the main differences between *Psephophorus calvertensis* and *Psephophorus polygonus* are no longer valid. This would indicate that both *Psephophorus calvertensis* and the Westerschelde specimen are *Psephophorus polygonus*. Therefore, a re-evaluation of this characteristic is necessary.

Re-evaluation of the ventral ridge architecture as taxonomic character

Wood et al. (1996) considered the taxonomic characteristics of *Psephophorus polygonus* to be the specific ridge architecture which he described as “prominent broad ridge, rounded at apex, whose crest undulates up and down along its length, and whose presence is not indicated on the visceral surface of the bony mosaic” (Wood et al., 1996). The taxonomic value of the visceral structure of the ridge ossicle in *P. polygonus* has already been questioned by Delfino et al. (2013) who assigned NHMW 2011/0151/0001 to *P. polygonus*, which has a strongly angled visceral surface (Figure 6, 7). The cross-sections of the standard *P. polygonus* ridge structure as in Wood et al. (1996), the Westerschelde specimen, and NHMW 2011/0151/0001 are shown in Figure 7. With the addition of the Westerschelde specimen, it is now argued that the visceral curvature is indeed not to be considered a taxonomic characteristic for *P. polygonus*. It can be seen that the Westerschelde specimen has a ridge cross-section with a curving visceral side, although the angle is less acute than in NHMW 2011/0151/0001. Possible variability in *P. polygonus* visceral angles from 180° (straight) to 125° (NHMW 2011/0151/0001) is analysed with use of the carapace architecture of a *Dermochelys coriacea* specimen.

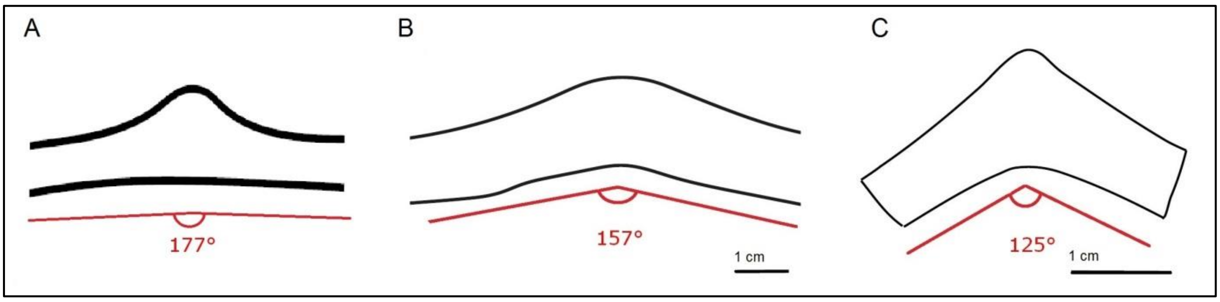

Figure 7. Schematic cross-sections of ridge ossicles and their corresponding visceral angles. A: standard ridge structure of *Psephophorus polygonus* according to Wood et al. (1996). B: ridge structure of the Westerschelde specimen. C: isolated ossicle NHMW 2011/0151/0001 identified as *Psephophorus polygonus* (Delfino et al., 2013)

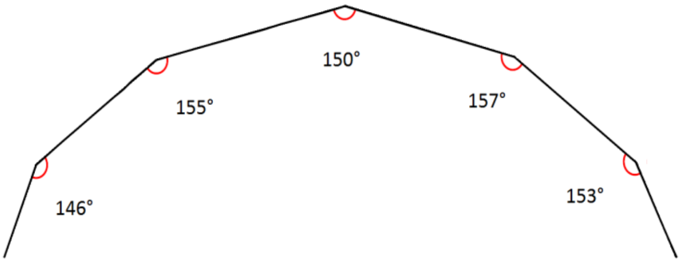

Figure 8. Schematic cross-section of a *Dermochelys coriacea* carapace (RBINS 268) with its corresponding angles of the ridges. Relative distances between ridges are an approximation.

In order to fully understand the angle variability within Dermochelyid ridges, a full *Dermochelys coriacea* specimen has been studied (RBINS 268). The only extant leatherback turtle has proven to be of use in the comparisons with *Psephophorus* (Delfino et al., 2013) and therefore it can be assumed that the (carapace) structure of *Dermochelys* is comparable to that of *Psephophorus*. Specimen RBINS 268 was used to measure each ridge angle (Figure 8). It shows that every ridge accommodates an angle resulting into the curved structure of the carapace, because normal (non-ridge) ossicles remain (relatively) straight. The curved structure of the carapace is thus generally created by the angles at the ridges. This shows that the near 180° angle as depicted by Wood et al. (1996) is not realistic, as there will always be an angle at which the plates in between ridges will vary relative to each other due to the curved shape of the carapace as a whole. The curved shape of the carapace is an evolutionary adaptation to keep the flow around the body laminar (Deraniyagala, 1936; Hendrickson, 1980) and provide increased hydrodynamic performance (Bang et al., 2016). The visceral side should therefore have an approximate curvature at all times.

The steep angle of NHMW 2011/0151/0001 is however not realistic either. The *Dermochelys* carapace counts 7 ridges, from which at least 5 have equal angles. Assuming similar proportions, a hypothetical *Psephophorus* carapace would have a structure encompassing over 300°, which is nearly circular. In contrast, the *Dermochelys* carapace encompasses only ±150° over the 5 equal angles (Figure 8). As there is no other ossicle specimen found like NHMW 2011/0151/0001, a definite conclusion on how this structure varies so significantly compared to the other specimens, cannot yet be drawn.

Cladistics

Based on several alterations (See Materials and Methods) and additional characteristics added to the matrix initially created by Wood et al (1996), a new matrix has been created (Table 1). The additional characteristics 21 to 24 are described below.

21. Ossicle size; big/intermediate/small. The size of the ossicles is a relative property, but the difference in size of the dermochelyid ossicles is so explicit, that we consider it appropriate to use it as taxonomic character. The outgroup, the Japan specimen, and *Eosphargis* have scuti and are therefore scored ‘not applicable’ (-); especially large ossicles are found in *Natemys peruvianus* and *‘Psephophorus’ rupeliensis* and are scored ‘0’; the New Zealand specimen, *Egyptemys, Cosmochelys,* the Alabama specimen, *Psephophorus polygonus, Psephophorus calvertensis,* and the Westerschelde specimen all have intermediately sized ossicles (= 1), while *Dermochelys* has very small ossicles (= 2).

22. Carapace shape; convex/convex between ridges/concave between ridges. Most sea-turtle's carapaces are convex. Ridge-bearing carapaces are mostly convexly shaped in between their ridges, such as *Egyptemys* and *Psephophorus*, whereas the extant *Dermochelys coriacea* has a concavely shaped structure in between ridges, but still an overall convex shape. The character 'carapace shape' is scored as follows: convex carapace without (lateral) ridges = 0; a carapace that is convex between its ridges = 1; and a carapace that is concave between its ridges = 2.

23. Thickness of the ossicles; thick/intermediate/small. Similar to ossicle size, the thickness of ossicles is also a relative property that is considered explicit enough to be considered as taxonomic character. The outgroup, the Japan specimen and *Eosphargis* have scuti, so they are scored '0'; *Natemys peruvianus* and *'Psephophorus' rupeliensis* have particularly thick ossicles and are scored '1'; The New Zealand specimen, *Egyptemys*, *Cosmochelys*, the Alabama specimen, *Psephophorus polygonus*, *Psephophorus calvertensis* and the Westerschelde specimen all have intermediately thick ossicles (= 2), while *Dermochelys* has highly reduced, thin ossicles (= 3).

24. Age; pre-Eocene/Eocene/Oligocene/Miocene/Recent. The age of a specimen is considered as taxonomic character because every species included originates from a relatively fixed timeframe. This is therefore argued to be taxonomically relevant. The hypothetical outgroup and the Japan specimen are assigned as pre-Eocene (= 0); *Eosphargis*, the New Zealand specimen, *Egyptemys oregonensis*, *Egyptemys eocaenus*, *Cosmochelys dolloi* and the Alabama specimen are all of Eocene age (Wood et al., 1996) and therefore scored '1'; *Natemys peruvianus* and *'Psephophorus' rupeliensis* are of Oligocene age (Wood et al., 1996) (= 2); *Psephophorus polygonus*, *Psephophorus calvertensis* and the Westerschelde specimen are of Miocene age (= 3); and *Dermochelys coriacea* is the extant species (recent = 4).

The resulting cladogram is shown in Figure 9. It bundles *Psephophorus calvertensis* together with *Psephophorus polygonus* and the Westerschelde specimen. A notable difference is the Alabama specimen not being as closely related to the *Psephophorus* clade anymore as in Wood et al. (1996). Considering that the Alabama specimen is from the Eocene whereas the other two originate from the Miocene, this is a likely position. It can be argued that the Alabama specimen is a predecessor of *Psephophorus*. However, it has to be described before this can be concluded.

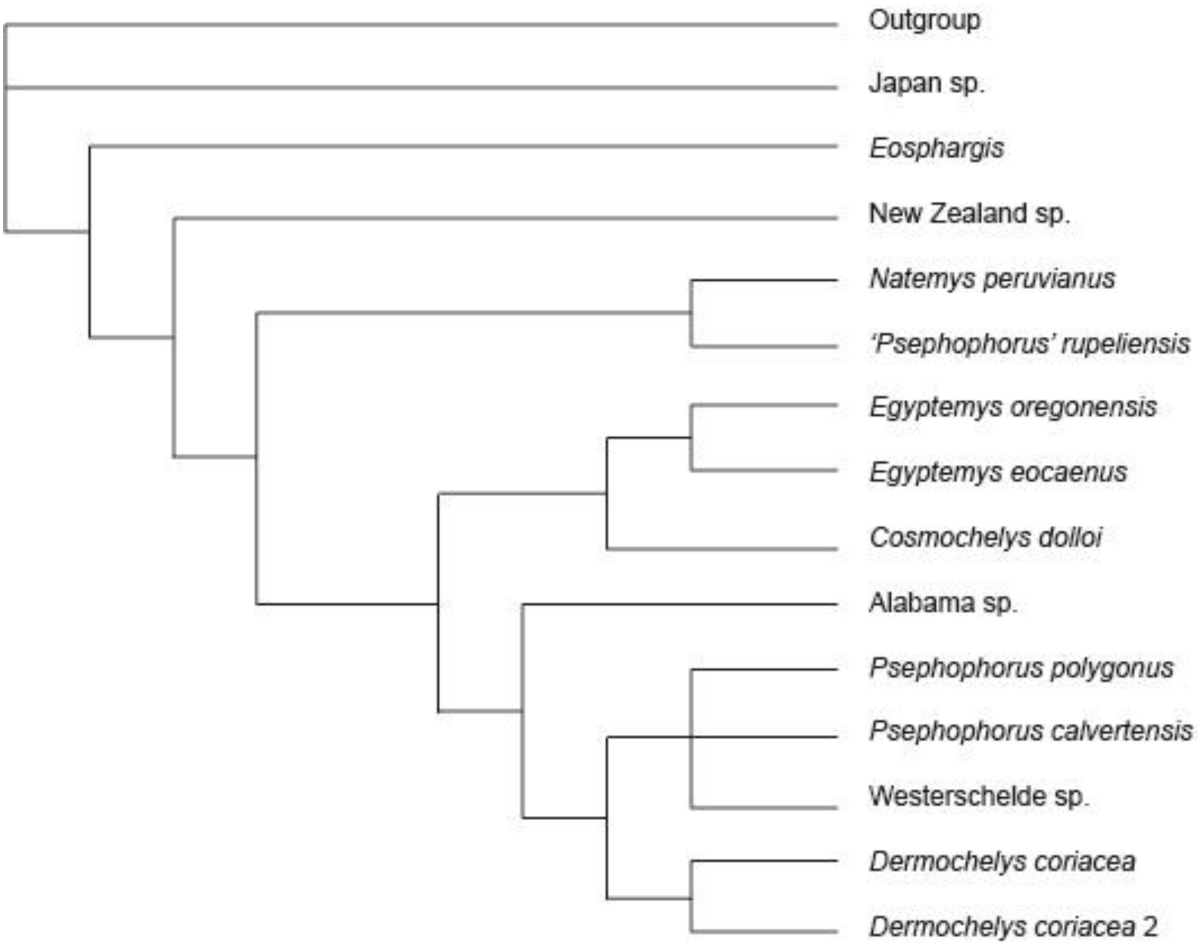

Figure 9. New cladogram based on Wood et al. (1996), showing the relationships within Dermochelyidae. All characters are described briefly in Appendix 1. For full descriptions, see Wood et al. (1996) and section Cladistics.

Different variations of the matrix of Table 1 have been executed in PAUP 4.0 to determine the influence of different characters on the resulting tree. The characters 14 and 15 of *Psephophorus polygonus* have been changed back to '?' similar to Wood et al. (1996). It becomes apparent that editing these characters does not provide any taxonomic relevance, because the resulting cladogram remains equally viable. This confirms the irrelevance of the visceral angle as taxonomic character for *Psephophorus polygonus*. Furthermore, characters 11 and 16 have been removed fully from the analysis to test the relevance of the ridge architecture in the overall dermochelyid taxonomy. This also resulted into the same cladogram, and is therefore not considered a key factor in dermochelyid evolution. The most important character to differentiate the group of *Psephophorus polygonus*, *Psephophorus calvertensis*, and the Westerschelde specimen from *Dermochelys coriacea* is the strong variability in ossicle size (character 19). This is a character that has been modified from Wood et al. (1996) for *Psephophorus calvertensis.* The Alabama specimen is in turn differentiated because of its lack of an undulating ridge crest (character 13) which is also a character that has been added for this study.

These results indicate that all factors that differentiated *Psephophorus calvertensis* from *Psephophorus polygonus* are no longer present. Based on the newly made cladogram (Figure 9), it is argued that *Psephophorus calvertensis* is within the genetic variability of *Psephophorus polygonus*, and is not a sister taxon. This is partly in agreement with Delfino et al. (2013) who proposed for *Psephophorus calvertensis* and *Psephophorus californiensis* to be junior synonyms of *Psephophorus polygonus*. As for *Psephophorus californiensis*, it is impossible to confirm whether this species belongs to *Psephophorus polygonus* too, because it is based on a femur (Gilmore, 1937). As for *Psephophorus calvertensis*, it can now be confirmed. The new specimen NMR 9988-0661 from the Westerschelde Estuary can therefore be assigned to *Psephophorus polygonus* too.

Discussion

Westerschelde reconstruction

Figure 8 indicates that the maximum angle variability for *Dermochelys coriacea* ridges is only 11°. The ridge angle of the Westerschelde specimen (157°) corresponds best with ridges 3 and 5, but due to the small variability, any of the ridges is a possible match. Therefore, the angle cannot help identify which ridge the one on NMR 9988-0661 corresponds to. The Westerschelde specimen must have had more space between its ridges than RBINS 268, because the measurements from the Westerschelde ridge to either side of the specimen exceed the measurements of Table 2. The extra spacing may have an effect on how the angles of the Westerschelde carapace are oriented, because the ridge angles of *Psephophorus* do not have to be the equal to the angles of RBINS 268. Due to the small angle variability and uncertainty about the influence of size, it is impossible to indicate the exact location of the Westerschelde fragment on the *Dermochelys* carapace.

The ridge on the Westerschelde specimen does not show a perfectly straight line along the anteroposterior axis (Figure 4A). Instead, a slight curve is present, which makes it unlikely to be the median ridge, as the latter is fully straight throughout the longitudinal axis. Furthermore, the ridge prominence appears to be weakening towards the posterior side of Figure 4A. This may be caused by erosion, or it could be indicative of its position on the carapace: far to the back of the turtle. It can be seen in *Dermochelys coriacea* that its ridges weaken towards the back of the carapace, where the outer ridges fully disappear and the middle ridges come together. The ridges stay fully intact towards the front of the carapace. Therefore, it is argued that the bottom as seen in Figure 4A is the posterior side, and the top is the anterior.

Table 2 shows the curved distances between ridges for two *Dermochelys coriacea* specimens. Based on the assumption that the *Psephophorus polygonus* carapace consisted of seven ridges just like *D. coriacea*, an approximate size reconstruction can be made with use of the relative size variations of RBINS 268 and RBINS 15516. For the Westerschelde specimen, the maximum measured distance from the middle of the ridge towards the edges of the fragment is 21.5 cm (lateral side) and 20.7 cm (medial side). Because there is no sign of a secondary ridge present in the Westerschelde specimen, these given distances are the minimum distances on either side of the ridge towards a hypothetical next ridge. Both these values exceed the maximum values of *D. coriacea*, as the average distances between the ridges for *D. coriacea* are 16.5 cm (RBINS 268) and 16.9 cm (RBINS 15516). With a hypothetical average of 21.1 cm for the Westerschelde specimen, the approximate curved carapace width would be 21.1*6 = 126.6 cm. RBINS 268 provides a length/width ratio: 140.2/105.3 = 1.33. Assuming an approximately constant length/width ratio, the Westerschelde specimen would have a curved carapace length of 126.6*1.33 = 168.6 cm. This value is considered a minimum size, because the specimen may originate from further towards the back of the turtle, where the width between ridges significantly decreases. In that case, the maximum average distance between ridges must be larger than 21.1 cm for the Westerschelde specimen.

Taphonomy

The different marks on the Westerschelde specimen are all believed to be secondary. None of the marks show signs of recovery, which indicates that the marks have been inflicted post-mortem or were the cause of its death.

Marks 1 (M1) - The structure of M1 suggests a pair of possible scores: where teeth of both sides of its jaw are dragged along the carapace, creating two grooves but not fully fracturing, yet still causing depressions on the bone. Since the scratches are elongated but not deep, scraping of an object (possibly teeth) with approximately 15 mm thickness is suggested. The thicknesses of the two separate scratches of M1b add up to the width of M1a, so it is suggested that scratch M1b is possibly created by a broken tooth like the scratch on Figure 4D of Drumheller & Brochu (2016). The parallel orientation of M1a+b and distance of 8.0 cm is a strong argument that M1 is created by a single organism with a jaw-width of approximately

8 to 10 cm. Potential predators include sharks, crocodiles, or predatory whales.

Marks 2 (M2) - M2 is a sub-parallel oriented pair of pits: it suggests teeth contacted the surface of the bone, leaving a depression approximately matching the shape of the teeth (Figure 4E). The depression never fully pierces through the bone. The shape resembles the ichnospecies *Nihilichnus nihilicus* (Mikuláš et al., 2006; Milàn et al., 2011) on a larger scale, so possibly originating from larger teeth. If these holes are indeed inflicted by teeth, they suggest a relatively circular shape and an approximately 4 mm wide crown. This reduces the probability for M2 to have been inflicted by sharks, as sharks do not have circular shaped teeth. The pairs of pits were situated 11.0 cm away from each other, suggesting a jaw width similar to M1. A physeteroid is a likely predator to have inflicted these marks. It is reasonable to assume that dermochelyids and physeteroids lived in the same waters in the Miocene because physeteroids were highly common in the Miocene. A Tortonian physeteroid specimen has been found in Italy in the Pietra Leccese sandstone (Varola et al., 1988), which is the same sandstone as from which the Italian *Psephophorus polygonus* findings of Chesi et al. (2007) originate. Another Italian physeteroid specimen was found close to the same locality (Bianucci & Landini, 2006). Recently, physeteroid teeth from the Westerschelde Estuary have been described (Reumer et al., 2017). Physeteroid teeth are rounded with a pointed crown, fitting the architecture of the pits of M2 (Bianucci & Landini, 2006; Reumer et al., 2017) which makes them a possible cause of the marks of the M2 type mark.

Marks 3 (M3) – The irregular structure of M3 shows variations in depression, with M3a cutting deeper into the bone, a structure that is similar to M1 (Figure 4E). Due to the presence of a curved shape in the structure, it is unlikely that a predatory action is the only cause. Instead, an invertebrate growth is suggested, as sea-turtles have a high variety of epibionts on their carapaces, such as molluscs, hydrozoans and algae (Caine, 1986; Frick et al., 1998; Frick et al., 2000). The resemblance with M1 suggests scraping. It is possible that more than one process has influenced the structure. A more precise identification of these marks is not possible.

Marks 4 (M4) – Much like M3, M4 has curved structures (Figure 4C, D). However, this structure has a relatively homogenous pattern in which bone has been removed equally along the whole pattern. The homogenous structure of M4 appears to follow the edges of the ossicles locally, although it also clearly crosses various ossicles at times (Figure 4C). This could be caused by an invertebrate epibiont that migrates along the surface of the carapace. By doing so, movement along the ossicle boundaries could be preferential, although sometimes an ossicle had to be crossed. The intersection of M4b with M1a indicates that M1 must have been formed prior to the formation of M4, because otherwise M1 would have eroded the structure of M4 completely. It is therefore probable that these marks have been formed over the whole timespan of the exposure of the fragment, rather than only just after the sea-turtle's death.

Paleobiogeography and evolution

With current understanding of *Psephophorus calvertensis* belonging to the species *Psephophorus polygonus*, a first step in determining all different kinds of *Psephophorus* is made. It can now be stated that *P. polygonus* ranged over the entire Atlantic Ocean, and possibly occupied the other oceans too. This is in agreement with Delfino et al. (2013) who also hypothesized for *Psephophorus* to have a broader geographic distribution than currently indicated (Delfino et al., 2013). The large size of *P. polygonus* similar to that of *Dermochelys coriacea*, along with the cosmopolitan ecology of both species, suggests a large resemblance. The carapace of *P. polygonus* must have been more massive than that of *D. coriacea* (Delfino et al., 2013), but due to its large size (Chesi et al., 2007; See above) it must have also been able to dive to great depths and swim across oceans.

A transition from thick, robust ossicles to small, thin, and thus more flexible ossicles is suggested as an evolutionary trait to allow deeper diving and higher survivability. With a thinner, flexible carapace, the pressure on its carapace would be reduced when diving to great depths and its geographical distribution could increase even more. However, the current data does not fully support this theory. The thickest ossicles in Table 1 are from *Natemys peruvianus* and *'Psephophorus' rupeliensis*, which are of Oligocene age (Wood et al., 1996). The older Eocene specimens already have intermediately thick ossicles. Therefore, this transition hypothesis is only valid from intermediate to thin ossicles from the Miocene to present.

Age complications and further research

The Westerschelde specimen has been dated by Munsterman (2017) who concluded it to originate from the SNSM12, 11.5-8.8 Ma. Another age measurement had been done by Veenhof (2015), who concluded it to be from zone SNSM10, which is 12.3-11.7 Ma. All other analysed material from the same locality originated from either SNSM13 or 14, which indicates Middle to Late Tortonian, rather than Early-Middle Tortonian age (Munsterman & Brinkhuis, 2004). Furthermore, a specimen described by Post et al. (2017) from the same Westerschelde assemblage has been dated Late Tortonian-earliest Zanclean (7.6-5 Ma), whereas Munsterman (2017) stated the same specimen to be of Late Tortonian age (8.1-7.4

Ma). Due to these inconsistencies of the dinocyst dating within the assemblage of the Westerschelde, it cannot be confidently proven that the Westerschelde sea-turtle carapace originates from the same assemblage. A thorough investigation on the whole Westerschelde collection must be performed to get a complete understanding of the Miocene fauna from the Westerschelde Estuary. With more data gathered, it will also be easier to determine possible variability in dinozones.

Currently, there are still too many *Psephophorus* variants, which causes for it to appear a wastebasket taxon. Without further study, this problem cannot be resolved. *'Psephophorus' rupeliensis* (Van Beneden, 1883) must be re-evaluated and likely to be re-named, because it is evident from both the current study as well as Wood et al. (1996) that it does not agree with the *Psephophorus* neotype. Furthermore, *Psephophorus californiensis* (Gilmore, 1937) and *Psephophorus scaldii* (Van Beneden, 1871) must be found in-situ along with a carapace fossil to be able to compare them with other specimens. It is possible that these bone-described species are described alongside a carapace-described species, while in fact they are the same. More fossils must be found and described in order to solve this ongoing problem in dermochelyid taxonomy.

Additionally, the XRD analysis has proven enough carbonate to be present to perform clumped isotope analysis on the specimen to reconstruct the body temperature of the sea-turtle. This can then be compared to the water temperatures reconstructed from carbonate analysis. It provides information on the animal's gigantothermy, which is the main reason for dermochelyids to be so successful worldwide (Pough et al., 2013). Due to its large body size, a dermochelyid can maintain its body warmth and thereby survive in colder environments than most other turtles. The contrast between its body temperature and the corresponding water temperature indicates the effect of gigantothermy on the animal. Furthermore, it provides another confirmation of its large size, because a large size is needed to create such a contrast in temperature. This will in turn provide more insight in leatherback turtles, and specifically the extinct genus *Psephophorus*.

Conclusions

The Westerschelde specimen is just a fraction of the entire Westerschelde assemblage from the trawling expedition in 2014 (Post & Reumer, 2016). After a thorough investigation, the sea-turtle carapace fragment is identified as *Psephophorus polygonus*. Based on cladistics analysis, it is suggested that the ridge architecture, especially ventral curvature, is not a reliable taxonomic character of *Psephophorus polygonus*. This concludes that the species

Psephophorus calvertensis is in fact also *Psephophorus polygonus*.

The Westerschelde specimen was rich in secondary surface lesions which are all considered post-mortem. Taphonomic analysis shows that M1 and M2 are likely to have been caused by a predator, where M2 is suggested to have been caused by a physeteroid. Marks M3 and M4 are suggested to be caused by invertebrate scavenging. The origin of these marks is suggested to have occurred over the whole timespan of the material's exposure, because of the overlap of M4 crossing over M1.

Dermochelyid specimens are still relatively scarce, and unless *Psephophorus californiensis* (Gilmore, 1937) and *Psephophorus scaldii* (Van Beneden, 1871) specimens are found together with carapace fragment(s), they can never be confidently assigned into the framework of *Psephophorus*. Therefore, more research is needed to learn whether these species also belong to *Psephophorus polygonus*.

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Appendix 1

Descriptions of the taxonomic characteristics used in Table 1 (edited from Wood et al., 1996).

1. Neural bones (present = 0, absent = 1)
2. Peripheral bones (present = 0, absent = 1)
3. Pleural bones (present = 0, absent = 1)
4. Shell scutes (present = 0, absent = 1)
5. Median plastral fontanelle (small or absent = 0, large = 1)
6. Plastral bones reduced to a rod-like peripheral framework (absent = 0, present = 1)
7. Broad, flat ribs (absent = 0, present = 1)
8. Shell composed of a mosaic of small bony ossicles (absent = 0, present = 1)
9. Anteroposterior ridges (or keels) on the ossicles of the carapace (absent = 0, anteroposterior keel on scuti = 1, present = 2)
10. Ridges expressed on external surface of carapace mosaic only (not applicable= -, absent = 0, present = 1)
11. Ridges either arched or tectiform (not applicable = -, absent = 0, present = 1)
12. Height of separate ridges (not applicable = -, uneven = 0, uniform = 1)
13. Undulating ridge crests (not applicable = -, absent = 0, present = 1)
14. Ridges rounded in cross-section on dorsal carapace surface but not expressed on underlying visceral surface (not applicable = -, absent = 0, present = 1)
15. Ridges rounded in cross-section of carapace with upward flexure of both dorsal and visceral surfaces (not applicable = -, absent = 0, present = 1)
16. Ridges pointed in cross-section (absent = 0, pointed keel on scuti = 1, present = 2)
17. Clusters of ossicles forming “sunflower” patterns (absent = 0, big and long = 1, small and circular = 2)
18. Some shell ossicles greatly elongated along anteroposterior axis (absent = 0, present = 1)
19. Ossicles vary greatly in size and shape (absent = 0, present = 1)
20. Number of ossicles between ridges (not applicable = -, 1 to 4 = 1, 5 or more = 2)
21. Ossicle size (not applicable = -, big = 0, intermediate = 1, small = 2)
22. Carapace shape (convex = 0, convex between ridges = 1, concave between ridges = 2)
23. Thickness of ossicles (scutes = 0, thick = 1, medium = 2, thin = 3)
24. Age of specimens (pre-Eocene = 0, Eocene = 1,Oligocene = 2, Miocene = 3, recent = 4)