A Miocene leatherback turtle from the Westerschelde (The Netherlands) with possible cetacean bite marks: identification, taphonomy and cladistics

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The Westerschelde Estuary in The Netherlands is well known for its rich yield of vertebrate fossils. In a recent trawling campaign aimed at sampling an assemblage of late Miocene marine vertebrates, over 5,000 specimens were retrieved, all currently stored in the collections of the Natuurhistorisch Museum Rotterdam. One of these is a well-preserved fragment of a dermochelyid carapace. The Westerschelde specimen is an interesting addition to the scant hypodigm of dermochelyids from the Miocene of the North Sea Basin. The carapace fragment is described and assigned to *Psephophorus polygonus* von Meyer, 1847. The secondary marks present on the fragment are suggestive of predation or scavenging. Furthermore, based on the physical traits of the Westerschelde specimen and a re-examination of specimens of *P. polygonus*, inclusive of the neotype held at the Naturhistorisches Museum Wien (Vienna, Austria), we argue that several previously assigned characteristics cannot be used as discriminative taxonomic properties amongst dermochelyids in general and of *P. polygonus* in particular. An improved cladistic analysis of dermochelyids is performed on the basis of previously defined and novel taxonomic characters. Our results indicate that *Psephophorus calvertensis* Palmer, 1909 is a junior synonym of *P. polygonus*. Hence, a new diagnosis of *Psephophorus polygonus* is proposed. The synonymy of *P. calvertensis* with *P. polygonus* also means that the latter had a cosmopolitan distribution, similar to the extant species *Dermochelys coriacea* (Vandelli, 1761).

KEY WORDS: Testudines, Dermochelyidae, *Psephophorus*, Cainozoic, North Sea Basin, taphonomy, systematics

Introduction

The Westerschelde Estuary is renowned for its rich yield of extinct vertebrates. During a trawling expedition by the Natural History Museum of Rotterdam in 2014, over 5,000 fossil mammalian remains were collected (Post & Reumer, 2016). This material is known to originate from a single locality, site 6d (Figs 1, 2) and, as such, is of great palaeontological and palaeoecological interest. The assemblage consists mostly of cetaceans, associated with vertebrae of an extinct shark and the present dermochelyid turtle carapace fragment, described in detail below.

The family Dermochelyidae is currently represented by a single extant species, *Dermochelys coriacea* (Vandelli, 1761). However, dermochelyids have been shown to have had a complex evolutionary history (Wood *et al*., 1996). The current record of extinct dermochelyid genera comprises the Palaeocene–Eocene *Arabemys* (see Tong *et al.,* 1999), the Eocene *Cosmochelys* (see Andrews, 1919), *Egyptemys* (see Wood *et al*., 1996) and *Eosphargis* (see Lydekker, 1889), the Oligocene *Cardiochelys* (see Moody, 1993) and *Natemys* (see Wood *et al*., 1996) and the Miocene *Psephophorus* (see von Meyer, 1847). ‘*Psephophorus*’ *rupeliensis* is of Oligocene age (compare Wood *et al*., 1996); this species has affinities to the genus *Natemys*, which, most probably, is of Miocene age (Olivier Lambert, pers. comm., 2018).

Dermochelys coriacea is the largest extant turtle, attaining a length of up to 240 cm and a weight of > 600 kg (Pough *et al*., 2013). Unlike other marine turtles, the carapace of the leatherback is made up of thousands of small bones (called ossicles) that are embedded in a leathery skin. The carapace of the extant species possesses seven ridges that extend from the front to the back. Currently, extant *Dermochelys* has a wider geographical distribution than any other ectothermal amniote (Pough *et al*., 2013), being resistant to cold waters and able to dive down to depths of up to 1,000 metres (Pough *et al*., 2013).

Psephophorus from the Miocene of Devínska Nová Ves (Slovakia) was first described in 1846, but no name was provided (von Meyer, 1846); a year later, the generic name was introduced (von Meyer, 1847). Unfortunately, no drawing has ever been published; the type specimen is merely known to have consisted of two slabs with approximately 70 ossicles and to have included a ridge. It was described in detail by Seeley (1880). At present, one of the two slabs described by Seeley (1880) is lost. The other is deposited in the collections of the Naturhistorisches Museum Wien under registration number NHMW 2011/0330/0001; this is currently considered the neotype of *Psephophorus polygonus* (compare Wood *et al*., 1996).

Only in three recent studies has material been assigned to *Psephophorus polygonus*. This is from Slovakia (von Meyer, 1846; Delfino *et al*., 2013), Italy (Chesi et al., 2007) and Denmark (Karl *et al*., 2012). Delfino *et al*. (2013) described additional topotypical material of *P. polygonus* contained in four European institutions. Generally, *Psephophorus* is treated as a wastebasket genus (Wood *et al*., 1996), which is demonstrated by the large number of diverse species attributed to it, such as *P. scaldii* (Van Beneden, 1871), *P. rupeliensis* (Van Beneden, 1883), *P. calvertensis* and *P. californiensis* (Gilmore, 1937). Taxonomic criteria on which to determine with confidence whether or not these species all belong to the genus *Psephophorus* are lacking, in part due to the fact that identifications were based on different parts of the skeleton, i.e., either appendicular bones or carapaces, which naturally cannot be compared.

In the present study, a new well-preserved fragment of a dermochelyid carapace from locality 6d in the Westerschelde is discussed and illustrated, followed by a thorough analysis to which species it belongs. Based on our phylogenetic analysis, a renewed study of the neotype of *P. polygonus*, and a reference specimen of *Dermochelys coriacea*, an emended diagnosis of the genus *Psephophorus* is proposed. By studying comparative material we hope to gain more insights into the complex history of dermochelyid evolution. With an additional taphonomic analysis of secondary markings on the carapace, a better understanding of the palaeoecology of the southern North Sea Basin (Westerschelde area) can be achieved.

***Abbreviations*:**

BMNH	The Natural History Museum, London, UK.
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
HMG	Hobetsu Museum, Hobetsu-cho, Hokkaido, Japan.
IRSNB	Institut Royal des Sciences Naturelles (Koninklijk Belgisch Instituut voor Natuurwetenschappen), Brussels, Belgium.
MHNP	Museo de Historia Natural, Lima, Peru.
NHMW	Naturhistorisches Museum Wien, Vienna, Austria.
NMR	Natuurhistorisch Museum Rotterdam, Rotterdam, the Netherlands.
RMNH	Rijksmuseum van Natuurlijke Historie, Naturalis Biodiversity Center, Leiden, the Netherlands.
UMMP	University of Michigan, Museum of Palaeontology, Ann Arbor, Michigan, USA.
USNM	United States Museum of Natural History (Smithsonian Institution), Washington DC, USA.
YPM	Peabody Museum of National History, Yale University, New Haven, Connecticut, USA.

Geological setting

The 'Western Scheldt River', or in Dutch 'Westerschelde', is a geologically dynamic estuary in the southwest of the Netherlands (Fig. 1). In the present study, only the Dutch name 'Westerschelde' will be used. Currently, the estuary is the only direct passage from the River Schelde (Scheldt) into the North Sea, and it is an important shipping route towards the port of Antwerp in Belgium.

The base of the Westerschelde is formed by the London-Brabant Massif which has experienced marine sedimentation since the latest Mesozoic, with chalks (Upper Cretaceous) and Cainozoic clayey sands and sandstones (Du Four *et al.,* 2006). A slight slope towards the North-North-East is present (Le Bot *et al*., 2003). The thickness of Palaeogene and Neogene strata varies between 10 and 30 metres, whereas Quaternary deposits attain thicknesses of up to 10 metres (Du Four *et al*., 2006).

Lithostratigraphical units present in the Westerschelde Estuary, from bottom to top, include the Rupel Formation (Rupelian), Breda Formation (Langhian–Zanclean), Oosterhout Formation (Zanclean–Piacenzian) and Maassluis Formation (Gelasian), with Holocene strata overlying (Drees, 1986). Figure 2 illustrates the deep cut of the River Schelde into these units, eroding the Breda Formation and exposing the underlying Rupel Formation (Du Four *et al*., 2006; Post & Reumer, 2016), which shows this locality to yield material of Oligocene to Miocene age.

The material from the trawling expedition by the Natuurhistorisch Museum Rotterdam originates from the Breda Formation of Langhian–Zanclean age (Post & Reumer, 2016). This unit is a regional lithostratigraphical entity; it consists mostly of marine, locally glauconitic (grey green to black green) sands, sandstones and claystones (Doppert *et al*., 1975), with some carbonate (Westerhoff, 2003). Occasionally, pyrite, phosphorite and vivianite, as well as isolated shark teeth and other unidentified bones can be found (Westerhoff, 2003).

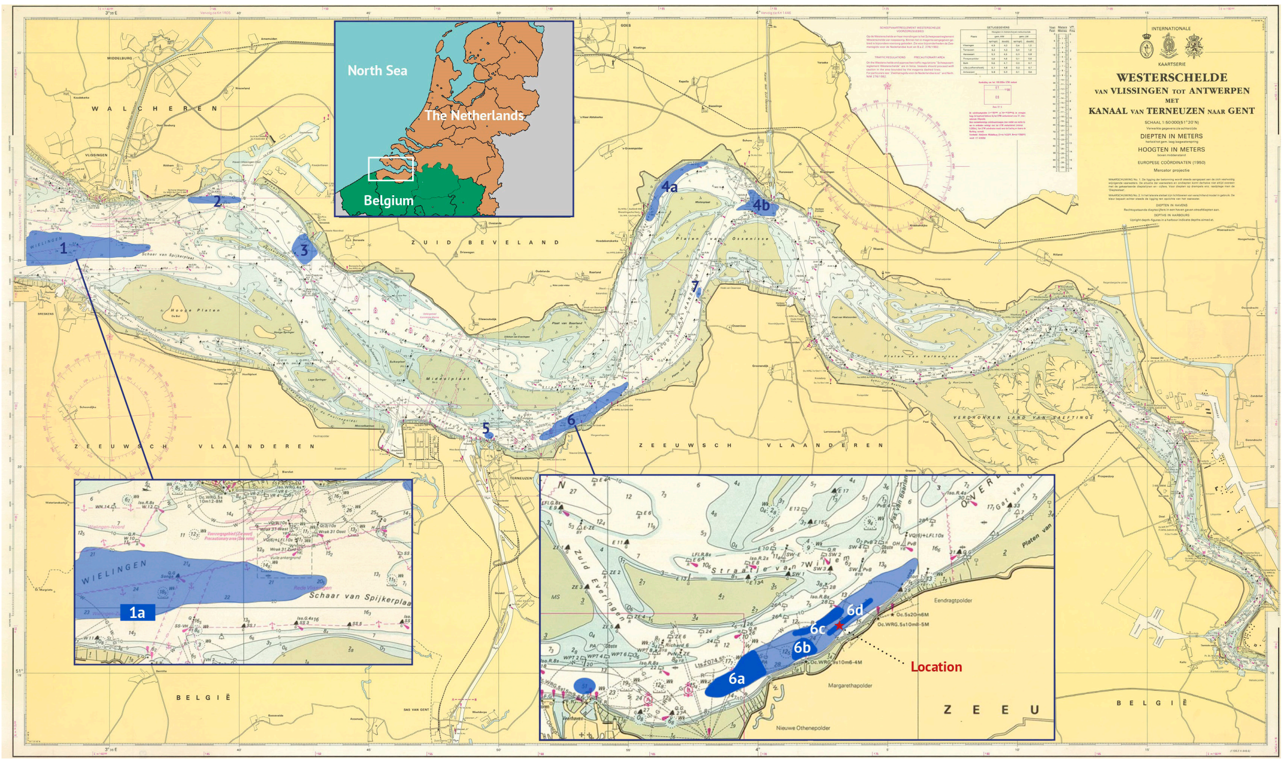

Figure 1. Map (from Post & Reumer, 2016) of the Westerschelde Estuary and trawling localities; specimen NMR 9988–0661 was retrieved in 2014 from site 6d.

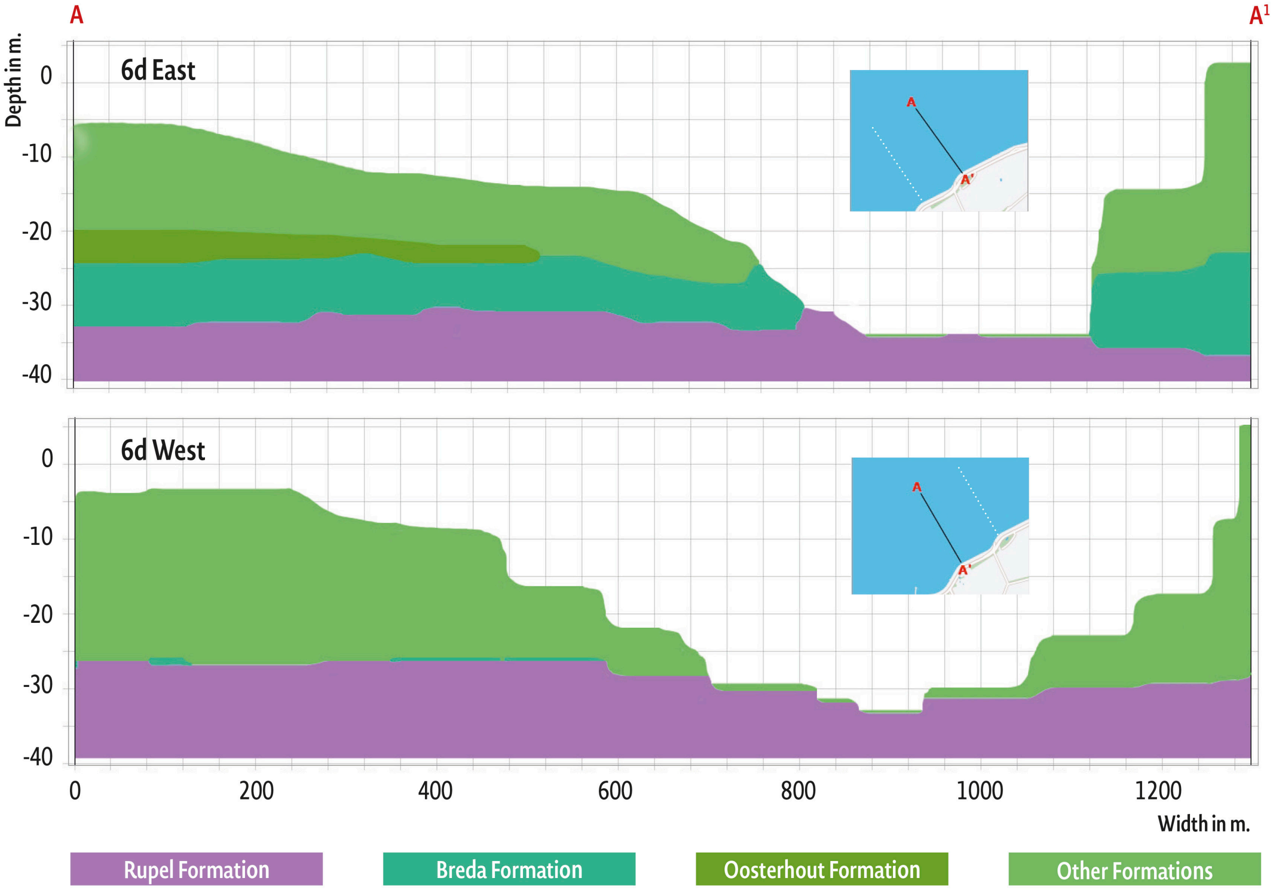

Figure 2. East and west cross sections of site 6d in the Westerschelde Estuary (after Post & Reumer, 2016).

A detailed stratigraphical analysis of Miocene strata of the North Sea Basin based on organic-walled dinoflagellate cysts was carried out by Munsterman & Brinkhuis (2004), who defined fourteen informal dinocyst zones for the southern North Sea Miocene (SNSM) which includes an age model (Munsterman & Brinkhuis, 2004) which was subsequently recalibrated to Ogg *et al*., (2016), enabling a more accurate dating based on dinocyst assemblages. The Westerschelde specimen has been assigned to zone SNSM12 (Munsterman, 2017), which has been documented for the Breda Formation and is dated as early-middle Tortonian (Munsterman & Brinkhuis, 2004; Munsterman, 2017). Zone SNSM12 is defined by the interval from the highest occurrence of *Cannosphaeropsis passio* to the highest occurrence of *Palaeocystodinium golzwense* (Munsterman & Brinkhuis, 2004).

The Westerschelde specimen was dated by Munsterman (2017), who dated it as 11.5–8.8 Ma. All other material from the same locality analysed originated either from SNSM13 or 14, which indicates middle to upper Tortonian, rather than lower to middle Tortonian (Munsterman & Brinkhuis, 2004). In addition, a cetacean specimen described by Post *et al*., (2017) from the same Westerschelde assemblage has been dated as late Tortonian to earliest Zanclean (7.6–5 Ma), whereas Munsterman (2017) had earlier stated the same specimen to be of late Tortonian age (8.1–7.4 Ma). Due to these inconsistencies of dinocyst dating within the assemblage of the Westerschelde, it cannot be confidently proved that the Westerschelde carapace originates from the same assemblage. A thorough investigation of the whole Westerschelde collection must be performed in order to obtain a complete understanding of the Miocene fauna from the Westerschelde Estuary. Once more data have been gathered, it will also be easier to identify possible variability in dinoflagellate zones.

Material and methods

We have performed a cladistic analysis. Data used are provided in the Supplementary Online Material (SOM), at www.wtkg.org/tijdschriften/cainozoic-research. We have scored 15 specimens in this analysis; eight of these have been coded on the basis of personal observation, the other seven from literature data.

Chelonia mydas Linnaeus, 1758: IRSNB 215 gamma; personal observations.

Caretta caretta Linnaeus, 1758: RMNH.RENA.38288; personal observations.

Mesodermochelys undulatus Hirayama & Chitoku, 1996: HMG 5, 6, 7, 8, 9, 342, 363, 365, 368, 369, 1053, 1062-1064; literature data (Hirayama & Chitoku, 1996: 597-622).

Eosphargis gigas (Owen, 1880): IRSNB R 1736, a near-complete skeleton; personal observations.

Natemys peruvianus Wood, Johnson-Gove, Gaffney & Maley, 1996: MHNP uncatalogued, a partial carapace; literature data (Wood *et al*., 1996: 270-276).

‘*Psephophorus*’ *rupeliensis* Van Beneden, 1883: CMNH 19750, a partial carapace; literature data (Wood *et al*., 1996: 276-277).

‘*Psephophorus*’ *rupeliensis* Van Beneden, 1883: IRSNB R 1655 and R 1656, partial carapaces; personal observations.

Egyptemys oregonensis (Packard, 1940), type specimen (= junior synonym of *E. eocaenus*; see Karl & Lindow, 2010: 57; literature data (Wood *et al*., 1996: 267-268).

Egyptemys eocaenus (Andrews, 1901): YPM 6212, a partial carapace; literature data (Wood *et al*., 1996: 268).

Egyptemys eocaenus (Andrews, 1901): UMMP 97538, a partial carapace; literature data (Wood et al., 1996: 269).

Cosmochelys dolloi Andrews, 1919: BMNH R-4338; literature data (Andrews, 1919; Tong *et al*., 1999: 915, fig. 2: 9a, b).

‘Alabama specimen’: USNM 23699, a partial carapace; literature data (Wood *et al*., 1996: 278-279).

Psephophorus polygonus von Meyer, 1846, neotype NHMW 2011/0330/0001, a partial carapace; personal observations and literature data (Seeley 1880).

Psephophorus calvertensis Palmer, 1909: USNM V6059; literature data (Palmer, 1909: pl. 31) and personal observations (NMNH - Paleobiology Department, Smithsonian Institution. 2015).

Dermochelys coriacea (Vandelli, 1761): IRSNB 268, a complete skeleton and carapace; personal observations.

Dermochelys coriacea (Vandelli, 1761): RMNH.RENA. 02517-4224, a partial carapace; personal observations.

Dermochelys coriacea (Vandelli, 1761): RMNH.RENA. 6180 and 13943, two neonates; personal observations.

New material – In the present study, we examine specimen NMR 9988–066, a dermochelyid carapace fragment referred to as the ‘Westerschelde specimen’, which was retrieved and prepared by staff of the Natural History Museum, Rotterdam (The Netherlands). All measurements were made by using a measuring tape: the carapace measures 51 x 34-43 cm and has various bite marks; in addition, it contains an internal mould of a large, inflated bivalve. In addition, the type specimen of *Psephophorus polygonus* (NHMW 2011/0330/0001) has been restudied, as well as four individuals of *Dermochelys coriacea* (see listing above).

Species of ‘*Psephophorus*’ not included in the analysis by Wood *et al*., (1996) comprise *Psephophorus scaldii* (Van Beneden, 1871), which is based on an isolated humerus and *Psephophorus californiensis* (Gilmore, 1937), based on a femur. As both of these forms lack associated carapace material, these cannot be included in our novel analysis. We have also excluded ‘*Psephophorus*’ *terrypratchetti* Köhler, 1995, as this form has been described on the basis of a very small carapace fragment that does not yield sufficient data for it to be included in the matrix (see Köhler, 1995).

Wood *et al*., (1996) carried out a cladistic analysis of dermochelyid phylogeny on the basis of 15 different terminal taxa, 13 of which belong to the family Dermochelyidae. Based on personal observations and new insights and in order to correct for some cladistic inconsistencies, modifications have been made for several characters and/or character state definitions. We have retained most characters of the matrix published by Wood *et al*., (1996). Seven of these have been copied unaltered, while the other ones have been modified to some degree (see SOM Appendix 1).

We have made the following modifications to the matrix used by Wood *et al*., (1996):

(a) For their characters 9 through 22, we have scored cheloniids, *Mesodermochelys* and *Eosphargis* 'not applicable = -', because they lack carapaces consisting of ossicles. Keratin scutes of cheloniids and basal dermochelyids are not homologous to the bony ossicles of more derived dermochelyids.

(b) Characters 14, 15 and 16 of Wood *et al*., (1996: 282) describe the cross section of the ridges. We have modified and merged these characters into two new ones. The first one describes the visceral side of the carapace and the ridges only, scoring cheloniids, *Mesodermochelys* and *Eosphargis* = - (not applicable, as they have scutes rather than ossicles); carapaces that are entirely flat viscerally are scored 0, those that are raised under the ridges are scored 1 (= new character 7). The second character describes the external side of the carapace only, scoring cheloniids, *Mesodermochelys* and *Eosphargis* = - (not applicable); carapaces that are entirely flat externally are scored 0, those with just a low elevation are scored 1, those with a low rounded ridge are scored 2 and those with an elevated, tectiform ridge are scored 3 (= new character 19).

(c) As far as the 'sunflower patterns' (Wood *et al*., 1996: 283, character 17) is concerned, a distinction has been made between: not applicable (cheloniids, *Mesodermochelys* and *Eosphargis*); absent = 0; large and elongated = 1 and small and circular = 2 (character 12 in our matrix).

(d) We have omitted character 7 ("broad, flat ribs", of Wood et al., 1996: 281), because this was uninformative with regard to parsimony.

(e) Characters 20, 21 and 22 of Wood *et al*., (1996) describe the number of ossicles between the ridges. In view of the fact that these three characters clearly represent the same homologous feature, we have united them into a single, new character (our character 15), comprising three character states: not applicable = -; 1 to 4 ossicles between two ridges = 0; 5 to 17 ossicles = 1; more than 17 ossicles = 2.

(f) For the Alabama specimen we consider that no undulating ridge crest is visible in the illustration supplied by Wood *et al*., (1996); thus, the undulating ridge crest is scored as 'absent' (character 11, state 0).

(g) For *Psephophorus calvertensis*, two characters have been edited: from '?' in Wood *et al.,* (1996) to containing an undulating ridge (character 11, state 1) and ossicles not varying greatly in size and shape (character 14, state 0). These changes are based on personal observations of new photographs of material.

(h) For *Psephophorus polygonus* we observe that this does have a raised ridge on the internal side (character 7, state 1) and that it does possess tectiform ('roof-shaped') ridges externally (character 19, state 3).

(i) Three new characters have been added: carapace shape (character 16), ossicle thickness (character 17) and ossicle size (character 18), defined as follows:

Character 16: 'Carapace shape': convex/convex between ridges/concave between ridges. Most carapaces of marine turtles are convex. Ridge-bearing carapaces are mostly convex between ridges, as in *Egyptemys* and *Psephophorus*, whereas the carapace surface in *Dermochelys coriacea* is concave between ridges, yet retains an overall convex shape. The character 'carapace shape' is scored as follows: convex carapace without (lateral) ridges (0); a carapace that is convex between ridges (1); and a carapace that is concave between ridges (2).

Character 17: 'Thickness of the ossicles': thick/intermediate/thin. Similar to ossicle size, ossicle thickness also is a relative property which is considered explicit enough to be considered of taxonomic value. *Natemys peruvianus* and '*Psephophorus*' *rupeliensis* have particularly thick ossicles and are scored (1); *Egyptemys*, *Cosmochelys*, the Alabama specimen, *Psephophorus polygonus*, *Psephophorus calvertensis* and the Westerschelde specimen all have intermediately thick ossicles (2), whereas *Dermochelys* has greatly reduced, thin ossicles (3); see Delfino *et al.* (2013, p. 769 and figs. 1,2). Cheloniids, *Mesodermochelys* and *Eosphargis* have scutes and are scored (0)

Character 18: 'Ossicle size': This is a relative property, but the difference in size of dermochelyid ossicles is explicit to such an extent that we here consider it appropriate to be used as a taxonomically important feature. Particularly large ossicles are seen in *Natemys peruvianus* and '*Psephophorus*' *rupeliensis* and are scored '0'; *Egyptemys*, *Cosmochelys*, the Alabama specimen, *Psephophorus polygonus*, *Psephophorus calvertensis* and the Westerschelde specimen all have intermediately sized ossicles (1), whereas *Dermochelys* has very small ossicles (2). Cheloniids, *Mesodermochelys* and *Eosphargis* have scutes and are therefore scored 'not applicable' (-).

NMR 9988–0661 was scored for all characters, with the exception of 5, 6 and 10, and included in the matrix as the 'Westerschelde specimen'. With this new matrix a maximum parsimony analysis, Bremer support values, bootstrap frequencies (1,000 replicates) and Jackknife frequencies (500 replicates) were calculated using heuristic searches in a phylogenetic analysis using PAUP 4.0 beta (Swofford, 2003). This phylogenetic analysis has resulted in two equally long, most-parsimonious cladograms (see Fig. 6 and SOM Appendix 4) with the following tree statistics: 15 taxa, 19 characters; tree length = 36; Consistency Index (CI), Retention Index (RI), Rescaled Consistency index (RC) = 1.0000; Homoplasy Index (HI) = 0.0000. All characters have been treated 'unordered' and with equal weight.

Systematic palaeontology

Order Testudines Linnaeus, 1758
Family Dermochelyidae Fitzinger, 1843
Genus *Psephophorus* von Meyer, 1847

Psephophorus polygonus von Meyer, 1847
Fig. 3

Neotype – NHMW 2011/0330/0001, a slab of carapace with both ridged and non-ridged ossicles (Wood *et al*., 1996).

Material studied – NMR 9988–0661.

Locality – Area 6d in the Westerschelde Estuary, province of Zeeland, The Netherlands (Fig. 1), collected during 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; see Munsterman, 2017).

Description

Carapace – Fragment only (Fig. 3A), measuring 51 cm in length and 34–43 cm in width, but well preserved. Carapace consisting of a mosaic of ossicles of varying sizes: medial side average being 16.7 mm (n = 22), lateral side average 18.5 mm (n = 22), resulting in overall average of 17.6 mm. A single circular 'sunflower' ossicle visible; a larger (30 mm) ossicle with scalloped margins surrounded by other ossicles (compare Wood *et al*., 1996). One prominent ridge in carapace centre; shape of ridge slightly tectiform with rounded top (Fig. 4). Apically, ridge thickness is 17 mm, laterally, 13 mm; slope extending far onto adjacent ossicles, a feature not seen in other dermochelyid carapaces, to a minimum thickness of 8 mm. Maximum distance from ridge to edges is 21.5 cm laterally and 20.7 cm on medial side (Fig. 3A). Ridge ossicles on average 24 mm in length (n = 11), but ossicle shape varying from elongate to semi-circular, with maximum diameters of 31 and 14 mm, respectively. In dorsal view, ridge not straight on anteroposterior axis, but slightly curved. In addition, ridge structure prominence weakens posteriorly (Fig. 4). Fragment damaged in several places, resulting in secondary features (described in detail below).

Secondary features – There are several secondarily inflicted marks on the carapace. Firstly, there is a pair of 'scratches' perpendicular to the ridge (Fig. 3B); these are here referred to as marks 1 (M1a, b). The top scratch 'M1a' consists of two different scratches scraping off the carapace surface, displacing some of the bone, but the ossicle boundary structures are still visible. M1a measures 19.5 cm in overall length and the two depressions are 0.7 cm and 0.5 cm wide (top and bottom, respectively). The lower scratch 'M1b' is one large depression from which material was removed rather than displaced. Ossicle boundaries are still visible, resulting in a 'ladder-like' pattern of deeper and shallower depressions where the ossicle boundary is cut through more deeply than the ossicle surface. M1b is 16 cm long and 1.6 cm wide. The two scratches appear different in character but are oriented parallel to each other. The distance between M1a and M1b is 8.0 cm.
Secondly, two bundles of deeper depressions occur, here referred to as marks 2 (M2a–b) (Fig. 3C). The bundles (M2a, b) consist of 3 to 4 aligned holes of 1 cm across, on average, with a slightly pointed V-shaped structure. They penetrate more than halfway into the bone. The two bundles are aligned near parallel, 11.0 cm apart. There is a single 'hole' visible on the anterior side (arrow in Fig. 3A) with a shape that is similar to that of the aligned holes. Therefore, it is possibly of the same origin and is considered to be part of M2 as well.

Phylogeny

The phylogenetic representation of dermochelyids by Wood *et al*. (1996) is basic, but because of carapace-specific identifications, clear variations in carapace morphology between different taxa are shown. Our Westerschelde specimen is of Tortonian age (Munsterman, 2017) and, based on features outlined by Wood *et al*. (1996), it corresponds best with *Psephophorus calvertensis*. The Westerschelde specimen also has a tectiform ridge; in cross section, this is visible on both the dorsal and ventral side of the carapace.
However, it should be noted that the definition of *Psephophorus polygonus* is currently based on merely a single slab and Seeley's (1880) description. In the recent literature it has been suggested that *P. polygonus* may also have tectiform ridges, curvatures on the ventral side (Delfino *et al*., 2013; personal observations of neotype) and sunflower patterns (Karl *et al*., 2012). All of these characteristics are also seen in the Westerschelde specimen. This begs the question whether *P. polygonus* had a more diverse morphology than previously suggested by von Meyer (1847) and Wood *et al*. (1996) or whether it is merely a wastebasket taxon. Furthermore, only a single specimen of *P. calvertensis* has been described from Maryland to date (Palmer, 1909), whereas *P. polygonus* has been recorded from several European localities.
Additionally, the geographical location of the Westerschelde Estuary during the Miocene was along the southern margin of the North Sea Basin with the sea inundating the entire territory of The Netherlands and Denmark.

Figure 3. A, Dorsal view of the Westerschelde specimen (NMR 9988–0661), a well-preserved carapace fragment. B, Two parallel scratches (M1a, b) that cut into the surface of the carapace bone; C, Two near-parallel rows of circular bite marks (M2a,b) penetrating over halfway into the bone. Black arrow points to single bite mark.

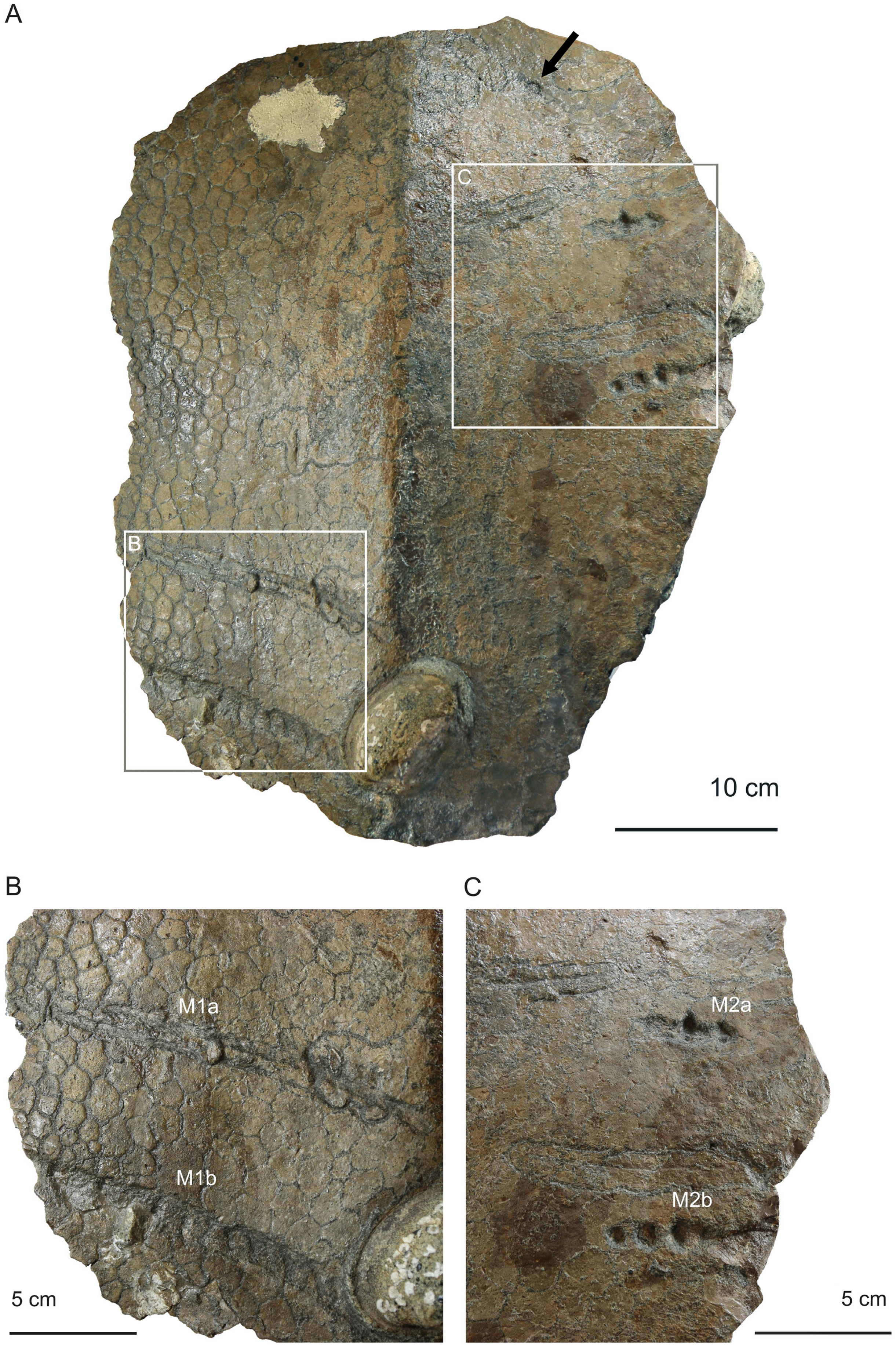
A
C
B
10 cm
B
M1a
M1b
5 cm
C
M2a
M2b
5 cm

Figure 4. Cross sections of ridge morphology of the anterior (above) and posterior (below) sides of the Westerschelde specimen (NMR 9988–0661). Note the clear variability in angle of the ridge on both sides of the specimen. White spots are scars of epifauna such as barnacles.

Figure 5. Oblique superposition of the Westerschelde specimen (NMR 9988–0661) on the carapax of a Recent individual of *Dermochelys coriacea* (IRSNB 268) showing its supposed position and the ridges.

The find of specimens of *P. polygonus* in the Gram Formation of Denmark (Karl *et al*., 2012) confirms the distribution of this species across the North Sea.

The only differences of importance between *Psephophorus calvertensis* and *P. polygonus* (as based on Wood *et al*., 1996) are the expression of the ridge on the external carapace surface only and the form of that ridge, i.e., either tectiform or arched. It has been suggested that *P. polygonus* would have lacked a visceral expression of the ridge, and no tectiform or arched ridge shape, whereas *P. calvertensis* does reveal both characters (Wood *et al*., 1996). However, according to Delfino *et al*. (2013), these differences between *P. calvertensis* and *P. polygonus* are no longer valid.

In order to substantiate this claim, the ridge architecture of a specimen of *Dermochelys coriacea* (RBINS 268) has been studied. It is highly curved, originating only from the angles created in the ridges (Fig. 5), these angles all being between 150 and 155 degrees. Assuming a similar morphology for the seven ridges in *Psephophorus polygonus*, the visceral angle cannot be straight (~180 degrees), because the curvature of the carapace diminishes. Alternatively, curvatures (~30°) can be interpreted as being created along its ordinary ossicles to compensate for the straight visceral side; this is not seen in any specimen of *P. polygonus* on record to date. Thus, we concur with Delfino *et al.* (2013) that the visceral angle of *P. polygonus* cannot be straight. This would suggest that *Psephophorus calvertensis* and the Westerschelde specimen are conspecific and should be referred to *Psephophorus polygonus*.

Cladistics

Our cladistic analysis has confirmed results obtained by Wood *et al.* (1996), except for the Alabama specimen, *Psephophorus polygonus* and *Psephophorus calvertensis*. In our novel analysis the Alabama specimen occupies a more basal position than the *Psephophorus* clade, as its crest is scored as non-undulating (character 11). *Psephophorus polygonus*, *P. calvertensis* and the Westerschelde specimen form a monophyletic group, united by a single synapomorphy, i.e., their ossicles do not vary greatly in size and shape (character 14 = 0). In contrast, all ossicles exhibit a more or less similar, subhexagonal shape. Some ossicles illustrated by Palmer (1909: pl. 31, under the name of *P. calvertensis*) appear to contradict this, but are, in fact, groups of ossicles that merged due to the old age of that particular specimen (Roger Wood, pers. comm., 2018; personal observations on unpublished Belgian specimens).

The resulting consensus tree is shown in Figure 6. It unites *Psephophorus calvertensis* with *P. polygonus* and the Westerschelde specimen into one clade. The corresponding matrix, consisting of 19 characters (rather than 24), is shown in SOM Appendix 3. The corresponding overview of character descriptions can be found in SOM Appendix 2.

Based on the new cladogram, it is here argued that *Psephophorus calvertensis* is within the range of morphological variation of *P. polygonus*, and is not its sister taxon. This is in agreement with Delfino *et al*. (2013), who proposed to treat *P. calvertensis* and *P. californiensis* to be junior synonyms of *P. polygonus*. However, *P.californiensis* cannot be shown to be a junior synonym of *P. polygonus*, as it is based on an isolated femur only.

Diagnoses

Based on the current data, a new diagnosis of *Psephophorus polygonus* is here proposed (see also SOM Appendices 2 and 3).

Emended diagnosis – Psephophorus polygonus is a species of Miocene age which is defined by the following set of characters:

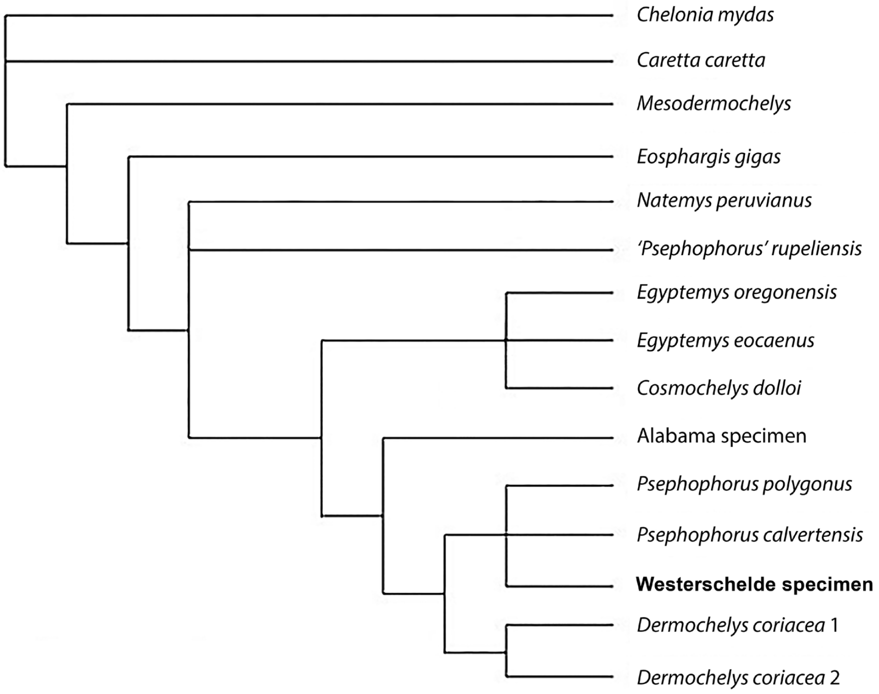

Figure 6. Cladogram (consensus tree) based on the new matrix, showing relationships amongst the Dermochelyidae, including the Westerschelde specimen ((in **bold**). The corresponding matrix is shown in SOM Appendix 3, with character descriptions in SOM Appendix 2. For full descriptions, reference is made to Wood *et al.* (1996) and the section Cladistics in the present text. The character change list and the apomorphy list are in SOM Appendices 5 and 6, respectively.

Pleural bones lacking (this character is shared by all species in the current analysis, except for cheloniids and *Mesodermochelys*).

Neural bones, peripheral bones and scutes lacking as well; carapace composed of bony ossicles (these characters are shared by all species in the current analysis, except for cheloniids, *Mesodermochelys* and *Eosphargis*).

Specimen lacking ossicles that are greatly elongated along the anteroposterior axis (this character is shared by all species in the current analysis, except for cheloniids and *Mesodermochelys*, *Eosphargis*, *Natemys* and '*Psephophorus*' *rupeliensis*).

The specimen has anteroposterior ridges on the carapace and ossicles are of intermediate size (these characters are shared by all dermochelyids with anteroposterior ridges: *Egyptemys oregonensis*, *Egyptemys eocaenus*, *Cosmochelys dolloi*, the Alabama specimen, *Psephophorus polygonus*, *Psephophorus calvertensis*, the Westerschelde specimen and *Dermochelys coriacea*).

The carapace is convex between the ridges and bony ossicles of the carapace are of medium thickness (these characters are shared by all dermochelyids with anteroposterior ridges, except for *Dermochelys*).

The ridges are separated by more than 5 and fewer than 17 ossicles (this character is shared by all dermochelyids with anteroposterior ridges, except for *Cosmochelys*, *Egyptemys* and *Dermochelys*).

Psephophorus polygonus also has ossicles internally raised under the ridges and small and near-circular 'sunflower patterns' (both characters are shared by the Alabama specimen, *Psephophorus polygonus*, *P. calvertensis* and *Dermochelys*).

The anteroposterior ridges are undulose and the section of the ridge ossicles is tectiform externally (these characters are shared by *Psephophorus polygonus*, *P. calvertensis* and *Dermochelys*).

Lastly, the ossicles do not vary greatly in size and shape (the latter is a synapomorphy of the *P. polygonus-calvertensis*-Westerschelde-clade).

Differential diagnosis – Psephophorus polygonus differs from all other dermochelyids in having ossicles that do not vary greatly in size and shape.

Dermochelys coriacea differs from *P. polygonus* in having concave rather than convex sections of the carapace between its ridges and in having a carapace composed of very thin bony ossicles. Moreover, it (generally) has more ossicles separating the ridges than the latter. The Alabama specimen differs from *P. polygonus* because it has ridges that do not undulate, ossicles that widely vary in size and possesses a low rounded ridge externally.

Cosmochelys dolloi, *Egyptemys oregonensis* and *E. eocaenus* have, unlike *P. polygonus*, ossicles that are viscerally flat, crests that do not undulate and lack 'sunflowers'. Their ossicles vary greatly in size and shape. In addition, they have an externally low elevated crest. The two last-named species might represent a single taxon, but the low crests of *Cosmochelys* differ in being pointed rather than rounded.

Natemys peruvianus and '*Psephophorus*' *rupeliensis* differ from *P. polygonus* in having ossicles that are viscerally flat, in lacking anteroposterior ridges on the carapace, in having crests that do not undulate, large and long ‘sunflowers’, greatly elongated ossicles arranged along the anteroposterior axis, ossicles that vary greatly in size and shape, one to four ossicles in between the ridges and a convex carapace that is composed of thick and large ossicles. In addition, the carapace is externally flat.

Eosphargis and the specimen of *Mesodermochelys* studied are even more distant relatives of *Psephophorus polygonus*. They represent very basal dermochelyids, which still retain horny scales (scutes), rather than bony ossicles, but share a large plastronal fontanelle with all other dermochelyids.

Chelonia and *Caretta* are both cheloniids and differ from all dermochelyids in lacking a large medial plastronal fontanelle.

Discussion

In this section, other subjects related to the Westerschelde specimen are discussed.

Former carapace position – The ridge on the Westerschelde specimen is not a perfectly straight line along the anteroposterior axis (Fig. 3A), but is slightly curved, which makes it unlikely for it to represent the median ridge, because the latter is fully straight along the longitudinal axis. Furthermore, the ridge prominence weakens posteriorly (Fig. 4). This may be indicative of its position on the carapace, i.e., (far) towards the back and right lateral side. In *Dermochelys coriacea* the ridges weaken towards the carapace posterior, where the outer ridges fully disappear and the median ones approximate. The ridges stay fully intact towards the carapace front. Therefore, it is argued that the bottom as seen in Figure 3A is the posterior side, and the top is the anterior side. Figure 5 shows the supposed position of the Westerschelde specimen on a carapace of *Dermochelys*.

Taphonomy – A large internal mould of a bivalve sticks to the dorsal (external) side of the carapace. This matches well-preserved material of *Arctica islandica* of Miocene age. This species is well known from the Miocene and Pliocene of the North Sea Basin, including several localities in or around the Westerschelde (Moerdijk *et al*., 2010).

The different marks on the Westerschelde specimen (Fig.3) are believed to be of a secondary nature. There are no signs of recovery, which indicates that the marks were either inflicted post-mortem or were the cause of death.

Marks 1 (M1) – M1 consists of a pair of possible scores: where teeth on both sides of an attacking predator’s (or scavenger’s) jaw were dragged along the carapace, creating two grooves not fully fracturing the bone, but causing depressions (Fig. 3B). Because the scratches are elongated, yet 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; thus, it is proposed that scratch M1b was possibly created by a broken tooth, similar to an example illustrated by Drumheller & Brochu (2016, fig. 4D). The parallel orientation of M1a/b and the constant distance of 8.0 cm is a strong argument that M1 was created by a single organism with a jaw width of approximately 8 to 10 cm. Potential predators (or scavengers) include sharks, crocodiles or small toothed whales.

Marks 2 (M2) – M2 is a subparallel-oriented pair of pits, which indicates that teeth contacted the surface of the bone, leaving two rows of depressions approximately matching the shape of the teeth (Fig. 3C). The depression never fully pierces the bone. If these holes were indeed inflicted by a bite, they suggest teeth with a relatively circular shape and an apex of approximately 4 mm in width. This reduces the probability for M2 to have been inflicted by sharks, because these do not have circular teeth.

One row shows four depressions, while the other has only three. They are between 10 and 15 mm in diameter at the surface of the bone and just 6.5 to 8.5 mm at the bottom of the depressions. The centres of successive aligned depressions are between 13.3 and 16.3 mm apart. Successive holes are separated by 5.4 to *c*.10 mm wide ridges. The two rows are separated from each other by some 97-103 mm (distance between two opposite depressions); they diverge by about 5 degrees, widening towards the crest. The pairs of pits are situated 11.0 cm away from each other, suggesting a jaw width similar to M1. A small predatory physeteroid or kentriodontid (Cetacea) might be a potential predator to have produced such marks. It is reasonable to assume that dermochelyids and physeteroids co-existed during the Miocene in the North Sea Basin. A Tortonian physeteroid has been recorded from the Pietra Leccese sandstone in Italy (Varola *et al*., 1988); this unit has also yielded material of *P. polygonus* (see Chesi *et al*., 2007). Another physeteroid has been described from a nearby locality (Bianucci & Landini, 2006) and, recently, physeteroid teeth have been recorded from the Westerschelde Estuary (Reumer *et al*., 2017). Teeth of physeteroids are rounded with a pointed, conical crown, which matches the architecture of the M2 pits (Bianucci & Landini, 2006; Reumer *et al.,* 2017).

We have considered the possibility that, while M2 is a typical bite mark, M1 could have been inflicted by the same or similar predator that did not have a firm grip, causing parallel longitudinal scratches. The M2 bite marks are about 100 mm apart, the two parallel scratches M1 between 85 and 88 mm. M2 in particular begs the question who is responsible for these? Numerous cetaceans possess rows of teeth, but these would need to conform to the following criteria:

1. the distance between successive tooth apices should be 13.3-16.3 mm.
2. the maxilla should preferably show a convex row of teeth in lateral view.

3. the left and right tooth rows should be about 100 mm apart.
4. the animals occurred during the late Miocene.

Physeterid genera such as *Acrophyseter* Lambert, Bianucci & De Muizon, 2008 and *Aulophyseter* Kellogg, 1927a have teeth that are too large and too far apart, although they do meet criteria 2, 3 and 4. The same applies to the delphinid *Orcinus citoniensis* (Capellini, 1883) which, in addition, lacks a convex maxilla and is of Pliocene age. The kentriodontid *Kentriodon pernix* Kellogg, 1927b and the delphinids *Hemisyntrachelus cortesii* (Fischer, 1829), *H. capellini* (Del Prato, 1897), *H. oligodon* (Pilleri & Siber, 1989) and *H. pisanus* Bianucci, 1996 would appear to come closest. Of these, the genus *Hemisyntrachelus*, which has been found to be abundant in the North Sea Basin, has not yet been recorded from the Miocene, which also holds true for the delphinid *Arimidelphis sorbinii* Bianucci, 2005. In other words, *Kentriodon* appears to be the best fit; kentriodontids have been recorded from the region where the turtle carapace was found, i.e. the southern part of the North Sea Basin (Lambert, 2006; Foekens, 2008; Louwye *et al*., 2010,; Kazár & Hampe, 2014; and personal observations by KP and MEJB).

Palaeobiogeography and evolution – With *Psephophorus calvertensis* synonymised with *P. polygonus*, the composition of the genus *Psephophorus* is better defined. It appears that *P. polygonus* ranged across the entire Atlantic Ocean and possibly inhabited other oceanic basins as well. This is in agreement with Delfino *et al.* (2013), who hypothesised that *Psephophorus* had a wider geographical distribution than previously assumed. The large size of *P. polygonus* is similar to that of *Dermochelys coriacea*, and, along with the cosmopolitan ecology of both species, points at a close resemblance. This is supported by the cladogram (Fig. 6), which recognises *D. coriacea* as a sister group to *P. polygonus.* Although closely similar, the carapace of *P. polygonus* must have been more massive than that of *D. coriacea* (Delfino *et al*., 2013), but, on account of its large size (Chesi *et al*., 2007), it must also have been able to dive down to great depths and traverse oceanic basins.

Taxonomic remarks – To date, numerous extinct dermochelyids are still attributed to the genus *Psephophorus*, some of which cannot be compared. In short, the genus appears to be rather a wastebasket taxon. Without further research and new, more complete finds that consist, at least, of a combination of humerus, skull and (partial) carapace, this taxonomic problem cannot be resolved. '*Psephophorus*' *rupeliensis* is need of re-evaluation and should be referred to another genus, because it differs in many respects from the neotype of *Psephophorus* (see Wood *et al*., 1996; present study). Furthermore, new, *in-situ* material of *Psephophorus californiensis* and *P. scaldii*, both erected on the basis of post-cranial elements, is called for, along with corresponding carapace material in order to define their generic placement confidently and determine whether they are conspecific with carapace-based taxa or not.

Conclusions

The Westerschelde specimen is a constituent of an abundant Westerschelde assemblage from the 2014 trawling expedition; it is here identified as *Psephophorus polygonus*. We suggest that ridge architecture, and ventral curvature in particular, is more variable than previously stated for this form, which corroborates the synonymy of *P. calvertensis*.

A cladistic analysis has been performed, based on a modified version of the matrix published by Wood *et al.* (1996), with the addition of new or adapted characters based on new observations. Additional characters have been defined: shape of the visceral side of the carapace, carapace shape, ossicle thickness and ossicle size. *Psephophorus polygonus*, the Westerschelde specimen and *Psephophorus calvertensis* form a separate clade, based on the identical undulating crest, the subhexagonal, near-equal-sized ossicles and the closely similar tectiform ridge shape. We consider them to represent the same species. Furthermore, the Alabama specimen occupies a more basal position than do the *Psephophorus* and *Dermochelys* clades.

The Westerschelde specimen possesses secondary surface lesions that are considered to be of a *post-mortem* nature. Taphonomic analysis shows that both marks M1 and M2 are bite marks, likely to have been produced by a predator or scavenger. The producer of M2 is suggested to have been a cetacean, possibly a kentriodontid.

Extinct dermochelyids are relatively rare; until post-cranial, appendicular material for *Psephophorus polygonus*, *P. californiensis* and *P. scaldii* is found in association with carapaces (or fragments), the precise generic status of the two last-named forms cannot be determined.

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