

***CARCHARIAS VORAX* (LE HON, 1871) (CHONDRICHTHYES, LAMNIFORMES), FROM THE MIOCENE OF BELGIUM: REDESCRIPTION AND DESIGNATION OF A NEOTYPE AND PARANEOTYPE.**

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(6 figures, 1 table, 3 plates)

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ABSTRACT. *Carcharias vorax* (Le Hon, 1871) is poorly defined with one single tooth only. The holotype could not be found in the Type Collection of the IRScNB (Brussels) and recognition of the holotype is impossible based on the poor drawing in Le Hon (1871). A neotype and paraneotype are designated for the lost holotype. A temporary outcrop at a construction site southeast of the city of Antwerp is chosen as type locality. The basal part of the Middle Miocene Antwerpen Sands Member is selected as type horizon. An artificial tooth set is constructed and illustrated, confirming the attribution of this species to the genus *Carcharias*. *Carcharias vorax* (Le Hon, 1871) appears to be closely related to *Carcharias cuspidatus* (Agassiz, 1843) and seems to have a restricted geographical and temporal distribution, focused on the North Sea Basin only during the Burdigalian-Tortonian interval. The disappearance of *Carcharias vorax* during the Late Miocene is discussed. A maximum total body length of approximately 280 cm is estimated for this Miocene shark species.

KEYWORDS: Elasmobranchii, Odontaspidae, *cuspidatus*, sandtiger shark, Antwerpen Sands Member, North Sea Basin

1. Introduction

Neogene selachian remains are very common in the Antwerp area in northwest Belgium (Fig. 1). These have been studied for more than 150 years (Le Hon, 1871; Leriche, 1926, 1951; Herman et al., 1974; Herman, 1979; De Ceuster, 1987; Nolf, 1988; Bosselaers et al., 2004; Reinecke & Hoedemakers, 2006; De Schutter, 2009). The Pliocene deposits of the Antwerp area have been extensively studied thanks to the continuous expansion works of the harbour (e.g. Herman et al., 1974; Herman, 1979; Ottema & in't Hout, 1987). The Miocene deposits however are only accessible in temporary outcrops (e.g. De Meuter et al., 1976; De Ceuster, 1987; Marquet, 1991; Louwye et al., 2010). In the Antwerp area (Fig. 1), the Miocene is divided into the Lower-Middle Miocene Berchem Formation and the Upper Miocene Diest Formation (De Meuter & Laga, 1976; Laga et al., 2001).

Although only a very limited number of sharks' teeth were found in the Lower and Upper Miocene deposits of Belgium (De Ceuster, 1987; Bosselaers et al., 2004; Reinecke & Hoedemakers, 2006), selachian remains are relatively common in the Middle Miocene Antwerpen Sands Member (De Ceuster, 1987; Nolf, 1988; Louwye et al., 2010), the upper member of the Berchem Formation (Laga et al., 2001).

Numerous odontaspidid teeth were recovered from the Miocene and the transgressive base of the Pliocene, that have been attributed by authors to *Carcharias vorax* (Le Hon, 1871), *Carcharias acutissimus* (Agassiz, 1843) and *Carcharias reticulatus* (Probst, 1879). Reinecke et al. (2005, p. 21) separated *Carcharias reticulatus* from *Carcharias acutissimus*, but synonymized the former with the Oligocene species *Carcharias gustrowensis* (Winkler, 1875). However, the Middle Miocene representatives of



Figure 1. Location of the study area near Antwerp in northern Belgium. The Posthofbrug outcrop (1) was located near the railway station of Berchem (N 51° 11' 38" – E 4° 26' 04").

this lineage appear to be sufficiently different from *Carcharias gustrowensis* to maintain their own specific name *Carcharias reticulatus*, but this requires further study. In this paper *Carcharias reticulatus* (Probst, 1879) will be used for the teeth originating from the Middle Miocene Antwerpen Sands Member (*sensu* De Ceuster, 1987).

The purpose of this paper is to present evidence for the validity of *Carcharias vorax* (Le Hon, 1871), a large but poorly known odontaspide shark from the Miocene of Belgium. *Lamna* (*Odontaspis*) *vorax* Le Hon, 1871 is poorly defined with one single tooth only (Fig. 3). A neotype and paraneotype are designated to define the nominal taxon objectively and to shed light on past confusions. An artificial tooth set of *Carcharias vorax* is constructed and its affinities with other odontaspide species discussed.

The abbreviation IRScNB stands for ‘Institut royal des Sciences naturelles de Belgique’ (Royal Belgian Institute of Natural Sciences, Brussels).

2. Locality and Stratigraphy

Marine Miocene and Pliocene deposits are restricted to the northern part of Belgium and were deposited in a shallow marine environment along the southwestern margin of the North Sea Basin (Laga et al., 2001; De Schepper et al., 2004). In the Antwerp area (Fig. 1), the Miocene is divided into the Lower-Middle Miocene Berchem Formation (Edegem Sands Member, Kiel Sands Member and Antwerpen Sands Member) and the Upper Miocene Diest Formation (Deurne Sands Member) (De Meuter & Laga, 1976; Laga et al., 2001). Based on dinoflagellate cysts, an early Burdigalian to Serravallian age is attributed to the Berchem Formation (Louwye &

Laga, 2008) and a Tortonian age to the Diest Formation (Louwye, 2002).

The Middle Miocene Antwerpen Sands Member is a slightly clayey, medium fine-grained sandy unit, rich in glauconite and specimens of the bivalve *Glycymeris baldii* Glibert & Van de Poel, 1965 (De Meuter & Laga, 1976; Louwye et al., 2010). This member can be divided into a lower part (late Burdigalian to early Serravallian) and an upper part (middle to late Serravallian) (Louwye & Laga, 2008).

The Posthofbrug section (Fig. 2) was a temporary outcrop at a construction site southeast of the city of Antwerp (Fig. 1), near the railway station of Berchem (N 51° 11' 38" – E 4° 26' 04"). The lithostratigraphy and biostratigraphy of this section were studied in detail by Louwye et al. (2010). The Middle Miocene Antwerpen Sands Member was well exposed and its base, unit 2 in Louwye et al. (2010), proved to be very rich in elasmobranch remains. The *in situ* Miocene *Carcharias* teeth used in this study, including the neo- and paraneotype, originate from this unit (Fig. 2). Unit 2 is further characterised by the presence of phosphoritic concretions and the gastropod *Turritella eryna* (d'Orbigny, 1852). Based on dinoflagellate cyst stratigraphy, the phosphoritic base of the Antwerpen Sands Member at the Posthofbrug site was deposited some time between 16.5 Ma and 15.1 Ma, *i.e.* during late Burdigalian to early Langhian times (Louwye et al., 2010).

The teeth used for dental reconstruction were collected between 2007 and 2009 in relocated sands originating from dredging of the Churchilldok harbour dock, located on the right bank of the river Scheldt, Antwerp. Due to the constant sedimentation process of the Scheldt river, maintenance- and capital dredging is continuously required. The extracted Neogene sands were dumped near the town of Hoevenen (Fig. 1). Although these teeth were found *ex situ*, the majority is presumed to originate from the Middle Miocene Antwerpen Sands Member, with shark remains typical for this fauna: *Carcharoides caticus*, *Hemipristis serra*, *Isurus oxyrinchus*, *Notorynchus primigenius*, *Carcharias reticulatus*, *Carcharhinus priscus*, *Alopias exigua*, *Galeocercus aduncus*, *Physogaleus hemmooriensis*, *Parotodus benedeni* (De Ceuster, 1987; pers. data).

3. Materials and methods

Initially, an artificial tooth set (*sensu* Welton & Farish, 1993) was assembled using more than 300 isolated teeth of *Carcharias vorax*, recovered from mixed Neogene sediments, in accordance with the “horizontal dentition method” of Cunningham (2000). The respective positions of the isolated teeth of *Carcharias vorax* were assigned comparing characters observed in the extant sandtiger shark *Carcharias taurus* Rafinesque, 1810. Elongated, more slender teeth were separated from teeth with a shorter crown and were assigned to anterior positions. The upper and lower teeth were grouped based on the amount of lingual curvature of the crown, recurvature of the crown-tip, and angle of the root-lobes. Teeth with a

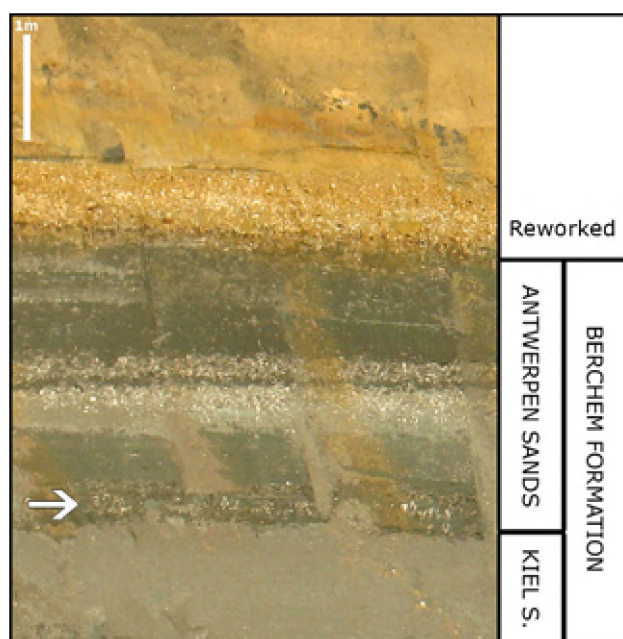


Figure 2. Lithostratigraphy of the Posthofbrug outcrop (after Louwye et al. 2010). The arrow indicates the *Turritella eryna* phosphoritic horizon, the type horizon of *Carcharias vorax*.

strong lingual curvature of the crown and strong lingual protuberance of the root were assigned to lower positions. The remaining teeth have strongly recurved crown tips which were assigned to the upper jaw. Their position was then determined by the increasing angle of root-lobe divergence in distal direction (see Cunningham, 2000). Subsequently, the reconstructed anterior dental series (Plate 2, figs 1-9) was duplicated using 140 well preserved teeth originating from the Middle Miocene Antwerpen Sands Member (Plate 1, figs 1-9), the presumed type horizon of Le Hon. Corresponding intermediate teeth were not found in this relatively small sample, probably because these small teeth are subject to collection bias (mesh width). Therefore, an intermediate tooth from a nearby locality was chosen to complete the reconstruction (Plate 1, fig. 4A-D).

The more than 300 isolated teeth of *Carcharias vorax* used for the initial reconstruction (Plate 2, figs 1-9), recovered from mixed Neogene sediments, are housed in the collection of the author. 140 isolated teeth, including the neotype and paraneotype, originate from the type locality and horizon and were used to reconstruct the species' anterior dental series (Plate 1, figs 1-9). These teeth are housed in the collection of the author and the private collections of L. Dufraing and G. Van den Eeckhaut, with the exception of the neotype and paraneotype that are deposited in the collections of the IRScNB, Brussels. Additionally, numerous specimens from the Burdigalian of Germany (Reinecke Collection) and the Tortonian of the Netherlands (Van der Vliet Collection) were examined for comparison purposes.

4. Systematic Palaeontology

Le Hon (1871, p. 5) figured a single lower anterior tooth that he described as *Lamna (Odontaspis) vorax*, found in the "Pliocene" of the Antwerp region (Fig. 3). By the short description of the single figured tooth, *Lamna (Odontaspis)*



Figure 3. Holotype of *Carcharias vorax* (Le Hon, 1871).

vorax is poorly defined and consequently, a lot of confusion arose in subsequent publications. Leriche (1926, p. 394) referred to this species as *Odontaspis acutissima* (Ag.) mut. *vorax* (Le Hon). Examination of the teeth figured in Leriche (1926, pl. 28, figs 31-49), housed at the IRScNB (Brussels), revealed that Leriche figured a mix of at least 3 different odontaspidid species. Only the teeth figured on plate 28, figs 33, 34, 39 and 44-46 appear to belong to *Carcharias vorax*. Most teeth are identified here as *C. reticulatus*, pl. 28, figs 31 and 38 belong to *Carcharias acutissimus* (Agassiz, 1843) and pl. 28, fig. 36 probably represents an upper intermediate tooth of *Carcharoides catticus* (Philippi, 1851). Cappetta (1970, p. 29) considered the teeth in Leriche (1926, pl. 28, figs 31-49) to be synonymous with *Carcharias acutissimus*. However, in 2006, Cappetta tentatively considered *vorax* a valid species based on the figure in Le Hon (1871). Nolf (1988, pl. 53, figs 1-7) correctly illustrated *vorax* using several of the specimens figured by Leriche (1926).

The holotype of *Carcharias vorax*, presumably deposited in the IRScNB (Brussels), could not be found in the Type Collection (see also Reinecke et al., 2005, p. 18).

The exact location and horizon of the type specimen are unknown. Although large parts of the collections at the IRScNB are well organised, the Neogene tooth collections are not by the lack of stratigraphic knowledge at the time of collecting. Leriche (1926, p. 371) examined these Neogene selachian collections and noticed that information about locality and horizon were mostly absent. According to Leriche (1926, p. 395), the "Pliocene" layers of Le Hon appeared to be Miocene sediments.

In his introduction, Le Hon (1871) mentioned the excavations for a siege wall and a 17 km long chain of fortresses around the city of Antwerp as basis for his study. He died in 1872, shortly after the publication of his preliminary report, and thus was unable to finish his more extensive memoir (see Leriche 1926, p. 375). For that purpose, the IRScNB had put all the selachian material housed in their collections that were recovered from the above excavations, to his disposal for study (Le Hon 1871, p. 2). Due to his sudden death, all teeth returned to the IRScNB. The unlabelled holotype of *C. vorax* may well have been included, but unfortunately mixed with the thousands of other Neogene teeth in the collection of the IRScNB. Based on the poor drawing in Le Hon (1871) only, recognition of the holotype in the collections is impossible and it must be considered as lost.

The current ring way (R1) around the city of Antwerp follows the line of the ancient siege wall (Lombaerde, 1997). Along its stretch, the shallow marine Berchem Formation of Lower-Middle Miocene age is widely exposed with the Edegem, Kiel and Antwerpen Sands Members (see De Meuter et al., 1976). The oldest Miocene deposits indicate a transgression; maximum flooding took place during the deposition of the Middle Miocene Antwerpen Sands Member (Louwye, 2005). This Member is most commonly exposed in the area (De Meuter et al., 1976) and it is the only Member where selachian remains

are relatively common (De Ceuster, 1987; pers. data). It is very likely that most of the authentic Miocene shark remains from older studies (e.g. Le Hon, 1871, Leriche, 1926) originated from these sands, except for those found in a limited area around Borgerhout and Deurne (Louwye et al., 2010). However, recently only a very limited number of sharks' teeth were found in a temporary exposure of the Deurne Sands (Bosselaers et al., 2004). The Early Miocene contains some sharks' teeth (De Meuter & Laga, 1976; De Ceuster, 1987; Reinecke & Hoedemakers, 2006), but this selachian assemblage remains poorly documented.

The "Pliocene" (= Miocene) species listed in Le Hon are typical for the fauna of the Middle Miocene Antwerpen Sands Member (De Ceuster, 1987; pers. data). The local presence of *Carcharias vorax* and *Carcharoides caticus* suggests a Burdigalian to Serravallian age for this faunal assemblage, which corresponds very well with the Antwerpen Sands Member (see Louwye & Laga, 2008).

It is obvious that the taxonomic status of the nominal species *Lamna* (*Odontaspis*) *vorax* Le Hon, 1871 needs to be clarified. A neotype and paraneotype from the Antwerpen Sands Member are designated to define the nominal taxon objectively and to shed light on past confusions. A temporary outcrop in the close proximity of the ring way at Berchem is chosen as type locality (Fig. 1), which is considered to be closest to the original type locality of the lost holotype. The basal part of the Middle Miocene Antwerpen Sands Member is selected as type horizon (Fig. 2).

The descriptive terminology follows Siverson (1999) and Cunningham (2000). Systematics follow Cappetta (2006).

Class **Chondrichthyes** Huxley, 1880

Order **Lamniformes** Berg, 1958

Family **Odontaspidae** Müller & Henle, 1839

Genus *Carcharias* Rafinesque, 1810

Carcharias vorax (Le Hon, 1871)

(Plates 1-3)

1871 *Lamna* (*Odontaspis*) *vorax* Le Hon: 5, 2 text-figs.

1926 *Odontaspis acutissima* (Ag.) mut. *vorax* (Le Hon); Leriche: 394, pl. 28, figs 33-34, 39, 44-46, 41? (non figs 31-32, 35-38, 40, 42-43, 47-49).

1934 *Odontaspis acutissima* var. *vorax* (Le Hon); Rocabert: 87, pl. 3, figs 27-28, 29-30?

1934 *Odontaspis cuspidata* (Agassiz); Rocabert, pl. 3, fig. 1.

1937 *Odontaspis* (*Synodontaspis*) *vorax* (Le Hon); Van de Geyn: 274, pl. 3, figs 5-6, 8-10, 12-14, 11? (non fig. 7).

1960 *Carcharias* (*Synodontaspis*) *acutissima vorax* (Le Hon); Kruckow: 56, text-figs 1-3.

1971 *Odontaspis* (*Synodontaspis*) *cuspidata cuspidata* (Agassiz); Schultz: 319, pl. 1, fig. 6.

1975 *Odontaspis vorax* (Le Hon); Van den Bosch et al., pl. 21, figs 4-5.

1976 *Odontaspis vorax* (Le Hon); De Ceuster: 123, pl. 1, figs 12-15.

1987 *Synodontaspis vorax* (Le Hon); De Ceuster: 236 (no figuration).

1988 *Odontaspis vorax* (Le Hon); Nolf: 53, figs 1-7.

1999 *Odontaspis vorax* (Le Hon); De Jong: 46, fig. 14.

Type species: *Carcharias taurus* Rafinesque, 1810, by monotypy (ICZN, 1912, Opinion 47, *Smithsonian Pub.*, (2060): 108).

According to Cappetta (2006), the species *vorax* is attributed to the genus *Carcharias*. This is confirmed by the generic diagnosis below.

Specific diagnosis: Species represented by isolated teeth only, showing a distinct monognathic heterodonty, as well as dignathic heterodonty. The grasping-cutting type dentition consists of three upper and four lower anterior teeth (see description below). The teeth are large, up to at least 34 mm in height. Except for some labio-basal folds on posterior teeth, the enameloid of all other teeth is smooth. Anterior teeth have elongated, slender cusps with cutting edges almost reaching to the base of the crown. Only the third upper anterior teeth and some of the second upper anteriors have cutting edges reaching from apex to base. The principal cusp on anterior teeth is flanked by a sharp, strongly hooked and lingually curved cusplet on each side, often accompanied by a marginal second one. The roots have a moderate to strong lingual protuberance. The root lobes are rounded and well separated by a deep nutrient groove. Upper lateral teeth are labio-lingually compressed with a distally inclined crown, while lower lateral teeth are thicker and more or less straight. The cusplets on upper lateral teeth vary from sharp and slender to broad and triangular shaped, or low and serrated. The crown's cutting edges of lateral teeth run from apex to base.

Neotype.

IRSNB P.8800 (ex De Schutter Collection)

Paraneotype.

IRSNB P.8801 (ex Dufrain Collection)

Type locality and horizon: Posthofbrug section, a temporary outcrop at a construction site southeast of the city of Antwerp (Fig. 1), near the railway station of Berchem (N 51° 11' 38" – E 4° 26' 04"); basal part of the Antwerpen Sands Member; *Turritella eryna* phosphoritic horizon (Fig. 2); unit 2 in Louwye et al. (2010); layers 2 and 3 in De Ceuster (1987). Based on dinoflagellate cyst stratigraphy, this unit was deposited some time between 16.5 Ma and 15.1 Ma, i.e. during late Burdigalian to early Langhian times (Louwye et al., 2010).

Description: The neotype IRSNB P.8800 (Fig. 4A-B; Plate 1, fig. 6A-D) is a second lower anterior tooth (LA2) from the left side of the jaw. This tooth is nearly symmetrical, except for the slightly longer and more diverging distal root lobe. The slightly distally inclined crown is elongated and wide. The crown is strongly

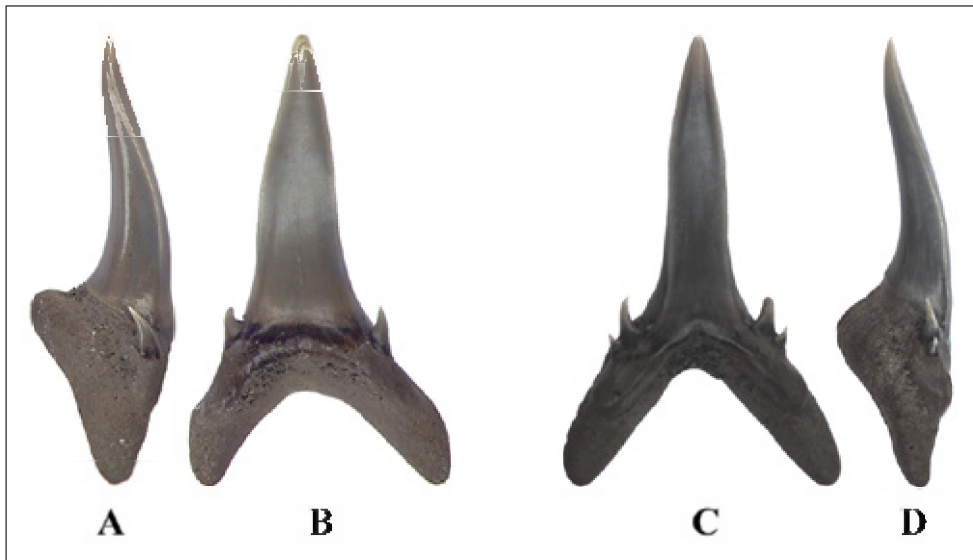


Figure 4. Neotype IRSNB P.8800 (A-B) and paraneotype IRSNB P.8801 (C-D). Lateral (A, D) and labial (B, C) views.

lingually directed, but the crown-tip is recurved labially. The crown surface is smooth. The cutting edges reach from apex to almost the base. A sharp, lingually curved cusplet flanks the principal cusp at each side. The root has a strong and high lingual protuberance with a well developed nutrient groove. Both root lobes are mesio-distally compressed.

The paraneotype IRSNB P.8801 (Fig. 4C-D; Plate 1, fig. 7A-D), a second or third lower anterior tooth from the left side of the jaw, is chosen to demonstrate the individual variation of the species. In contrast with the neotype, this tooth has a slender and narrow crown and two pairs of cusplets: a principal pair that is high, sharp and lingually curved, and a marginal secondary pair.

Dimensions (Table 1):

Distribution: *Carcharias vorax* (Le Hon, 1871) has a rather restricted temporal distribution ranging from Early Miocene Burdigalian to Late Miocene Tortonian (Reinecke et al., 2008, p. 11; pers. data). It seems that the geographical distribution of this species is focused on the North Sea Basin, being reported from Belgium (Le Hon, 1871; Leriche, 1926; De Ceuster, 1987; Nolf, 1988; present study), the Netherlands (Van de Geyn, 1937; Van den Bosch et al., 1975) and northern Germany (Kruckow, 1960; Reinecke et al., in prep.). However, *C. vorax* seems to occur occasionally in the Miocene of France (pers. data) and Spain (Rocabert, 1934), and in Burdigalian to Langhian deposits of the Central Paratethys exposed in Austria (Schultz, 1971) and southern Germany (T. Reinecke, pers. comm. 2009), although not being reported from the western Atlantic.

Description of tooth- and dentition-design: The dentition of *Carcharias vorax* (Le Hon, 1871) consists of three upper (UA1-3) and four lower (LA1-4) anterior teeth (Fig. 5), which reach up to 34 mm in height for the largest examined specimen (LA3, Plate 1, fig. 8A-D). There is at least one intermediate file.

Sexual dimorphism was not found in more than 500 dentitions of extant *Carcharias taurus* Rafinesque, 1810 (see Sadowsky, 1970), but a considerable individual variation in tooth- and dentition design instead. While the number of anterior files appears to be constant, the numbers of lateral and posterior files are not (Bass et al., 1975). This implies that the latter has no taxonomic value, especially as the number of posterior teeth may increase during lifetime (Applegate, 1965). Thus the number of lateral and posterior teeth on *Carcharias vorax* remains speculative. Based on the above observations on extant *Carcharias*, between 6 to 8 upper lateral and 5 or 6 lower lateral teeth might have been present on each side of the jaw. Posterior teeth are the most variable of the teeth in extant *Carcharias* and differ largely in number, from 6 to 19 on each side of the upper and from 4 to 14 on each side of the lower jaw (Applegate, 1965; Bass et al., 1975). These posteriors are easily distinguished from the lateral teeth by their altered morphology (Applegate, 1965; Cunningham, 2000). It can not be concluded if *Carcharias vorax* possessed the same low-crowned crushing-type posterior teeth as *C. taurus*. If present, then it is impossible, when no lingual folds are present, to distinguish this type of teeth from those of *Carcharias acutissimus* and *C. reticulatus*. *Carcharias vorax* as well exhibits individual differences. Within teeth of the same tooth position, a strong variation was observed on the number and shape of

Specimen	Figure	Height	Width
Neotype IRSNB P.8800	Fig. 4A-B; Plate 1, fig. 6A-D	26.7	15.4
Paraneotype IRSNB P.8801	Fig. 4C-D; Plate 1, fig. 7A-D	24.9	15.3

Table 1. *Carcharias vorax* (Le Hon, 1871) – Measurements (mm)



Figure 5. Anterior tooth positions from the left side of the jaw. Mixed Neogene, *ex* Churchill-dok, Hoevenen (lingual views).

the cusplets, the width of the crown (UA2, LA2-3, UL), the amount of lingual curvature of the crown, and the length of the cutting edges (UA2, UA3).

Upper anterior teeth (Plate 1, figs 1-3; Plate 2, figs 1-4)

The upper anterior teeth have elongated and slender cusps with a smooth enameloid. In profile, these teeth are slightly lingually curved with a strong labial recurvature of the crown tip. They possess one sharp, lingually curved, often strongly hooked cusplet on each side of the principal cusp. Usually, a marginal secondary one is present. The cutting edges do not reach the base with the exception of the third upper anterior teeth (UA3) and some of the second upper anteriors (UA2) of which the cutting edges generally reach the base of the crown. The first upper anterior teeth (UA1, Plate 1, fig. 1A-D) are slightly smaller in size than the remaining upper anterior teeth, reaching up to 20 mm versus 30 mm for the largest second upper anterior. The first upper anterior teeth are almost symmetrical with root lobes that are approximately equal in length. The second and third upper anterior teeth (UA2 and UA3) have a longer mesial lobe. Third upper anterior teeth (UA3, Plate 1, fig. 3A-F) appear to curve mesially as the crown has a straight or slightly concave mesial edge and a convex distal edge. This interlocks with the distal margin of the anterior hollow in the palatoquadrate (Siverson, 1999, fig. 3A). Second (UA2) and third (UA3) upper anterior teeth occasionally possess a tiny cusplet between the base of the crown and the lateral cusplets (Plate 1, figs 2E-3E). The roots have a moderate to strong lingual protuberance. The root lobes are rounded, well separated, and divided by a deep nutrient groove.

Only few intermediate teeth (Plate 1, fig. 4A-D; Plate 2, fig. 5A-D) are recovered suggesting the presence of only one intermediate file. However this feature seems to be very variable within the extant *Carcharias taurus* (Arambourg, 1952; Applegate, 1965; Sadowsky, 1970). These labio-lingually flattened teeth originate on the

intermediate bar between the anterior and latero-posterior hollow of the palatoquadrate (Siverson, 1999, fig. 3A). These intermediate teeth are assigned to *Carcharias vorax* by their size (up to 12 mm) and smooth lingual crown face. The lingual root surface is large and flat limiting the depth of the interspace between the root lobes.

Lower anterior teeth (Plate 1, figs 5-9; Plate 2, figs 6-9)

The lower anterior teeth possess strongly lingually curved and slightly narrower crowns than the upper anterior ones. The enameloid of the lower anterior teeth is smooth. The cutting edges do not reach the base of the crown. The lingual protuberance of the root is stronger than in upper anterior teeth. The root lobes are rounded, well separated, and divided by a deep nutrient groove. They possess one sharp, lingually curved, often strongly hooked cusplet on each side of the principal cusp. Regularly, a marginal secondary one is present. Due to their parasymphseal position the first lower anterior teeth (LA1, Plate 1, fig. 5A-D) are very small compared to the remaining anteriors, reaching up to 15 mm versus 32 mm for the largest second lower anterior. The root lobes are strongly mesio-distally compressed. By their particular morphology, these teeth usually lack sufficient diagnostic characters to distinguish them from first lowers of *Carcharias reticulatus* and *Carcharias acutissimus*. Due to individual variation the second (LA2) and third lower anterior teeth (LA3) are very difficult to separate. The teeth need to be very well preserved to distinguish a difference between root lobes length. Also the difference of root lobe divergence is minimal and thus hard to recognize. Usually the teeth at the LA3 position have a smaller lingual protuberance and a deeper interspace between the root lobes. Its mesial root lobe is visibly longer than the distal one and both lobes are equally diverging, resulting in an almost symmetrical appearance. The teeth at the LA2 position have a more asymmetrical root with a more diverging distal lobe slightly longer than the mesial one. The fourth lower

anterior teeth (LA4, Plate 1, fig. 9A-D) are more distally inclined than second and third lower anteriors, having a longer mesial root lobe.

Upper lateral teeth (Plate 3, figs 1-8)

The separation of lateral teeth is gradational and therefore somewhat subjective. Upper lateral teeth strongly vary in crown width. The crowns are broader than those of lower lateral ones. Upper lateral teeth have a distally inclined crown with smooth enameloid. The cutting edges reach the base of the crown. The cusplets of upper lateral teeth show significant variations: sharp and slender, broad and triangular, or low and serrated. The cusplets often bend towards the principal cusp. Serrations are sometimes present at the base of the crown's cutting edge (e.g. Plate 3, fig. 5E). In profile, the roots of upper lateral teeth are relatively flat. The root lobes are widely diverging.

Lower lateral teeth (Plate 3, figs 9-14)

Lower lateral teeth exhibit less individual variation than upper laterals. The teeth have a more or less straight crown with smooth enameloid. The cutting edges reach the base of the crown. They possess one lingually curved cusplet on each side of the principal cusp, often accompanied by a marginal second one. In profile, the roots of lower lateral teeth are thicker than those of upper laterals. The root lobes are widely diverging.

Generic diagnosis: The first upper anterior teeth of *Carcharias vorax* are only slightly smaller in size than the two remaining upper anterior teeth, whilst *Odontaspis* has strongly reduced first upper anterior teeth. Lower anterior teeth of *Odontaspis* have a deeper interspace between the root lobes. *Carcharias vorax* anterior teeth have shorter and strongly hooked cusplets, often accompanied by a marginal second one as opposed to *Odontaspis* teeth which have multiple sharp and very tall cusplets that are straight or weakly curved. The dental formula and dental morphology of *Carcharias vorax* allows attributing this species to the genus *Carcharias*.

Differential diagnosis: The type specimen in Le Hon (1871) can be recognized as different from the contemporaneous living odontaspidid sharks *Carcharias acutissimus* (Agassiz, 1843), *C. cuspidatus* (Agassiz, 1843) and *C. reticulatus* (Probst, 1879). The Middle Miocene teeth of *Carcharias acutissimus* (Fig. 6) are practically indistinguishable from those of extant *Carcharias taurus* Rafinesque, 1810 and therefore might better be referred to *Carcharias taurus* as Miocene representative of this *Carcharias* lineage (*sensu* Kemp, 1991; Cappetta & Nolf, 1991; Ward & Bonavia, 2001). The root lobes of second lower anterior teeth of *C. vorax*, and in particular the distal lobe, are much more divergent when compared to the more symmetrical teeth of the LA2 position in *C. taurus* (compare Plate 1, fig. 6A-B with Fig. 6A-B). The diverging root lobes of the holotype as illustrated in Le Hon (1871) correspond well with the neotype of *C. vorax*. The holotype represents a second or third lower anterior tooth. Due to individual variation, the teeth of the LA2 and LA3 positions in *C. vorax* are very difficult to distinguish. Unfortunately, the root lobes of the holotype appear to be damaged, disabling to establish differences in length of the root lobes. The lingual root protuberance of the holotype in Le Hon is similar to the lower anterior teeth of *C. vorax*. By comparison, the protuberance of teeth of *C. taurus* is more developed. In profile, the visible lobe and the lingual protuberance of the root form an almost straight line in *C. vorax* (Fig. 4A), whilst they form an obtuse angle in *C. taurus* (Fig. 6C). Generally, teeth of Miocene *C. taurus* have strong folds on the lingual crown face. The holotype of *C. vorax* appears to possess smooth lingual and labial crown surfaces as folds are absent on the illustration nor mentioned by Le Hon. Anterior teeth of *C. taurus* only possess a single cusplet on each side of the crown, while teeth of *C. vorax* usually have a marginal secondary pair.

The holotype in Le Hon, figured in natural size, measures 29 mm in height, which significantly differs from *Carcharias reticulatus* (Probst, 1879). The largest specimen of the syntypes of *C. reticulatus* illustrated by Probst (1879, pl. 2, fig. 27), a second lower anterior tooth,



Figure 6. *Carcharias acutissimus/taurus*, second lower anterior tooth (LA2). Middle Miocene, Antwerpen Sands Member, Berchem (scale bar = 5 mm). Lingual (A), labial (B), lateral (C) and basal (D) views.

is 19 mm high (T. Reinecke, pers. comm. 2010). Not a single tooth in a sample of more than 300 *C. reticulatus* specimens from the Neogene of Belgium is higher than 23 mm.

The Miocene species *Carcharias vorax* seems closely related to the Oligocene-Early Miocene species *Carcharias cuspidatus* (Agassiz, 1843). This resemblance was already observed by Leriche (1926, p. 395). *Carcharias cuspidatus* is recorded from the Early Oligocene (Rupelian) of Belgium (Leriche, 1910; Baut & Génault, 1999), the Oligocene of France (Merle et al., 2002) and the Early Oligocene to Early Miocene of Germany (Reinecke et al., 2001, 2005, 2008). The similarity in tooth- and dentition design, as well as their respective ages strongly suggests that *Carcharias cuspidatus* is the direct ancestor of *Carcharias vorax*. Cappetta (1970, p. 33), describing Miocene teeth from southern France, noted that *C. cuspidatus* disappeared in the area at the end of the Aquitanian or by the beginning of the Burdigalian. Reinecke et al. (2008, p. 11) placed the first appearance of *Carcharias vorax* in the North Sea Basin in the Burdigalian.

The teeth of *Carcharias cuspidatus* might reach well over 50 mm in height (pers. data) and are more massive in appearance than the more slender teeth of *C. vorax*, which rarely exceed 30 mm in height. Compared to *C. vorax*, the root lobes of *C. cuspidatus* are more strongly developed, particularly on lateral teeth. The crowns of *C. vorax* are more elongated and narrower in appearance. The cusplets of anterior teeth are higher and sharper and the marginal secondary cusplets are more frequently present and more developed in *C. vorax* than in *C. cuspidatus*. In relation to the height of the crown, the cusplets of anterior teeth of *C. cuspidatus* are small. In both species, i.e. *C. vorax* and *C. cuspidatus*, the cusplets of upper lateral teeth exhibit a wide morphological variation. This typical feature led to the suggestion that a separate genus for the species *C. cuspidatus* would be more appropriate (Suárez et al., 2006).

Purdy et al. (2001) reported *Carcharias cuspidatus* from both the Early Miocene Pungo River and Early Pliocene Yorktown formations at the Lee Creek mine. Its occurrence in the latter formation is doubtful as the single tooth illustrated by Purdy et al. (2001, p. 103, fig. 18b-d) is a third upper anterior tooth of *C. taurus*. After examining more than 200 Lee Creek sandtiger teeth, most of these appear very similar to the Oligocene *C. cuspidatus* teeth from Belgium and a minority is identical to *Carcharias taurus*. The artificial reconstruction of *C. cuspidatus*' dentition in Purdy et al. (2001, p. 103, fig. 18a) is missing a correct first upper and first lower anterior tooth. Also the tooth set of *Carcharias cuspidatus* proposed by Reinecke et al. (2001, pl. 16-17) is not fully accurate. Their "first lower anterior" seems to be a first upper and an appropriate first lower anterior tooth is missing.

Local extinction: *Carcharias vorax* occurred in the North Sea Basin until the Tortonian (pers. data) and its extinction could possibly be correlated with the contemporaneous

disappearance of the only extant representative of the genus, *Carcharias taurus*. Both species are found together in Miocene deposits, but do not seem to survive into the Pliocene of the area. During Late Miocene times, the North Sea evolved to an almost isolated basin with only a connection to the Atlantic via the north (Ziegler, 1990). A permanent connection with the Atlantic via the Channel may not have existed until the Pleistocene (Gibbard, 1995). The latest Tortonian to Messinian coastal environment at the southernmost border of the North Sea Basin, probably characterized by a shoaling phase, matches the global record of regressive phases during the Messinian, which are linked to cooling and increasing global ice volume (Louwye et al., 2007). Zachos et al. (2001) reported a gradual cooling after the late Middle Miocene climatic optimum and the re-establishment of an Antarctic ice sheet, related with a global lowering of the sea level (Vandenberghe et al., 1998). Extant *C. taurus* occurs in warm-temperate and subtropical waters (Compagno, 2001). The temperature in today's North Sea is too low for *Carcharias taurus* to survive. Compared to the Early Pliocene, North Atlantic Ocean surface temperature cooled down by about 6°C (Lawrence et al., 2009). Cold water seems to form a barrier for the extant *C. taurus* (Cione et al., 2007) and this species seems not to subsist above the 45°N latitude (Compagno, 2001). Mating in subtropical waters, a viable population apparently needs a temperate warm nursery area within reach of migrating sharks (Bass et al., 1975). Populations of *C. taurus* might not have been able to escape the North Sea Basin via the north and could not migrate to areas with a more optimal temperature, causing the number of the species to decline. As *C. taurus*, also *C. vorax* might have suffered from these changing conditions, global cooling and isolation. A similar, local extinction of *Carcharias taurus* occurred during the Pliocene in the eastern Pacific and was caused by a drop in global temperature and sea level, and isolation due to the forming of the Panama Isthmus in the north and the cold water in the south (Cione et al., 2007).

Remarks: In extant *Carcharias taurus*, Applegate (1965, fig. 5) developed an empirical relation between the tooth height of the tallest tooth in the jaw (LA3) and the total body length of the shark (TL), while Shimada (2004, p. 132) developed a similar relation between the crown height and the TL. The largest *C. vorax* tooth (LA3, Plate 1, fig. 8) reaches 34 mm in height with a crown height of 29.5 mm (measured *sensu* Shimada, 2004, fig. 1B). Assuming that the tooth- and crown height in *C. vorax* have a comparable relationship to the total body length as in *C. taurus*, the equation of Shimada (2004) suggests a TL of 286 cm, while a TL of almost 280 cm would be obtained with the equation of Applegate (1965).

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Plate 1. *Carcharias vorax* (Le Hon, 1871) - anterior dental series.

Middle Miocene, basal Antwerpen Sands Member.

Lingual (A), labial (B), lateral (C) and basal (D) views.

Scale bar = 5 mm.

1A-D. First upper anterior tooth (UA1), Posthofbrug outcrop, Berchem. Van den Eeckhaut Collection.

2A-E. Second upper anterior tooth (UA2), Posthofbrug outcrop, Berchem. Dufraing Collection. Detail of mesial cusplet (E).

3A-F. Third upper anterior tooth (UA3), Posthofbrug outcrop, Berchem. De Schutter Collection. Detail of distal cusplet (E) and occlusal view (F).

4A-D. Upper intermediate tooth, Berchem (Geological Survey of Belgium, 28 E 126'). Herman Collection.

5A-D. First lower anterior tooth (LA1), Posthofbrug outcrop, Berchem. Dufraing Collection.

6A-D. **Neotype**. IRSNB P.8800. Second lower anterior tooth (LA2), Posthofbrug outcrop, Berchem. *Ex* De Schutter Collection.

7A-D. **Paraneotype**. IRSNB P.8801. Second or third lower anterior tooth, Posthofbrug outcrop, Berchem. *Ex* Dufraing Collection.

8A-D. Third lower anterior tooth (LA3), Posthofbrug outcrop, Berchem. Dufraing Collection.

9A-D. Fourth lower anterior tooth (LA4), Posthofbrug outcrop, Berchem. Dufraing Collection.



Plate 2. *Carcharias vorax* (Le Hon, 1871) - anterior dental series.
Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.
Lingual (A), labial (B), lateral (C) and basal (D) views. Detail of distal cusplet (E).
Scale bar = 5 mm.

- 1A-D. First upper anterior tooth (UA1).
- 2A-D. Second upper anterior tooth (UA2)
- 3A-D. Third upper anterior tooth (UA3)
- 4A-E. Third upper anterior tooth (UA3)
- 5A-D. Upper intermediate tooth
- 6A-D. First lower anterior tooth (LA1)
- 7A-D. Second lower anterior tooth (LA2)
- 8A-D. Third lower anterior tooth (LA3)
- 9A-D. Fourth lower anterior tooth (LA4)

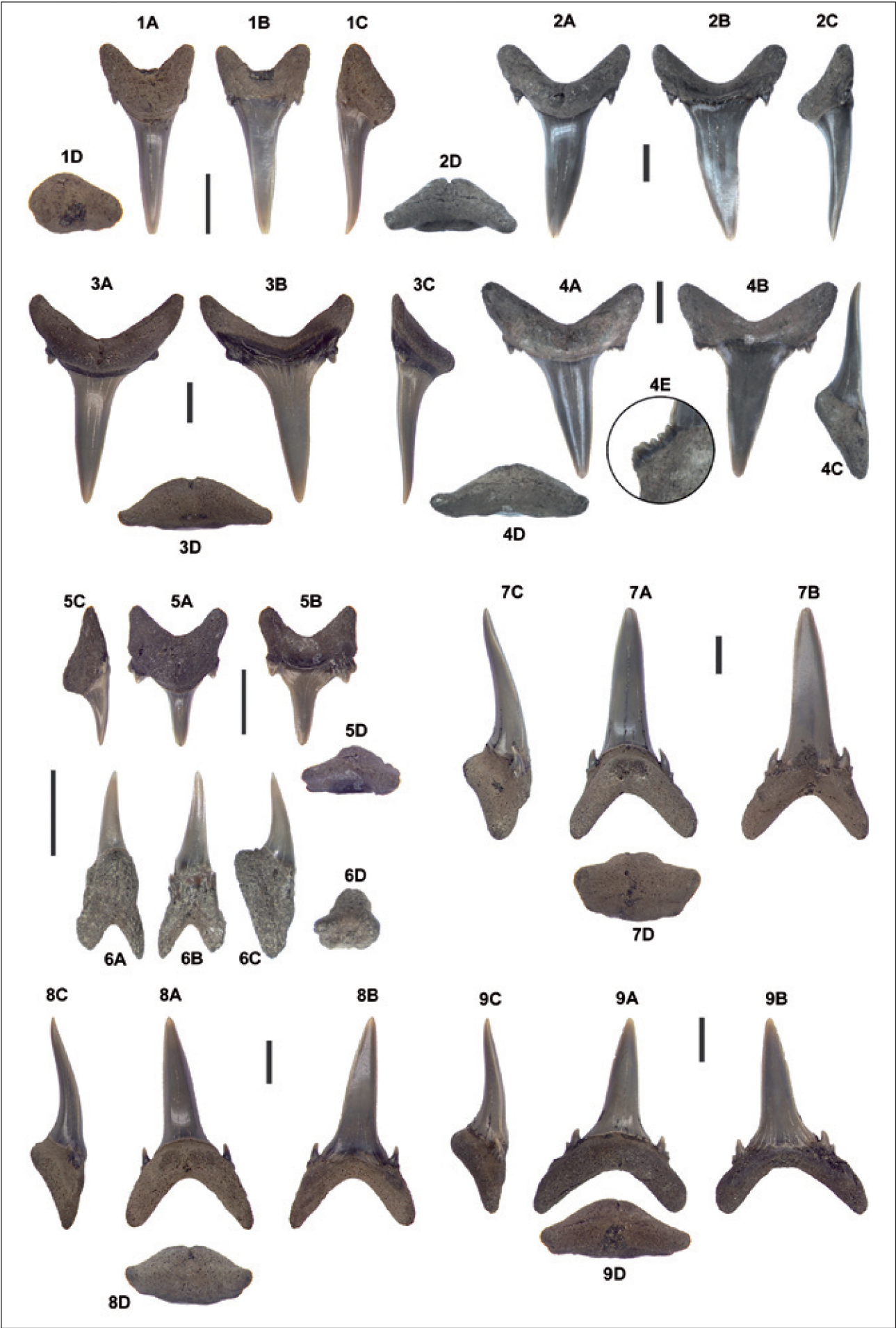


Plate 3. *Carcharias vorax* (Le Hon, 1871) - lateral teeth.

Lingual (A), labial (B), lateral (C) and basal (D) views.

Scale bar = 5 mm.

1A-D. Upper lateral tooth, Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.2A-D. Upper lateral tooth, Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.3A-E. Upper lateral tooth, Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.
Detail of distal cusplet (E).4A-E. Upper lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.
Detail of mesial cusplet (E).5A-E. Upper lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.
Detail of mesial cusplet (E).

6A-D. Upper lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.

7A-E. Upper lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.
Detail of distal cusplet (E).

8A-D. Upper lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.

9A-D. Lower lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.

10A-D. Lower lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. De Schutter Collection.

11A-D. Lower lateral tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection.

12A-D. Lower lateral tooth, Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.13A-D. Lower lateral tooth, Mixed Neogene, *ex* Churchilldok, Hoevenen. De Schutter Collection.

14A-D. (?Lower) posterior tooth, Middle Miocene, basal Antwerpen Sands Member, Posthofbrug outcrop, Berchem. Dufrain Collection. Scale bar = 2 mm

