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Dental evolution of the ‘serrated’ mako shark, *Isurus subserratus* aka *I. escheri* (Chondrichthyes, Lamnidae) in the late Neogene of the North Sea Basin

This paper is dedicated to the memory of Arie W. Janssen, as a token of appreciation for sharing his passion for and longstanding contributions to the Tertiary stratigraphy of the Netherlands and Belgium.

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The locality of Langenboom (Noord-Brabant, the Netherlands), also known as Mill, is famous for the massive number of isolated shark teeth recovered between 1995 and 2015 by fossil collectors from dumped upper Miocene and lower Pliocene sands. At this locality, the crenulated teeth of the extinct mako shark *Isurus subserratus* (Agassiz, 1843), commonly listed in the palaeontological literature with the specific name of *escheri*, are exceptionally common. Owing to scarcity of these teeth outside the Netherlands, Belgium and Germany, this species is poorly known, and its generic attribution has been for a long time the subject of debate. Based on the morphology and taphonomic condition, we identified four well defined consecutive morphotypes of *Isurus subserratus* teeth in the abundant Langenboom material. We observe that over time, the size increases, particularly on upper anterior teeth, together with a broadening of the crown. Lower teeth become more massive in appearance, the crenulations on the cutting edges get coarser and more irregular, and lateral cusplets disappear in all tooth positions. These four Langenboom types are also recognised in the sparse existing literature on *in situ* collected specimens. The gradual dental evolution clearly shows that the species descended from *Isurus oxyrinchus* Rafinesque, 1810 and is not related to the *Carcharodon* lineage. *Isurus subserratus* probably originated in the Serravallian of the North Sea Basin and its occurrence was restricted to the Atlantic coastline of Europe and the United States. By the middle Zanclean, the species seems to have disappeared. The genus *Carcharomodus* Kriwet, Mewis & Hampe, 2015, recently created to accommodate these teeth, is discussed and discarded.

KEY WORDS: Elasmobranchii, Tortonian, Zanclean, Breda Formation, Diessen Formation, *oxyrinchus*, Mill, Langenboom

Introduction

Between 1995 and 2015, Miocene and Pliocene selachian remains were extensively collected from a fossil site near the village Langenboom (municipality of Mill en Sint Hubert, Noord-Brabant, the Netherlands) (Wijnker *et al.*, 2008; Peters, 2013). The sharks’ teeth are recovered from dumped sands which were underwater excavated from various depths in the adjacent flooded sandpit ‘De Kuilen’. At this locality, also known as Mill, teeth of *Isurus subserratus* (Agassiz, 1843), usually listed in the palaeontological literature with the specific name of *escheri* Agassiz, 1843, proved to be abundantly present (Wijnker *et al.*, 2008) and represent the youngest occurrence of the species (Kriwet *et al.*, 2015).

The fossil distribution of *Isurus subserratus* seems restricted to the middle Miocene – lower Pliocene of the northern Atlantic and has been reported from Belgium (*e.g.,* Le Hon, 1871; Leriche, 1926; De Ceuster, 1976), the Netherlands (*e.g.,* Van den Bosch, 1969; Van den Bosch *et al.*, 1975), Germany (*e.g.,* Kruckow, 1960; Kriwet *et al.*, 2015), Denmark (Bendix-Almgreen 1983), France (Priem, 2012; Canevet, 2011, 2016) and the United States (Kent, 2018).

Teeth of *Isurus subserratus* are exceptionally common at the Langenboom locality. This large sized shark may have preferred deeper water as the assumed coastline during deposition of the upper part of the Diessen Formation (early late Miocene) was some 125 km south of Langenboom (Zagwijn & Hager, 1987; Wijnker *et al.*, 2008).

Also, in the roughly contemporary Deurne Sand Member of the Diest Formation in Belgium (Louwye, 2002), teeth of this species are amongst the most common larger teeth found (Hoedemakers & Dufraing, 2015; pers. obs. PDS).

The chondrichthyan fossil record generally consists of isolated teeth and vertebrae only, which are occasionally available as isolated, associated or semi associated tooth sets (Shimada, 2005). Such a unique associated set of 42 teeth and 49 vertebrae of *Isurus subserratus* was recovered from Miocene clays (Serravallian/Tortonian boundary) in Groß Pampau, Germany (as *escheri*; Andres, 2002; Mewis & Klug, 2006; Mewis, 2008) and published by Kriwet *et al.* (as *escheri*; 2015). The genus *Carcharomodus* was created to accommodate these teeth (Kriwet *et al.*, 2015).

The generic attribution of this species is poorly understood and is for a long time subject of debate, which focuses on whether or not *subserratus* (= *escheri*) is related to the *Carcharodon* lineage (*e.g.,* Leriche, 1926; Purdy *et al.*, 2001; Andres, 2002; Cappetta, 2012; Ehret *et al.*, 2012; Kriwet *et al.*, 2015). The morphological evolution of *Isurus subserratus* teeth, that is coarsening of the crenulation and broadening of the crown, was already noticed and summarised by Van den Bosch (1969, 1978, 1980), Van den Bosch *et al.* (1975) and Andres (2002). The abundant material from Langenboom enabled us to identify four well defined consecutive evolutionary types of *Isurus subserratus* teeth clearly showing that the species descended from *Isurus oxyrinchus* Rafinesque, 1810 and is not related to *Carcharodon* Smith *in* Müller & Henle, 1838.

Locality and stratigraphy

The sandpit 'De Kuilen' at Langenboom (51°41'54.5" N, 5°44'42.8" E), municipality of Mill en Sint Hubert, is situated in the southeastern part of the Netherlands (Fig. 1), near the southern margin of the North Sea basin, in the northwestern part of the Lower Rhine Embayment. The Langenboom site is located on the Peel Fault Block, in an area characterised by tectonic activity (Wijnker *et al.*, 2008).

The excavated sands at Langenboom originate from the Miocene Diessen Formation (formerly known as Breda Formation, see Munsterman *et al.*, 2019) of early-middle Tortonian age (Unit A) and overlying Pliocene Oosterhout Formation (Units B-C) ranging from early Zanclean to Piacenzian age (Fig. 2; Wijnker *et al.*, 2008; King, 2016; Munsterman *et al.*, 2019). The Diessen Formation at Langenboom (dinocyst zone SNSM12 of Munsterman & Brinkhuis, 2004) can be correlated with the Deurne Sand Member and probably also with the underlying and recently proposed Borsbeek Sand Member of the Diest Formation in the Antwerp area in Belgium (Louwye, 2002; Wijnker *et al.*, 2008; Goolaerts *et al.*, 2020). The boundary with the overlying Oosterhout Formation can be associated with the Late Miocene Unconformity (LMU) and approximates the boundary Miocene/Pliocene. The base of the Oosterhout Formation (Unit B) is assigned an early (or middle) Zanclean age, and the higher part of the formation a middle to late Zanclean age (King, 2016; Munsterman *et al.*, 2019). The transgressive base contains many reworked late Miocene and early Pliocene taxa in a very heterogeneous taphonomic condition (Wijnker *et al.*, 2008; Hoedemakers, 2013). Unit B corresponds in age to the Kattendijk Formation, except for the top shell bed, whose molluscan assemblage indicates the equivalent of the Oorderen Member in the Antwerp area in Belgium (King, 2016). Unit C is probably of early Piacenzian age (Wijnker *et al.*, 2008; King, 2016), but is decalcified and doesn't seem to contain many macrofossils (Wijnker *et al.*, 2008).

Figure 1. Location of the Langenboom locality (indicated by L), also known as Mill, in the southeastern part of the Netherlands (51°41'54.5" N, 5°44'42.8" E; See Wijnker *et al.*, 2008). Map data: Google, customised with Google Styled Maps API.

See Wijnker *et al.* (2008) for details on the location, stratigraphy and geological setting of the locality and to Peters (2013) for details on the history.

Materials and methods (Table 1)

The teeth used in this study were collected at the Langenboom locality between 1995 and 2015. More than 2300 isolated teeth of *Isurus subserratus* were recovered during that period. The specimens illustrated on Plates 1 to 4 are deposited in the collection of Oertijdmuseum De Groene Poort (Boxtel, the Netherlands) under registration numbers MAB 12059-12097. The remaining teeth are housed in the private collection of the second author (RV).

When the suction dredger reached a particular depth, often remaining in place for several weeks, all teeth recovered were kept together. In that way samples of *sub-*

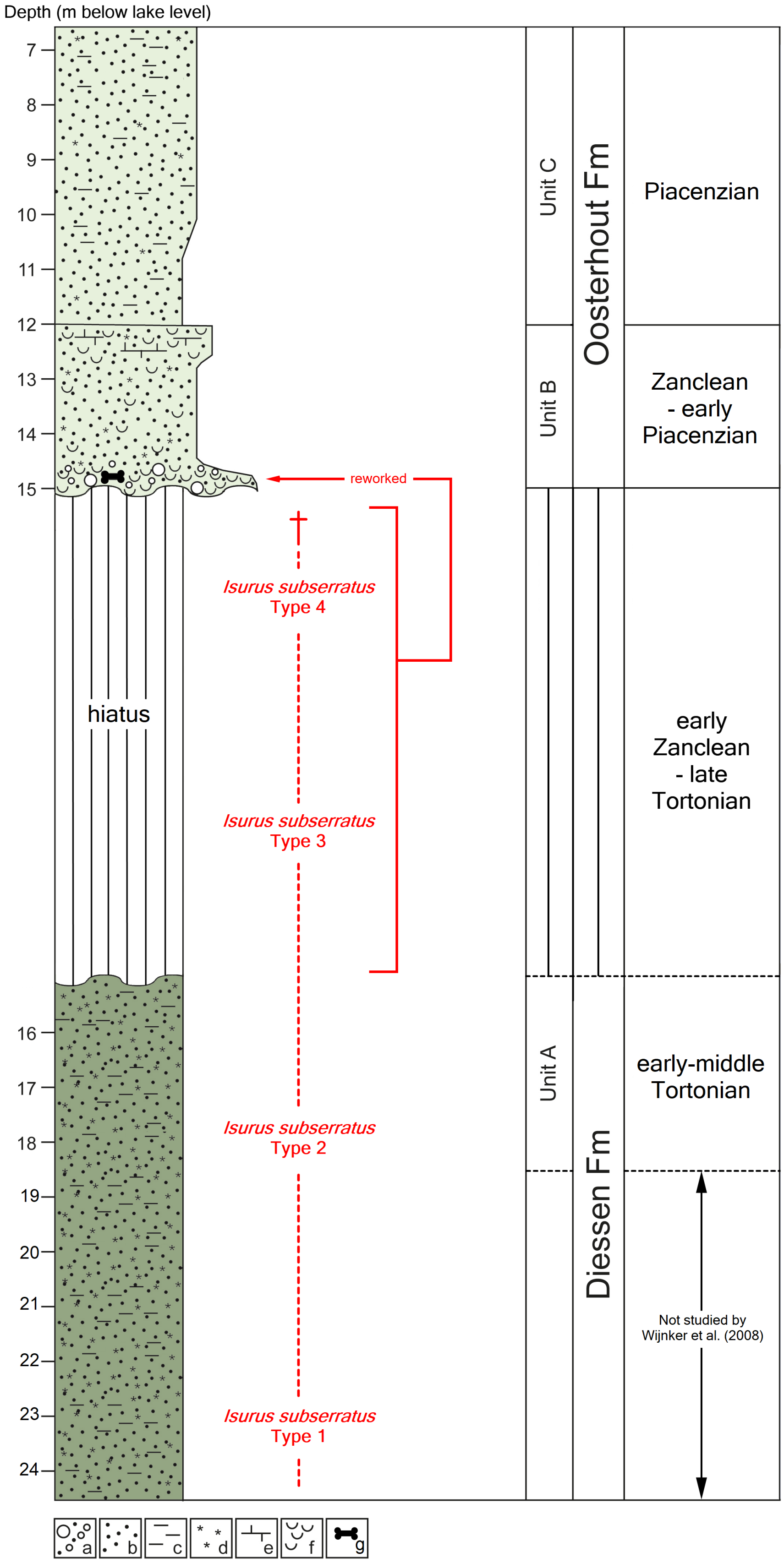

Figure 2. Lithological column and stratigraphic interpretation of the Diessen and Oosterhout Formations in the Langenboom section (based on Wijnker *et al.*, 2008). Often the suction dredger reached a depth of 20 m and occasionally even 24 m (pers. obs. RV), but this lowest interval could not be sampled by Wijnker *et al.* The probable origin of the four types of *Isurus subserratus* teeth (this study) is indicated. Caption: a = gravel; b = sand; c = silt; d = glauconite; e = carbonate cement; f = shells; g = bone.

Type	Sample size (Coll. RV)	Depth of the suction dredger (m)	Ratio *Isurus subserratus* - *Carcharodon plicatilis*
1	68	16-24	1:2
2	612	16-20	1:3
3	1441	14-15	1:8
4	228	14-15	1:10

Table 1. Ratio of *Isurus subserratus* (Agassiz, 1843) vs *Carcharodon plicatilis* (Agassiz, 1843) teeth.

serratus teeth from various depths were obtained. The morphology of the teeth from the different samples could then be compared; however, contamination from other levels cannot be excluded.

An isolated tooth set (see Shimada, 2005) was assembled using more than 600 Type 2 *subserratus* teeth (Plate 6). The reconstruction is based on the assumption that *I. subserratus* is a member of the Lamnidae (Kriwet *et al.*, 2015). The differentiation between lateral and posterior teeth is quite subjective (*e.g.,* Shimada, 2002) and are therefore combined here as lateral teeth. While the number of anterior files appears to be constant, the lateral files are not (*e.g.,* Applegate, 1965).

The following abbreviations are used:

RV	Rene van der Vliet, Uden, the Netherlands
PDS	Pieter De Schutter, Aalst, Belgium
MAB	Oertijdmuseum De Groene Poort, Boxtel, the Netherlands
NHMUK	The Natural History Museum, London, UK
UA	upper anterior tooth
LA	lower anterior tooth
UL	upper lateral tooth
LL	lower lateral tooth

Systematic palaeontology

Systematics and anatomical tooth terminology follow Cappetta (2012).

Class Chondrichthyes Huxley, 1880
Order Lamniformes Berg, 1958
Family Lamnidae Bonaparte, 1835
Genus *Isurus* Rafinesque, 1810
Type species: *Isurus oxyrinchus* Rafinesque, 1810, by monotypy.

Synonymy: Oxyrhina Agassiz, 1835; *Carcharomodus* Kriwet, Mewis & Hampe, 2015 (see Discussion).

Isurus subserratus (Agassiz, 1843)

Agassiz (1843: p. 260, pl. 36, figs 14-15) erected the species *Carcharodon subserratus* based on a single specimen supposedly originating from the Eocene London Clay of Sheppey, UK (NHMUK P. 2356), which is refigured in Fig. 3. However, the morphology and heavily mineralised preservation of the holotype do not occur in the London Clay; the specimen is probably collected from Miocene deposits in Belgium or the Netherlands, imported to Sheppey and sold with local fossils in the 19th century (Ward in Cappetta, 2012; Ward in Kent, 2018). The heavily mineralised preservation of the holotype with a matt black root showing pyrite decay and a slightly polished crown (pers. comm. D.J. Ward, 2021), suggests that this tooth might have originated from a clayey deposit. A possible source could be East Netherlands where shark teeth from late Miocene deposits were already mentioned in the late 18th century literature (*e.g.,* De Luc, 1779).

Agassiz (1843: p. 260, pl. 36, figs 16-21) also erected the species *Carcharodon escheri* based on two incomplete teeth allegedly from the Burdigalian of Switzerland and Germany (Molasse Basin), without precise locality information. The holotype is refigured in Kriwet *et al.* (2015, fig. 4), the whereabouts of the second tooth are unknown (Kriwet *et al.*, 2015). However, no other specimens are known to have been found in the Molasse Basin (Leriche, 1927; Höltke *et al.*, 2020; Kriwet *et al.*, 2015), rendering the provenance of these two teeth very questionable.

Woodward (1889) regarded these species conspecific and synonymised, on the basis of both page and figure priority, the species *escheri* under *subserratus*, an opinion followed by Priem (1912) and Kent (2018). We agree that *subserratus* is a senior synonym of *escheri* and that consequently the specific name *subserratus* must be used for these crenulated *Isurus* teeth.

Selected references

*1843	*Carcharodon subserratus* Agassiz 1843, p. 260, pl. 36, figs 14-15.
1843	*Carcharodon Escheri* Agassiz 1843, p. 260, pl. 36, figs 16-21.
1926	*Oxyrhina hastalis* Agassiz var. *Escheri* Agassiz – Leriche, p. 409, pl. 33, figs 1-8.
1937	*Isurus hastalis* (Ag.) mut. *Escheri* (Ag.) – Van de Geyn, p. 277, pl. 4, figs 11-14.
1969	*Oxyrhina escheri* (Agassiz) – Van den Bosch, p. 30, figs 27-39, 53, 55, 58-59.
1975	*Isurus escheri* (Agassiz) – Van den Bosch *et al.*, p. 99, pl. 23, figs 5-7.
1976	*Isurus escheri* (Agassiz, 1844) – De Ceuster, p. 130, pl. 3, figs 7-14; p1. 4, figs 1-6.
2011	*Carcharodon escheri* (Agassiz, 1843) – Canevet, p. 66, pl 1, figs 2-3.
2012	*„Carcharodon“ escheri* – Cappetta, p. 211, fig. 199.
2015	*Carcharomodus escheri* (Agassiz, 1843) – Kriwet *et al.*, p. 861, figs 4, 10-12.
2015	*Carcharomodus escheri* (Agassiz, 1843) – Hoedemakers & Dufraing, p. 15, pl. 1, fig. 5.
2018	*Carcharomodus escheri* – Pollerspöck & Gille, p. 17, fig. 3e.

Figure 3. Holotype of *Carcharodon subserratus* Agassiz, 1843. NHMUK P. 2356. Lingual (A1) and labial (A2) view. Scale bar 10 mm. Original drawing from Agassiz 1843 (B).

2018 *Carcharodon subserratus* Agassiz, 1843 – Kent, p. 75, figs 2.10F-H.

Description (Plates 2 and 6)

Upper anterior teeth (UA1-UA3) (Plate 2, figs 1-3) have a wide, triangularly shaped crown. In profile, these teeth are more or less straight with a strong labial recurvature of the crown tip. In lingual view, the cusp of first upper anterior teeth is slightly distally directed or more or less straight with a distally inclined apical part (Plate 2, fig. 1A). The cusp of the second upper anterior teeth is stronger distally directed (Plate 2, fig. 2A). Upper anterior teeth may possess a pair of tiny cusplets (*e.g.,* Plate 2, fig. 3E). The root is high and wide, with a small basal concavity separating the short, labio-lingually flattened root lobes. The basal root extremities are flat or slightly rounded. The lingual root protuberance is weak. Upper teeth exhibit fine crenulations along the cutting edge of the crown, from apex to base. The third upper anterior tooth (Plate 2, fig. 3) is reduced in size compared to the first and second upper anteriors. Besides the presence of marginal lateral cusplets and very fine crenulations along the crown's cutting edge, teeth of this tooth position are morphologically very close to those of the genus *Carcharodon* (see *e.g.,* Bass *et al.*, 1975, pl. 8; Bor & Peters, 2015, fig. 5). The crown is triangularly shaped, slightly distally directed or more or less straight with a distally inclined apex. There is a marked flattening of the root at the level of the lingual protuberance.

Upper lateral teeth (Plate 2, fig. 4) have a low crown with a wide base and a strongly distally inclined apical part, giving these teeth a hooked appearance. In profile, these teeth are straight and flat. The root is high and wide with a flat basal edge. A small basal concavity separates the short, labio-lingually flattened root lobes.

Lower anterior teeth (LA1-LA3) (Plate 2, figs 5-7) are recognisable by their massive root and slender crown. The lingual root protuberance is very strong. The well-developed root lobes are slender and rounded; longer and more separated than those on upper anterior teeth. The crown has a labio-lingually thick, and mesio-distally wide base and a narrow, elongated apical part. The crown's cutting edge is finely crenulated, often only at the base, while the apical part has none or weak crenulations, sometimes hardly visible with the naked eye. Generally, the crenulations are slightly more developed on upper than on lower teeth. Lingually seen, the cusp of the first lower anterior teeth (Plate 2, fig. 5A) is more or less straight while the second and third lower anterior teeth (Plate 2, figs 6A-7A) have a slightly distally inclined crown. In profile, these teeth are strongly lingually curved. The lateral cusplets on lower anterior teeth are very low and reduced. The cutting edge of the crown of some lower anterior teeth mesio-distally contracts. This is well visible in labial view, from where the lingual crown surface can be seen (*e.g.,* Plate 2, fig. 5B).

Lower lateral teeth (Plate 2, fig. 8) have a more or less straight crown in labio-lingual view. In profile, these teeth are lingually curved. Compared to upper lateral teeth, the crown is narrow and slender, the lingual root protuberance is stronger, and the root lobes are narrower, rounded instead of flattened, and more separated. The lateral cusplets on lateral teeth, and especially on lower laterals, can be relatively well developed (*e.g.,* Plate 2, fig. 8B).

Heterodonty

The dentition of *Isurus subserratus* is characterised by a strong dignathic and gradual monognathic heterodonty (Plate 6). Ontogenetic heterodonty is reflected in the upper anterior teeth by a straightening and broadening of the crown, relative to root width, as teeth get larger. Upper anterior teeth of juvenile sharks have a slender, elongated crown, often being asymmetrical (Plate 1, figs 9-10), while adult individuals acquire broad cusped, more symmetrical upper anterior teeth. In fact, teeth of juveniles resemble those of *Isurus oxyrinchus* Rafinesque, 1810, suggesting a similar diet for these small individuals largely based on teleost fish (Compagno, 2001). Adult teeth of *I. subserratus* are primarily of a cutting design, but the massive roots and very thick but narrow crown of the lower anteriors would be very suitable for holding large prey (Plate 6, figs 13-15). The upper jaw would than serve as a blade by the complete and crenulated cutting edges (Plate 6, figs 1-12). Its feeding style seems intermediate between those of *Isurus* and *Carcharodon* (Kriwet *et al*., 2015; as *escheri*).

Evolution (Plate 5)

Despite its abundance in Burdigalian strata (Reinecke *et al*., 2011; Everaert *et al*., 2019), teeth of *Isurus oxyrinchus* are quite rare in the upper Miocene of Langenboom, as in other middle and upper Miocene deposits of the North Sea Basin (*e.g.,* Reinecke *et al*., 2011; Bor *et al*., 2012). The species *Isurus subserratus* seems to evolve from a northeastern Atlantic population of *I. oxyrinchus* during the early Miocene. In the Burdigalian Kiel Sand Member of the Berchem Formation in Belgium (Everaert *et al*., 2019), a surprisingly large number of teeth of *I. oxyrinchus* exhibit a tiny lateral cusplet on the distal or both distal and mesial side of the crown (*e.g.,* Plate 5, fig. 2B-3B). This feature can be considered as the onset of the evolution to *I. subserratus*. The teeth acquire lateral cusplets, first observed on lateral, later also on anterior teeth. All teeth gradually develop a crenulated cutting edge (Fig. 4).

Upper anterior teeth gradually increase in size. In *Isurus oxyrinchus* typical asymmetrical upper anterior teeth with a narrow, elongated and strongly distally inclined crown evolve into more symmetrical teeth with a wide, triangularly shaped crown that is more or less straight (UA1, Plate 5, figs 1A-F) or slightly distally inclined (UA2-3). The root lobes reduce in length and evolve from rounded to labio-lingually flattened. The basal concavity separating the root lobes becomes less clear and there is a marked flattening of the root at the level of the lingual protuberance. A juvenile first and second upper anterior tooth are figured on Plate 1, figs 9-10. These are still morphologically very close to those of *I. oxyrinchus*, but already possess fine crenulations along the crown's cutting edge.

One of the tooth positions that demonstrates important morphological changes is the third upper anterior tooth (Plate 5, figs 2A-F). In *Isurus oxyrinchus* (Plate 5, fig. 2A), these teeth have a narrow, elongated and strongly distally inclined crown (hooked appearance). The root lobes are slender and well separated. At first, these teeth acquire a pair of marginal lateral cusplets (Plate 5, fig. 2B) and the crown's cutting edge gets very finely crenulated (Plate 5, fig. 2C), before evolving into a *Carcharodon*-like UA3 (see *description*) (Plate 5, figs 2D-F). Teeth of this position are relatively large compared to those of *I. oxyrinchus*.

The crown on lower anterior teeth (e.g., LA2, Plate 5, figs 4A-F) slightly shortens. The base of the crown gets mesio-distally wider and labio-lingually thicker. The apical part of the cusp remains narrow and elongated. Compared to *Isurus oxyrinchus*, the root increases in size and acquires a massive appearance. The root lobes are slightly more divergent.

Equally as observed in upper anterior teeth, also upper lateral teeth show a decrease in depth of the interspace between the root lobes (Plate 5, figs 3A-F); the root lobes are shorter, labio-lingually flattened and less separated from each other. As for lower anterior teeth, also lower laterals acquire a more massive root (Plate 5, figs 5A-F). The crown gets slightly more triangular.

Another important feature is the evolution of the labial crown overhang, which is typical for teeth of the genus *Isurus*. The labial crown overhang decreases in size, starting with the upper tooth positions, and finally disappears, similar as seen on corresponding teeth of *Carcharodon*. It remains, however, slightly visible on teeth of the lower tooth positions.

Morphological types (Table 2, Plates 1 to 5)

In the Langenboom material, four well-defined types of *Isurus subserratus* teeth are identified based on morphology and taphonomic condition. While the upper anterior teeth gradually gain in size with every type, acquiring very large teeth, the maximum size of the lower anterior teeth does not seem to change a lot, except that the root gets more massive in appearance. There is also a broadening of the crown in upper anterior teeth, the crenulations get coarser and more irregular (Fig. 4), and the lateral cusplets tend to disappear in all tooth positions.
This dental evolution happened gradually, over time, and a clear separation between all four types of *I. subserratus* is impossible, because they overlap both morphologically and probably also chronologically. This makes the attribution of a single specimen from a particular stratigraphic horizon difficult. Also, clearly identifiable *in situ* collected specimens are rare in the existing literature and consist mostly of one or two specimens, apart from Kriwet *et al.* (2015). This gradual morphological change over time could be linked to a shift in diet and feeding style, shifting from a grasping-cutting type to a cutting-type dentition, resulting in broad-bladed teeth ideal for preying upon marine mammals. The observed dental transition might be closely tied to the evolution of cetaceans.

Type 1 (Plate 1, figs 1-11) - The teeth are large, up to 45 mm in height for the upper jaw (UA2) and 38 mm for the lower jaw (LA2). Upper teeth exhibit fine crenulations along the cutting edge of the crown, from apex to base. On lower teeth, generally only the base of the cutting edge is finely crenulated. The crenulations are slightly more developed on upper than on lower teeth. Besides the lateral teeth, also some anterior teeth develop a marginal pair of lateral cusplets. The crown on upper anterior teeth increases in width and is nearly straight or only slightly distally inclined; however, typical *oxyrinchus*-like teeth with a slender and stronger distally inclined crown are also present, mostly representing sub-adult specimens (Plate 1, figs 9-11).

Type 1 teeth are very well preserved and show no signs of reworking. The crown is greyish, light blue coloured

	Type 1 **(Plate 1, figs 1-11)** **Early *Isurus subserratus***	**Type 2** **(Plate 2, figs 1-12)** **At the height of its evolution**	**Type 3** **(Plate 3, figs 1-8)**	**Type 4** **(Plate 4, figs 1-8)**
General morphology teeth	Close to *Isurus oxyrinchus*	Typical *Isurus subserratus*, morphology stable	Starts to resemble *Carcharodon*, less reminiscent of *Isurus*	*Carcharodon*-like, morphology very variable
Maximum height UA2/LA2	45 mm 38 mm	50 mm 43 mm	54 mm 43 mm	65 mm 42 mm
Morphology UA3	*I. oxyrinchus*-like; slender and distally inclined crown; well-developed root lobes.	Crown wider with decreased inclination; basal root concavity decreased in size.	*Carcharodon*-like; triangular shaped crown; shorter root lobes, basal root concavity further decreased in size.	*Carcharodon*-like; increased in size; basal root concavity indistinct
Cutting edges	Fine crenulations, full in some upper teeth, only near the base in lowers.	Fully crenulated, coarser in upper teeth, still very fine in lowers.	Coarse crenulations.	Coarse and irregular crenulations
Lateral cusplets	Lateral and anterior teeth start to develop a marginal pair.	More frequently present, (very) small in lower anterior teeth, sometimes well developed in upper anteriors.	Very rarely present.	Absent
Labial crown overhang	Distinct, *I. oxyrinchus*-like.	Less distinct, especially in upper tooth positions.	Absent in upper tooth positions (*Carcharodon* -like), indistinct in lowers.	Absent
Upper anterior teeth	Crown increased in width, nearly straight or slightly distally inclined; *I. oxyrinchus*-like slender and stronger distally inclined crowns also present.	Crown and root increased in width; root lobes shorter, labio-lingually flattened and less separated; basal concavity decreased in depth.	Crown increased in width, more triangularly shaped.	Thick and massive root
Upper lateral teeth	Slightly more robust and crown base mesio-distally wider than corresponding teeth of *I. oxyrinchus*.		*Carcharodon*-like, crown widens; decrease in distal crown inclination.	
Lower anterior teeth		Crown shorter, wider and thicker at the base; root increased in size with wider diverging root lobes; lingual root protuberance more developed.	Crown base wide, apex elongated.	Thick and massive root
Lower lateral teeth		Crown less distally inclined; lingual root protuberance more developed.	Crown straight, *Carcharodon*-like, no distal inclination; root more massive.	

Table 2. Summary of the dental characteristics of the four types of *Isurus subserratus* (Agassiz, 1843) teeth identified in the Langenboom material.

with occasionally a beige tint. Teeth of this type don't occur in the Pliocene basal gravel (Oosterhout Formation, base unit B, see Fig. 2) and may originate from the lowest part of unit A (Diessen Formation, see Fig 2) and from sediments several meters below the section described by Wijnker *et al.* (2008). The known stratigraphy goes down to about 18 m below surface (Fig. 2), but often the suction dredger reached a depth of about 20 m (Wijnker *et al.*, 2008, p. 168) and occasionally even 24 m (pers. obs. RV). Type 1 teeth were only found when the suction dredger reached these greater depths (pers. obs. RV).

Van den Bosch *et al.* (1975), when describing *Isurus subserratus* (as *escheri*) teeth from the Eibergen Member, of most likely Serravallian age (King, 2016), noted that the crenulation on the teeth's cutting edge is still rather indistinct and suggested the species is still in an earlier evolutionary stage. This corresponds well with our observations at Langenboom, suggesting Type 1 *subserratus* teeth evolved during the Serravallian.

Type 2 - See *Description* (Plate 2, figs 1-12; Plate 6, figs 1-23). We consider this type as the typical *Isurus subserra-*

tus. The teeth show much less variation than those of Type 1. It seems that the species stabilised at this moment in its evolution. The holotype of “*Carcharodon subserratus*” in Agassiz (1843), representing an upper anterior tooth, can be assigned to Type 2 based on the well-developed crenulations, and the width of the root and crown base. Also, the holotype of “*Carcharodon escheri*” in Agassiz (1843), refigured in Kriwet *et al.* (2015, fig. 4), representing an upper lateral tooth, can be assigned to Type 2 based on the coarse crenulation and crown height/width ratio.

There is an increase in tooth size (up to 50 mm in height for the UA2 and 43 mm for the LA2). A significant difference with teeth of Type 1 is the presence of complete crenulated cutting edges on both upper and lower teeth. These crenulations are regularly distributed along the cutting edge. The crenulations on upper teeth are more developed but remain very fine on lower teeth.

Lateral cusplets are more frequently present, often remaining very small, but occasionally well developed. The lateral cusplets in upper anterior and lower lateral teeth are more developed compared to those in lower anterior and upper lateral teeth.

The crown on upper anterior teeth widens and is nearly straight or only slightly distally inclined. The root and crown widen equally. Upper anterior and lateral teeth show a decrease in depth of the interspace between the root lobes, which are shorter, labio-lingually flattened and less separated from each other.

The crown on lower anterior teeth slightly shortens. The crown remains narrow, but its base widens and is slightly thicker in profile view. The root continues to increase in size with more widely diverging root lobes. The lingual root protuberance on lower anterior teeth, and to a lesser degree on lower laterals, is more developed. The crown’s cutting edge on some lower anterior teeth contracts to the centre of the tooth. This is well visible in labial view, from where the lingual crown surface can be seen (Plate 2, fig. 5B).

Type 2 teeth have an identical taphonomic condition as those of the previous type, being very well preserved showing no signs of reworking. Teeth of this type do not occur in the Pliocene basal gravel (Oosterhout Formation, base unit B, see Fig. 2) and may originate from (the upper part of) unit A (Diessen Formation, see Fig 2). These teeth are slightly more evolved than those of the preceding type.

In situ finds of this type are known from the Tortonian of Belgium (Hoedemakers & Dufraing, 2015; pers. obs. PDS) and the Serravallian of France (Canevet, 2011). The second upper anterior tooth (op. cit., pl. 1, fig. 2), measuring 42 mm in height, possesses marginal lateral cusplets, exhibits a complete but fine crenulation along the crown’s cutting edge, a distally directed cusp and short and reduced root lobes.

The partial dentition published by Kriwet *et al.* (2015), as *Carcharomodus escheri*, found near the boundary Serravallian/Tortonian, seems intermediate between types 2 and 3 at Langenboom by the broad-based crowns and well-developed and fairly coarse crenulations along the crowns cutting edges.

Van den Bosch *et al.* (1975) noted the stable morphology of the species (as *escheri*) in the Zenderen Member of Tortonian age (King, 2016), which corroborates our observations of Type 2 *subserratus* at Langenboom, indicating a correlation with the Deurne Sand Member of the Diest Formation in the Antwerp area in Belgium. The Diessen Formation at Langenboom (dinocyst zone SNSM12 of Munsterman & Brinkhuis, 2004) can indeed be correlated with the Deurne Sand Member (Louwye, 2002; Wijnker *et al.*, 2008; Goolaerts *et al.*, 2020).

Type 3 (Plate 3, figs 1-8) – Teeth of the third type start to resemble those of *Carcharodon*. The crown on upper teeth continues to widen, giving the upper anterior teeth a more triangularly shaped crown. The crown base on lower anterior teeth widens, while the crown apex elongates. The root of lower anteriors is more massive. Distal crown inclination on lateral teeth decreases. Upper anterior teeth slightly increase in size, up to 54 mm for the UA2, while the maximum tooth height of lower anteriors (LA2) remains unchanged at 43 mm. The cutting edge is stronger, but less regularly crenulated. Lateral cusplets are uncommon and are in the process of disappearing. The UA3 tooth position resembles those of *Carcharodon,* by acquiring a wide triangularly shaped crown. The root lobes shorten, and the basal root concavity decreases in size (Plate 3, fig. 3).

Most teeth of this type are worn, suggesting a reworking in the basal shell bed of Unit B (Oosterhout Formation, see Fig. 2). The crown is black, or steel blue coloured, often with an olive-green tint. These reworked teeth likely originate from missing parts of the upper Miocene, reworked in the Pliocene basal bed (see Fig. 2), as Wijnker *et al.* (2008) noticed the presence of many reworked Miocene taxa at the transgressive base of the Oosterhout Formation. However, some teeth of Type 3 are well-preserved and might originate from the uppermost part of Unit A (Diessen Formation, see Fig. 2).

Teeth of this morphology have been reported *in situ* from Tortonian sediments in Germany (Pollerspöck & Gille, 2018, fig. 3e). The *Carcharodon*-like third upper anterior tooth is more or less symmetrical with a triangular shaped crown, root lobes are short and more or less equal in length, basal root concavity is still well recognisable. The first upper anterior tooth has a wide crown base and root, with short lobes. Both teeth are slightly distally directed.

Type 4 (Plate 4, figs 1-8) - Very large sized upper anterior teeth, up to 65 mm in height for the UA2. To the contrary, the height of the lower anterior teeth remains unchanged with 42 mm as maximum (LA2). The teeth have a very variable morphology; it is practically impossible to find two similar teeth. The crenulations on the cutting edges are coarse and irregular, cusplets have (almost) disappeared. Besides the lower anterior teeth, also the upper anteriors have a thick and massive root. Teeth of the fourth type represent the final evolutionary stage of *Isurus subserratus*.

These teeth are very worn, suggesting a heavy reworking at the base of Unit B (Oosterhout Formation, see Fig. 2). The colour of the crown is mainly yellow ochre and olive green. It has to be noted that this yellow ochre colour aspect doesn't occur on teeth of the previous types. Type 4 teeth probably originate from missing parts of the lower Zanclean reworked at the base of the Oosterhout Formation (Unit B). As Type 4 teeth are more worn than those of Type 3, they probably originate from higher levels of the missing succession (Fig. 2) and hence were reworked for a longer period of time before they were deposited at the base of Unit B.

In situ specimens of latest Miocene or early Pliocene age are rare in the current literature, and in general, Type 4 teeth are almost absent. Van den Bosch *et al.* (1975) and Van den Bosch (1978) noted the rare presence of *Isurus subserratus* (as *escheri*) in the Delden Member, which is probably of Zanclean age (King, 2016), but unfortunately did not illustrate any specimens. De Ceuster (1976) and Cappetta (2012) figure tooth sets (as *escheri*) originating from Rumst (Belgium), indicating a Zanclean age (Cappetta, 2012, p. 211). This age is very questionable as these teeth originate from a basal gravel with many reworked Miocene fossils. In addition, when comparing these teeth to our series at Langenboom, both types 3 and 4 are recognised.

Extinction

At Langenboom, only Unit A and the transgressive base of Unit B contained *Isurus subserratus* teeth. When the suction dredger reached the upper part of Unit B, not a single *subserratus* tooth was found that day (pers. obs. RV). Many teeth of *Carcharodon plicatilis* (Agassiz, 1843) have remains of sediment firmly attached to the root and crown surface, which is characteristic for that part of Unit B; not a single *subserratus* tooth possesses this feature.

Unit B, apart from the top shell bed, corresponds in age to the Kattendijk Formation in Belgium of middle Zanclean age (King, 2016). With the exception of reworked specimens in the basal lag, not a single *Isurus subserratus* tooth is known to have been found in the Kattendijk Formation (Herman *et al.*, 1974; pers. obs. PDS). This corresponds with our observations at Langenboom that, apart from reworked specimens at the base, *I. subserratus* teeth are lacking in Unit B.

Van den Bosch *et al.* (1975) noted the rare presence of *I. subserratus* (as *escheri*) in the Delden Member which they interpreted as probably Pliocene. Bosch & Wesselingh (2006) confirmed that the assemblage includes taxa recorded only from the Pliocene, as did King (2016) indicating a possible Zanclean age for this member. However, the presence of *I. subserratus* in the Delden Member suggests an early Zanclean age for this deposit as by the middle Zanclean, the species seems to have disappeared. Unlike the earlier types, teeth of Type 4 are very large and irregular, variable in morphology. It is not known why it became extinct in the early or middle Zanclean, however, it may have been a result of competition with *Carcharodon plicatilis* (Agassiz, 1843) and *C. carcharias* (Linnaeus, 1758).

Discussion

De Ceuster (1976) mentioned a narrow and broad form of "*Isurus hastalis*" that he found in a post-Miocene basal gravel in Rumst, Belgium, as did Van den Bosch (1978, 1980) and Van den Bosch *et al.* (1975) when describing Neogene teeth from the eastern part of the Netherlands. The narrow form, *Carcharodon hastalis* (Agassiz, 1838), is reported from Burdigalian to Langhian strata in a.o. Belgium and the Netherlands (*e.g.,* Leriche, 1926; Van de Geyn, 1937; Van den Bosch *et al.*, 1975; De Ceuster, 1987; Bor *et al.*, 2012). These teeth attain a larger size and acquire wider crowns in Serravallian to Tortonian strata (*e.g.,* Leriche, 1926; Van den Bosch *et al.*, 1975). Purdy *et al.* (2001) proposed the name "*Isurus xiphodon*" to accommodate these teeth, considered a *nomen dubium* by Ward & Bonavia (2001). Cione *et al.* (2012) proposed *Carcharodon plicatilis* (Agassiz, 1843) as an available and valid name for this broad form. *C. plicatilis* has teeth with very wide triangular crowns and very short and flat root lobes compared to the early form *C. hastalis*, with a narrower crown and longer, rounded root lobes.

By the end of the Miocene, the tooth morphology of *subserratus* resembles that of the genus *Carcharodon* and is less reminiscent of *Isurus*. These teeth have probably led to the confusion in the past when authors suggested a relation with the species *hastalis* (*e.g.,* Leriche, 1926; Casier, 1960; Purdy *et al.*, 2001). Despite the resemblance of these teeth with those of *Carcharodon hastalis* and *C. plicatilis*, these evolving similarities are merely the result of convergence.

When comparing teeth of *Isurus subserratus* with those of the broad form *Carcharodon plicatilis* from the upper Miocene of Peru figured in Cappetta (2012, p. 215 as *hastalis*), several substantial differences are observed. Upper anterior teeth of *subserratus* are thicker and have a much narrower crown than those of *plicatilis*. The basal concavity separating the root lobes is less marked than observed in corresponding *subserratus* teeth. Lower anterior teeth of both genera have a very different morphology. Lower anteriors of *subserratus* have a much thicker root and crown base and possess a narrow cusp that only widens at the base. Lower anteriors of *Carcharodon* are flat and have a wide and triangular crown. In profile, lower anterior teeth are stronger lingually curved than corresponding *plicatilis* teeth. The labial crown surface overhanging the root is not observed in *Carcharodon* teeth.

Typical *Isurus subserratus* teeth from the Tortonian share some characters with the narrow form, *Carcharodon hastalis*, ranging from Burdigalian to Langhian (*e.g.,* Reinecke *et al.*, 2011). It must be noted that the stratigraphic ranges of these two morphotypes do not or only slightly overlap. When comparing teeth of *subserratus* with those of *hastalis* from the Burdigalian of Germany figured in Reinecke *et al.* (2011, pls 29-32), we notice that the upper anterior teeth are similar, but the lower anteriors are not. Lower anterior teeth of *hastalis* possess a higher and much wider crown and a less massive root. The lower part of the crown is labio-lingually thicker in *subserratus*. In profile, lower anterior teeth are stronger lingually curved than corresponding *hastalis* teeth. Upper lateral teeth of *subserratus* have a narrower crown, often with a strongly distally inclined apical part. Also, lower lateral teeth have a narrower crown and a thicker root than corresponding *hastalis* teeth. The root lobes are rounded instead of labio-lingually flattened as seen in *hastalis*. The labial crown surface overhanging the root is not observed in *Carcharodon* teeth.

Carcharodon carcharias derived, through an intermediate form named *Carcharodon hubbelli* Ehret *et al.*, 2012, from a Pacific population of *C. hastalis*. Besides the presence of a serrated cutting edge, *C. carcharias* teeth are almost identical to those of its ancestor (*e.g.*, Ehret *et al.*, 2012). *Isurus subserratus* has been suggested as a possible sister taxon to *C. carcharias*, mainly based on the presence of crenulations along the teeth’s cutting edge (Mewis, 2008). However, the crenulations of *I. subserratus* differ considerably from the serrations in *C. carcharias* and appear to have evolved separately (Ehret *et al.*, 2012) (Fig. 4). Serrations and crenulations evolved independently in many shark lineages (Cappetta, 2012).

Leriche (1926) noted the difference between the crenulations in “*Oxyrhina hastalis* var. *Escheri”* and the serrations in *Carcharodon*, considering the former as a variety of “*Oxyrhina hastalis”*. An understandable conclusion, as Leriche based his observations on “*hastalis”* (= *C. plicatilis*) teeth from the upper Miocene (probably Deurne Sand Member), when *I. subserratus* teeth had evolved to a morphology similar to those of *C. plicatilis*. However, Leriche observed that the crown of “*Escheri*” (= *I. subserratus*) lower teeth is narrower and thicker than those of “*hastalis*” (= *C. plicatilis*). Also, Van den Bosch (1969) noticed the difference between “*Oxyrhina escheri*” (= *I. subserratus*) and both the species *Carcharodon carcharias* and ”*Oxyrhina hastalis*”. Van den Bosch *et al.* (1975), discussing selachian material from the Winterswijk-Almelo region in the eastern part of the Netherlands, situates the first occurrence of “*Isurus escheri”* (= *I. subserratus*) in the Eibergen Member of the Diessen Formation, most likely Serravallian in age (King, 2016), adding that the crenulation on the teeth’s cutting edge is still rather indistinct giving him the impression that the species is still in an early evolutionary stage. While in the overlying Zenderen Member of probably Tortonian age (King, 2016), the species is very common and represents a very typical morphology (Van den Bosch, 1969). In the subsequent Delden Member of most likely Zanclean age (King, 2016), *Isurus subserratus* becomes a rare species (Van den Bosch *et al.*, 1975).

This compares well with our observations in Langenboom (Table 2), where the largest part of unit A (lower to middle Tortonian) can be correlated with the Zenderen Member. In contemporaneous sediments the species is very common, and its teeth have a stable morphology.

Van den Bosch (1969) noted that in the Zenderen Member only 1/3rd of the upper teeth possess lateral cusplets, while on lower teeth 2/3rd have them. Indeed, lateral cusplets are variably present, range between none and 3 pairs, and are more pronounced in the lower teeth (Mewis, 2008). Also, the crenulations vary in length along the cutting edge and in appearance. Van den Bosch (1969, 1980) differentiated late Miocene specimens as being weakly crenulated from early Pliocene teeth being strongly crenulated, an observation that was questioned by Ehret *et al.* (2012).

Ratio* Isurus subserratus *vs* Carcharodon plicatilis *(see Table 1)

Van den Bosch (1980) mentioned that “*Isurus escheri*”

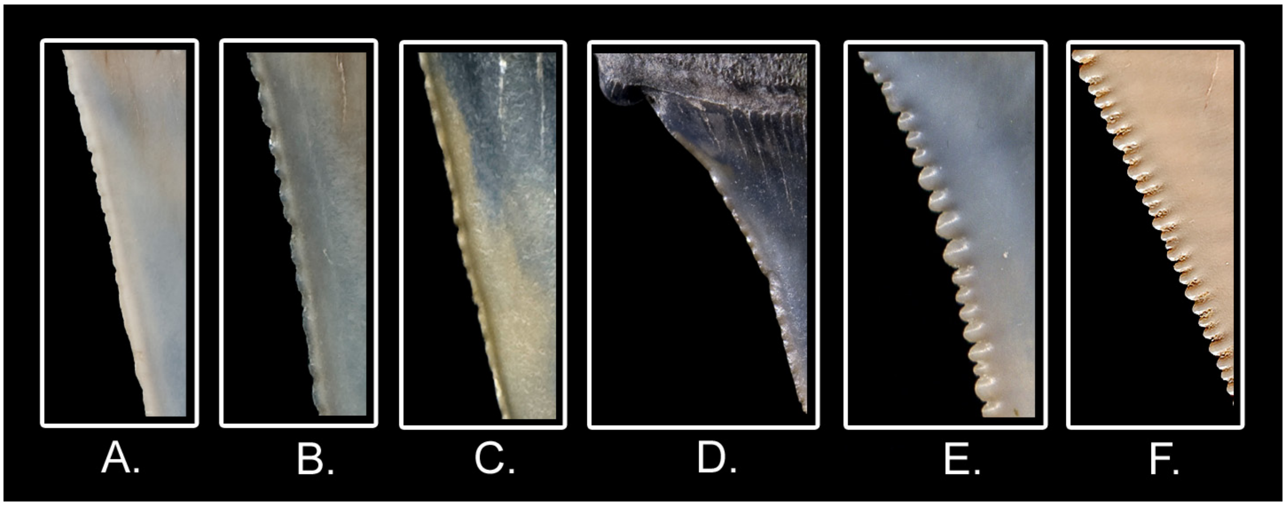

Figure 4. Detail and comparison of the crown’s cutting edge: *Isurus subserratus* (Agassiz, 1843) – Type 1 (A), Type 2 (B), Type 3 (C) and Type 4 (D), *Carcharodon carcharias* (Linnaeus, 1758) (E) and *Otodus megalodon* (Agassiz, 1843) (F).

and "*I. hastalis*" display a demonstrable evolutionary trend and show a typical ratio in the eastern part of the Netherlands: In the Eibergen Member, the ratio *I. subserratus* vs *C. plicatilis* is 1:10, in the overlying Zenderen Member 1:2, and in the subsequent Delden Member 1:22 (ratios calculated from table 1 in Van den Bosch, 1980). He claimed that a small number of teeth of these species is already sufficient for a stratigraphical interpretation. The ratio for the Zenderen Member corresponds reasonably well with our results for Type 2 in Langenboom and the ratio for the Delden Member shows the same trend as for Type 4 in Langenboom. However, the ratio for the Eibergen Member differs considerably from our results for Type 1 in Langenboom. In the Langenfelder Stufe from northwestern Germany, coeval with the Eibergen Member, the ratio *I. subserratus* vs *C. plicatilis* is approximately 1:3 (Kruckow, 1960).

Generic assignment

Owing to the scarcity of these teeth outside the Netherlands, Belgium and Germany, this species is very poorly known. This has led to a lot of confusion in current available literature.

In the past, "*Isurus escheri*" has been included in the genera *Carcharodon* (Agassiz, 1843), *Oxyrhina* (*e.g.,* Leriche, 1926; Glikman 1964) and *Cosmopolitodus* Glikman, 1964 (*e.g.,* Wijnker *et al*., 2008), has been related to *C. hastalis* (Ehret *et al*., 2012) and considered as the transitional form leading to *Carcharodon carcharias* (*e.g.,* Casier, 1960), until the genus *Carcharomodus* was created to accommodate these teeth (Kriwet *et al*., 2015). The reconstructed dentition as given in Kriwet *et al.* (2015, fig. 12) is not correct. The tooth labelled as L2 is an upper anterior tooth position, very probably UA1, and might not belong to the same individual.

The differential diagnosis between the genera *Carcharomodus* and *Isurus* given by Kriwet *et al.* (2015) is partly based on the presence of lateral cusplets and a crenulated cutting edge. These two characteristics occur widely in lamniform sharks (Cappetta, 2012), thus are not useful for establishing phylogenetic relationships and don't warrant the creation of a new genus. In many extant *Isurus* sharks, teeth with tiny cusplets are observed, both in large individuals (Bass *et al*., 1975) and juveniles (Espinosa-Arrubarrena, 1987). In fact, *Isurus subserratus* fits well within the generic diagnosis of *Isurus* as summarised by Cappetta (2012, p. 218). The third upper anterior teeth evolve from small, slender and hook-like (*Isurus oxyrinchus* type) to broad, flattened and triangular (resembling those of *Carcharodon*) (present study), rendering this feature useless in a differential diagnosis (see also Purdy *et al*., 2001).

Furthermore, the described dignathic heterodonty with upper teeth similar to those of *Carcharodon hastalis* and *C. plicatilis* is commonly seen in extant *Isurus oxyrinchus* where large (over 3m TL) sharks acquire very broad, more flattened and triangular upper teeth, more suitable for dismembering large prey (Compagno, 2001). This ontogenetic diet shift is also observed in fossil *Isurus oxyrinchus* from the lower Miocene of the Antwerp area in Belgium (pers. obs. PDS) and the lower Pliocene of Lee Creek, USA (Purdy *et al*., 2001).

The morphological similarity between the teeth of juvenile *Isurus subserratus* and *I. oxyrinchus* suggests a similar diet for these small individuals largely based on teleost fish. Adult individuals of *I. subserratus* acquired broad and triangular upper anterior teeth, suggesting a diet shift from teleosts to larger fish like tuna and sturgeons, particularly common at the Langenboom locality (Peters, 2013; pers. obs.), and marine mammals like pinnipeds. This comparable diet shift happened much earlier in the lifetime of a *subserratus* than observed for *oxyrinchus*, where only sharks of the largest size class are capable of preying on marine mammals (Compagno, 2001). Nevertheless, both species seem to have responded to the rise of marine mammals during the Miocene (Arnason *et al*., 2006).

The creation of a new genus for a single short-living evolutionary side branch of *Isurus* doesn't help in understanding and clarifying shark phylogeny. Especially in view of recent changes in nomenclature, *e.g.,* the *Carcharodon hastalis-carcharias* and *Otodus obliquus-megalodon* lineages, where the genera *Cosmopolitodus, Carcharocles* Jordan & Hannibal, 1923, *Megaselachus* Glikman, 1964 have been discarded for the same reason. We agree with Kent (2018, p. 75) that there seems to be little justification for this monotypic genus. Combined with the above observations, we prefer to retain the species *subserratus* within the genus *Isurus* and the genus *Carcharomodus* is synonymised under the older name *Isurus*.

Fossil record of **Isurus subserratus** *outside of northwestern Europe*

Teeth assigned to *Isurus subserratus,* commonly listed with the specific name of *escheri*, were reported from several Neogene localities outside of northwestern Europe:

Portugal, Setúbal district – Serralheiro (1954, p. 48, pl. 1, fig. 13) assigned a single tooth from the lower Tortonian at Caparica to *Isurus hastalis* var. *escheri*. Antunes & Jonet (1970, p. 140-143, pl. 6, fig. 21) documented an incomplete upper lateral tooth from the lower Tortonian at Mutela as *Isurus* cf. *oxyrhinchus* var. *escheri*. This specimen has a slightly serrated cutting edge and shows a broad lateral cusplet. From the descriptions and illustrations, we cannot positively identify these Portuguese specimens as *Isurus subserratus*.

Spain, Huelva province – García *et al.* (2009, p. 681, figs 5c-d) reported *Isurus escheri* from the Zanclean at Bonares, based on a single slightly crenulated lamniform tooth lacking lateral denticles. Toscano *et al.* (2016, p. 88, pl. 10, fig. 10) reported on five *Carcharomodus escheri* teeth from Messinean and Zanclean deposits at Huelva, Gibraleón and Corrales. The author mentions that the teeth are morphologically similar to *Carcharodon hastalis*, but smaller, the only difference being the presence of a very fine, regular, undulating serration on the smooth cutting edges, almost imperceptible to the naked eye. In our opinion, these Spanish specimens should be assigned to the *Carcharodon carcharias* lineage.

United States, Maryland – Kent (2018, p. 75, figs 2.10F-H) reports three *Carcharodon subserratus* teeth from Serravalian and Tortonian deposits of Calvert Cliffs. We can positively identify these American specimens as *Isurus subserratus*.

Australia, Victoria – Kemp (1991, p. 517, pl. 19, fig. H) documented the occurrence of a single *Isurus escheri* tooth from the lower Pliocene near Hamilton. However, based on the large size and broad triangular shape of the crown, this tooth should be assigned to the *Carcharodon carcharias* lineage.

Japan, Nagano and Kanagawa prefectures – The presumed presence of *Isurus escheri* in the upper Miocene-lower Pliocene of central Japan is based on a few teeth morphologically similar to *Carcharodon carcharias* but having a fine undulating serration on the cutting edge (Goto *et al*., 1993, p. 512, text-fig. 10, pl. 2, fig. 3; Tanaka & Mori, 1996, p. 70, pl. 3, fig. 3). From the descriptions and figures we may conclude that these authors erroneously used the name *escheri* for *Carcharodon hastalis-carcharias* transitional teeth, now referred to as *Carcharodon hubbelli*.

Peru – Brand *et al.* (2011, p. 420) mentioned *Isurus escheri* from the Pisco Formation (upper Miocene-lower Pliocene) in Peru. A description and figures are lacking, but we assume that they were also referring to *Carcharodon hubbelli*.

We follow Nyberg *et al.* (2006) in restricting *Isurus subserratus* to specimens occurring along the northern Atlantic coastline of Europe and the United States and agree with Ehret *et al.* (2012) that all other specimens assigned to this species should be transferred to a different taxon.

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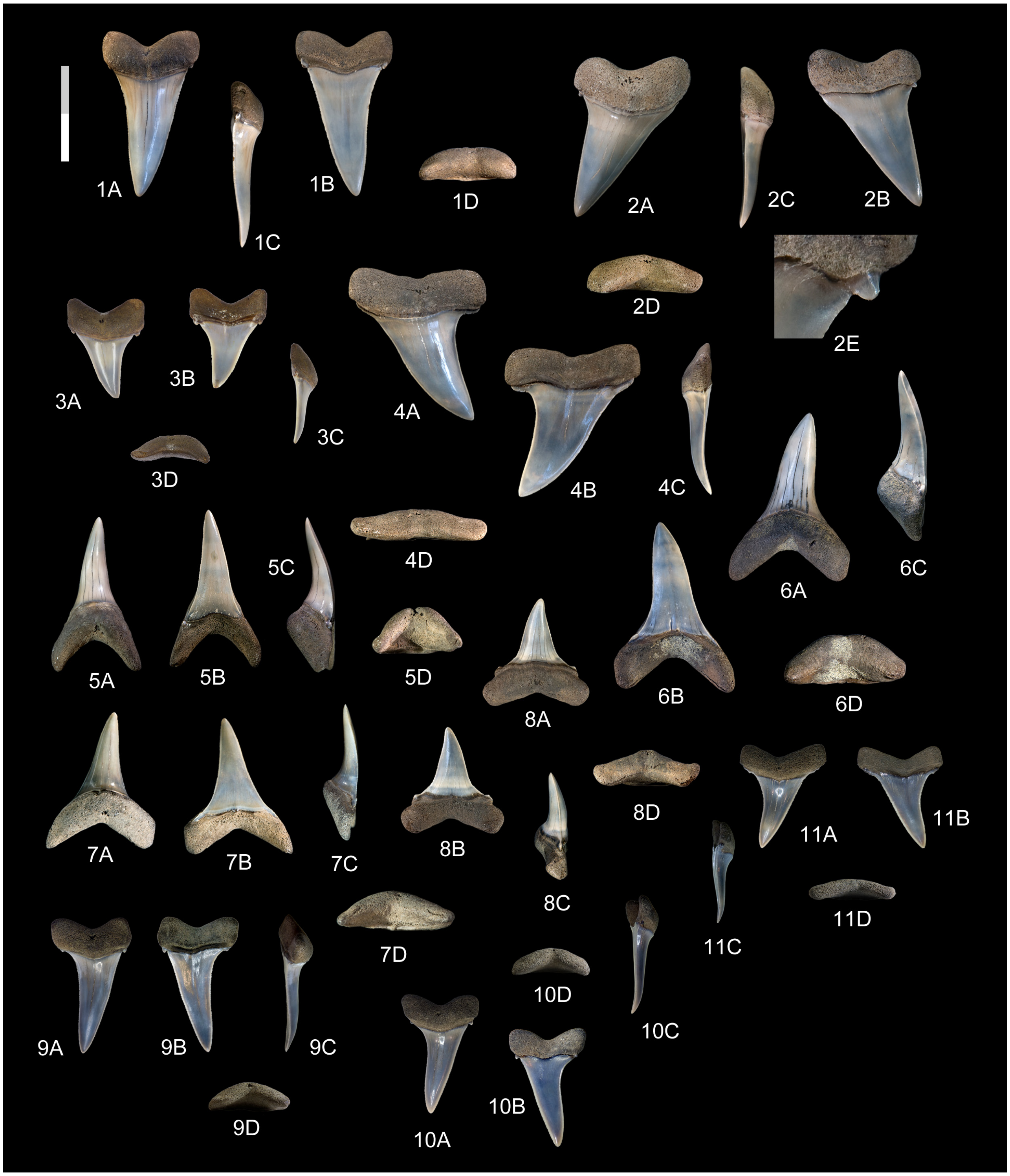

Plate 1. *Isurus subserratus* (Agassiz, 1843) - Type 1 - UA1 (1A-D), UA2 (2A-E), UA3 (3A-D), UL2 (4A-D), LA1 (5A-D), LA2 (6A-D), LA3 (7A-D), LL1 (8A-D), UA1 (9A-D), UA2 (10A-D) and UL2 (11A-D). Lingual (A), labial (B), lateral (C) and basal (D) views, detail of lateral cusplet (E). Figs 1-8 teeth of adult individuals, figs 9-11 teeth of juvenile or sub-adult sharks. All specimens from Langenboom, MAB 12059-12069. Scale bar 20 mm.

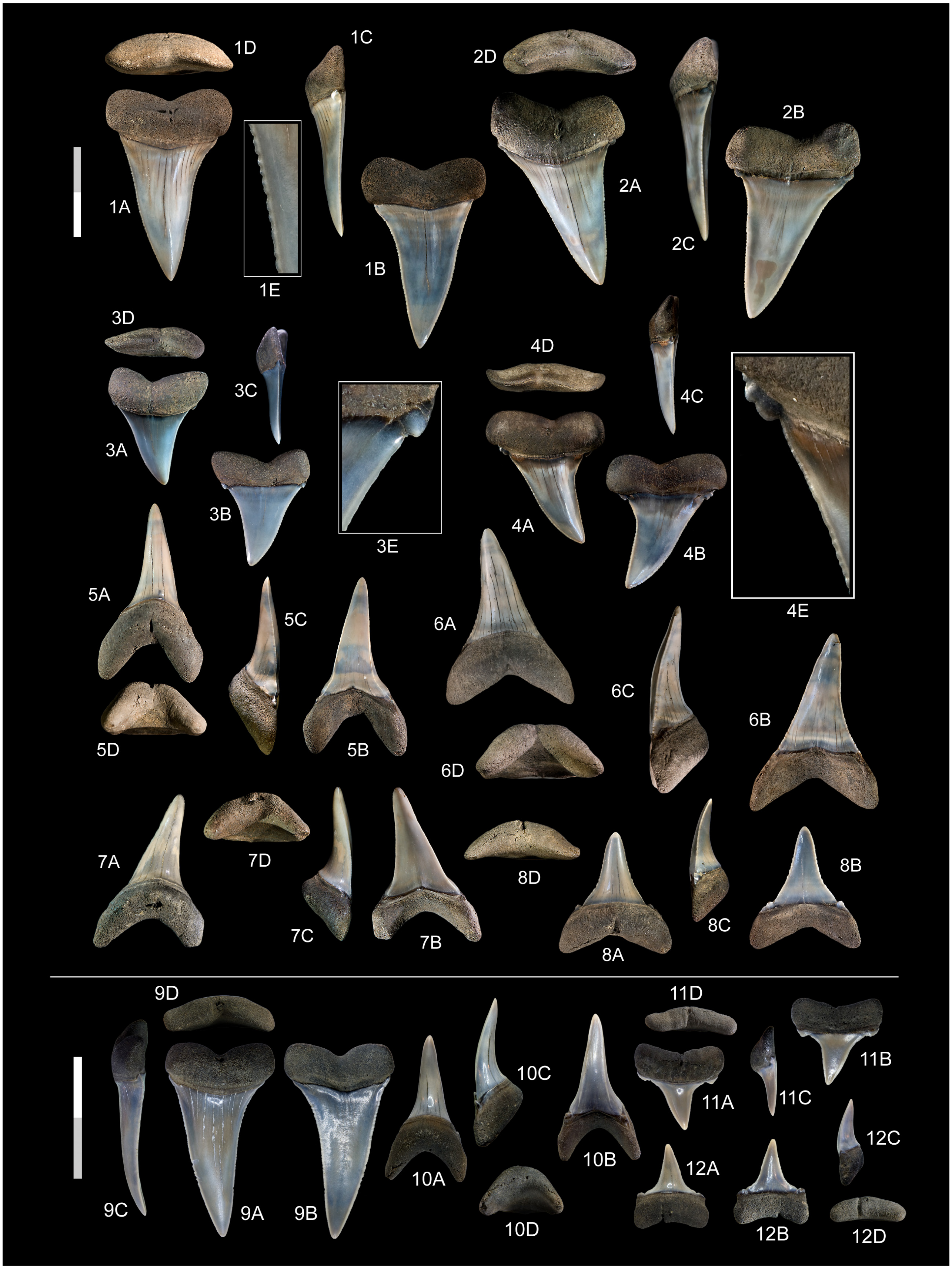

Plate 2. *Isurus subserratus* (Agassiz, 1843) - Type 2 - UA1 (1A-E), UA2 (2A-D), UA3 (3A-E), UL2 (4A-E), LA1 (5A-D), LA2 (6A-D), LA3 (7A-D), LL1 (8A-D), UA1 (9A-D), LA2 (10A-D), UL (11A-D) and LL (12-A-D). Lingual (A), labial (B), lateral (C) and basal (D) views, detail of cutting edge and/or lateral cusplet (E). Figs 1-8, 11-12 teeth of adult individuals, figs 9-10 teeth of juvenile or sub-adult sharks. All specimens from Langenboom, MAB 12070-12081. Scale bar 20 mm.

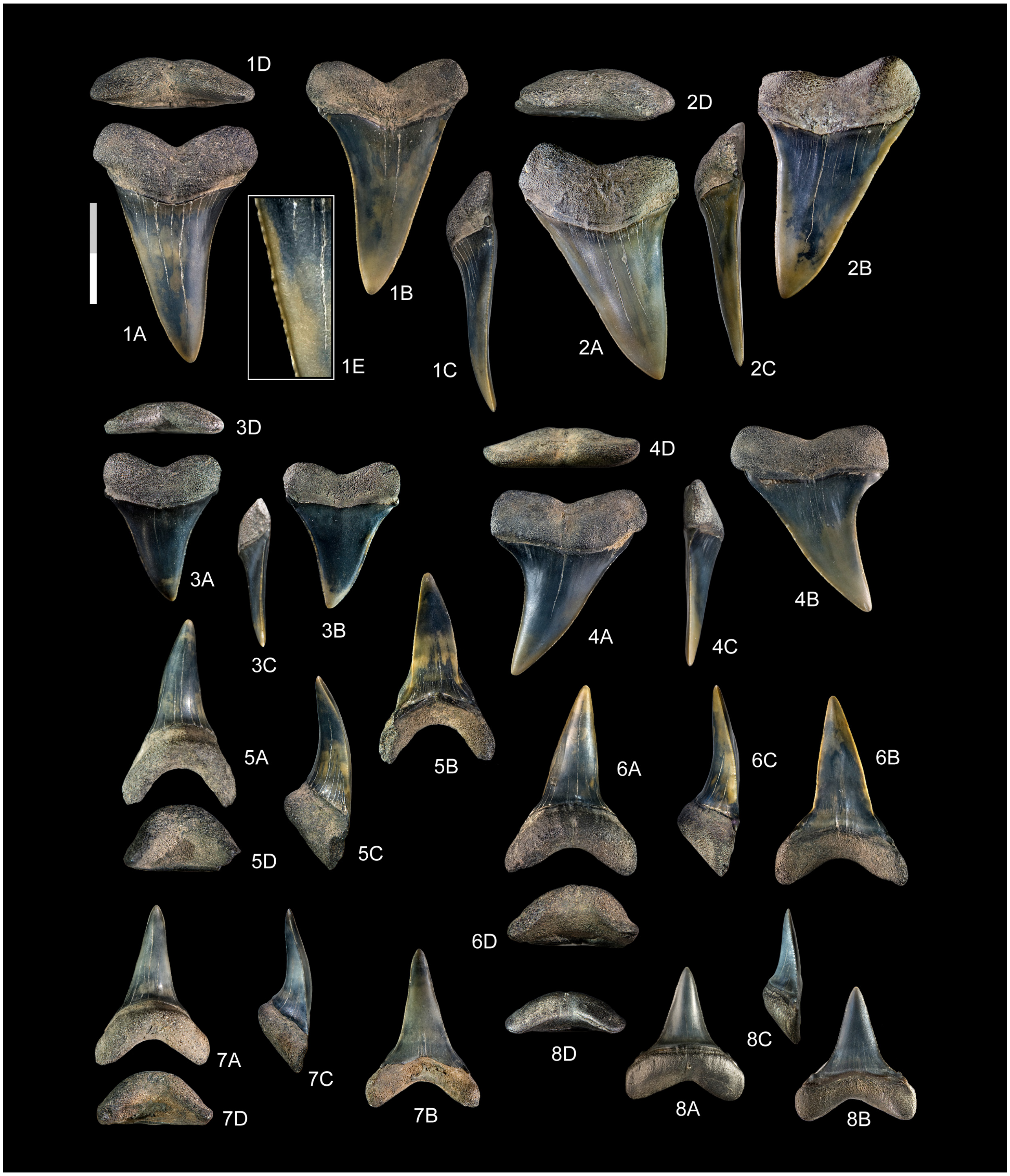

Plate 3. *Isurus subserratus* (Agassiz, 1843) - Type 3 - Adult teeth - UA1 (1A-E), UA2 (2A-D), UA3 (3A-D), UL2 (4A-D), LA1 (5A-D), LA2 (6A-D), LA3 (7A-D), LL1 (8A-D). Lingual (A), labial (B), lateral (C) and basal (D) views, detail of cutting edge (E). All specimens from Langenboom, MAB 12082-12089. Scale bar 20 mm.

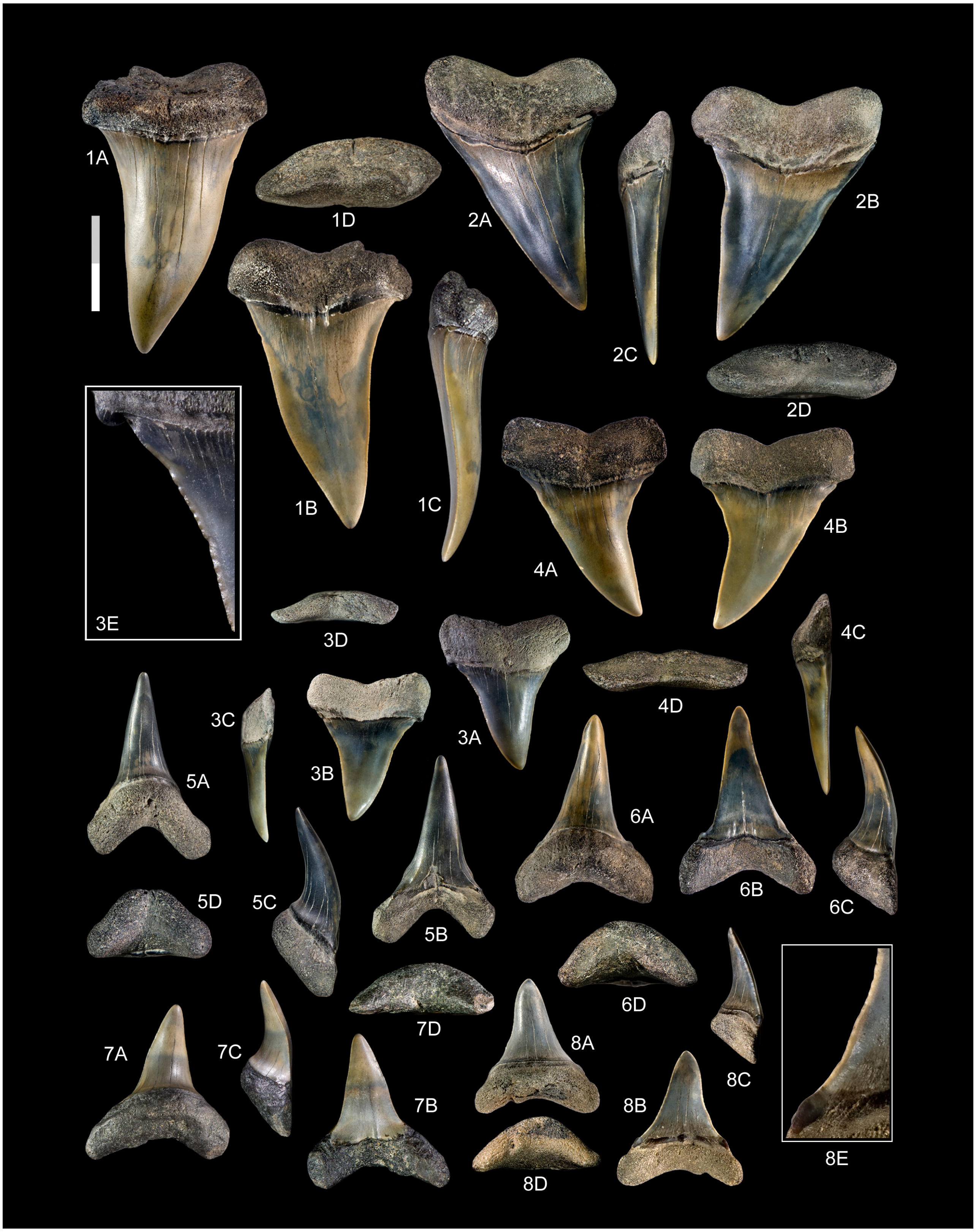

Plate 4. *Isurus subserratus* (Agassiz, 1843) - Type 4 - Adult teeth - UA1 (1A-D), UA2 (2A-D), UA3 (3A-E), UL2 (4A-D), LA1 (5A-D), LA2 (6A-D), LA3 (7A-D), LL1 (8A-E). Lingual (A), labial (B), lateral (C) and basal (D) views, detail of cutting edge (E). All specimens from Langenboom, MAB 12090-12097. Scale bar 20 mm.

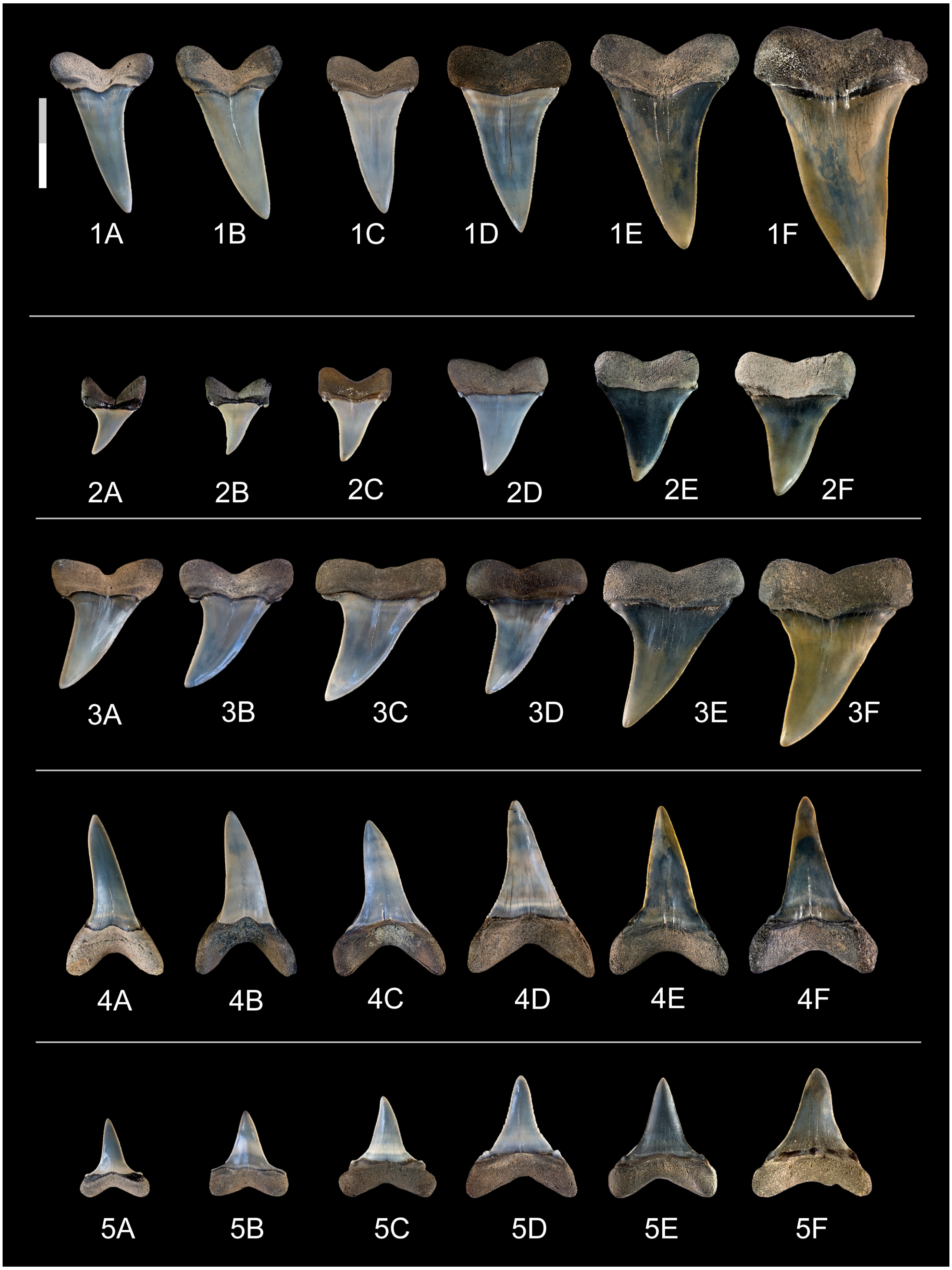

Plate 5. *Isurus subserratus* (Agassiz, 1843) – dental evolution of UA1 (1A-F), UA3 (2A-F), UL2 (3A-F), LA2 (4A-F) and LL1 (5A-F). *Isurus oxyrinchus* Rafinesque, 1810 (A-B), *I. subserratus* Type 1 (C), Type 2 (D), Type 3 (E) and Type 4 (F). *I. subserratus* from Langenboom; *I. oxyrhinchus* from Stabroek ('Tabaksnatie'), early-middle Miocene. Specimens 1D, 1E, 3E and 4D are digitally *mirrored* for comparison purposes. Private collection RV. Scale bar 20 mm.

Plate 6. *Isurus subserratus* (Agassiz, 1843) - Type 2 - Isolated tooth set. UA1-UA3 (1-3), UL1-UL9 (4-12), LA1-LA3 (13-15), LL1-LL8 (16-23). Labial (A), lingual (B), basal (C) and mesial (D) views. All specimens from Langenboom, private collection RV. Scale bar 20 mm.