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A partial skeleton of a new lamniform mackerel shark from the Miocene of Europe

JÜRGEN KRIWET, HEIKE MEWIS, and OLIVER HAMPE



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Cenozoic lamniform sharks are mostly represented by isolated teeth and vertebrae, whereas articulated skeletal remains are usually very scarce. Here, we describe a partial skeleton of an extinct lamniform shark consisting of 42 slightly disarticulated teeth, 49 vertebrae, and additional unidentifiable cranial and postcranial remains. The specimen originates from the Miocene mica-clay of Groß Pampau (North Germany), which is of late Langenfeldian age (= Serravallian-Tortonian boundary; middle–late Miocene). A total of 13 measurements of each tooth, as well as morphological features, were used to reconstruct the dentition of this specimen and to provide detailed taxonomic information. Additionally, the total body size and age at death were established using methodologies based on vertebral and tooth measurements and vertebral centra growth ring counts, respectively. The specimen undoubtedly represents the most complete individual of "*Carcharodon* (= *Isurus*) *escheri*", previously known only from a few isolated teeth. The dental pattern (e.g., marked dignathic and monognathic heterodonty patterns; only slightly labio-lingually compressed upper teeth; upper teeth slender with distally inclined or curved main cusps; massive, hook-like upper intermediate tooth; main cusps with crenulated cutting edges; lateral cusplets in teeth of all ontogenetic stages) clearly separates this shark from all hitherto known Cenozoic and Recent lamnids and a new genus, *Carcharomodus*, consequently is introduced. *Carcharomodus escheri* comb. nov. is a characteristic element of late early Miocene to the Pliocene Western and Central European fish faunas. All previously identified Pacific occurrences represent a different taxon. We estimate that the specimen had a total body length of about 4 m and that it was older than 10 years and thus might have reached maturity before death, as indicated by all available evidence.

Key words: Chondrichthyes, Lamniformes, Lamnidae, *Carcharomodus*, postcranium, Miocene, Langenfeldian, Germany.

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Introduction

Teeth of neoselachian chondrichthyans (sharks, skates, and rays) are often impressive components of marine Cenozoic sediments, whereas their poorly mineralised cartilaginous cranial and postcranial skeleton is rarely fossilised (e.g., Cappetta 2012). Neoselachians, as with all chondrichthyans, are characterised by continuous tooth replacement patterns, with teeth being arranged in multiple rows (Smith et al. 2013). Consequently, teeth of neoselachians are quite abundant in the fossil record. Numerous studies have shown that these teeth bear important taxonomic and phylogenetic signals and generally are used for palaeoecological interpretations (e.g., Straube et al. 2008; Klug et al. 2009; Klug 2010). Tooth morphologies, however, are not the only important features for taxonomic identification, but, dental pattern and arrangement of teeth in the jaws are also important. Accordingly, isolated teeth are often used to reconstruct complete dentitions, so-called artificial tooth sets, to overcome taxonomic problems caused by isolated teeth (e.g., Cunningham 2000; Schutter 2001). Artificial tooth sets, however, are often not repeatable, and so can only be regarded as hypotheses (Shimada 2005a). Reliable reconstructions may only be possible if the taxa have close extant relatives. It is not possible to rule out that teeth of different individuals, different sizes, different ages, and/or genders are combined, inevitably leading to false interpretations. Additionally, the assumption that most fossil neoselachian

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teeth, especially those from the Cenozoic, represent living taxa has led to incorrect artificial tooth arrangements (e.g., Purdy et al. 2001; Reinecke et al. 2001) with subsequent ambiguous taxonomic or systematic interpretations with possible convergences and parallelisms often being undetected when concentrating on isolated teeth. Glikman (1957) was one of the first to postulate that many Cenozoic lamniform taxa, which were classically associated with extant species on the basis of superficial similarities, in fact represent different extinct groups displaying morphological characters similar to those of extant forms.

So far, only a few completely or partially articulated as well as associated tooth sets of Cenozoic lamniform sharks have been recovered that represent the key to unsolved problems in their evolution (e.g., an associated dentition of *Carcharias acutissima* (Agassiz, 1843) described by Leriche (1910), a disarticulated dentition of *Carcharias cuspidate* (Agassiz, 1843) figured by Hovestadt et al. (2010), a disarticulated dentition of *Carcharias gustrowensis* (Winkler, 1875) described by Hovestadt and Hovestadt-Euler (2010), a single completely preserved dentition of *Carcharodon hubelli* Ehret, MacFadden, Jones, Devries, Foster, and Salas-Gismondi, 2009 (see also Ehret et al. 2012), one partial tooth set and associated vertebrae of *Carcharocles auriculatus* (Blainville, 1818) described by Storms (1905), associated tooth sets of *Carcharocles angustidens* (Agassiz, 1843) described by Leriche (1910) and Gottfried and Fordyce (2001), a disarticulated dentition of *Cetorhinus parvus* Leriche, 1910 described by Hovestadt and Hovestadt-Euler (2012), an associated tooth set of *Isurus flandricus* (Leriche, 1910), associated tooth sets of *Megaselachus megalodon* (Agassiz, 1835) (described by Uyeno et al. 1989; Purdy 1996; Purdy et al. 2001) and a very incomplete odontaspidid specimen including few disarticulated teeth described by Hansen et al. (2013)). The discovery of a partly articulated dentition of "*Carcharodon escheri*" (Agassiz, 1843) comb. nov., which undoubtedly belongs to a single individual, is the first and, until now, only record of a specimen of this taxon including more than a few isolated teeth. The systematic position of "*Carcharodon escheri*" was disputed for more than a century because of the peculiar crenulated cutting edges of its teeth and superficial similarities to either *Carcharodon* or *Isurus* (e.g., Leriche 1926; Casier 1960; Purdy et al. 2001; Ehret et al. 2009; Cappetta 2012). The intentions of this paper are to present (i) a re-evaluation of the taxonomy and systematic position of this lamniform shark based on this partial skeleton and additional information from isolated teeth and (ii) estimates its body size based on vertebral and dental measurements.

Institutional abbreviations.—ETZ, Earth Science Collections of the ETH Zurich, Switzerland; MNU, Museum für Natur und Umwelt Lübeck, Germany.

Other abbreviations.—CH, crown height (mm); MVW, maximum vertebral widths (mm); TL, total body length (m).

Geographic and geological setting

The fossil remains were recovered from a mica-clay horizon ("Oberer Glimmerton" in regional geological terms) in the commercial gravel pit of the company Kieswerke Ohle & Lau GmbH in Groß Pampau (Schleswig Holstein, northern Germany; Fig. 1) during excavation of fossil whales in 1989 (Höpfner 1991a, b). The "Oberer Glimmerton" is of late Langenfeldian age, which is a local stratigraphic unit in northwest Germany approximately equivalent to the middle–late Miocene boundary and thus is dated approximately to 11.6 Ma (Lourens et al. 2004). The Langenfeldian in northern Germany consists of fully marine sediments originally deposited in a depth of approximately 50–200 m. In addition to several cetacean skeletons, a diverse neoselachian fauna was discovered (Moths 1998), including, e.g., *Cosmopolitodus hastalis* (Agassiz, 1843), "*Carcharodon escheri*" (Agassiz, 1843), *Araloselachus vorax* (Le Hon, 1871), *Carcharias acutissima* (Agassiz, 1844). The specimen of *Carcharomodus escheri* is the only relatively complete shark found in Groß Pampau. Figure 2 depicts the position in which the specimen was deposited and found. The arrangement of skeletal elements supports the interpretation that the vertebrae and teeth belong to a single individual.

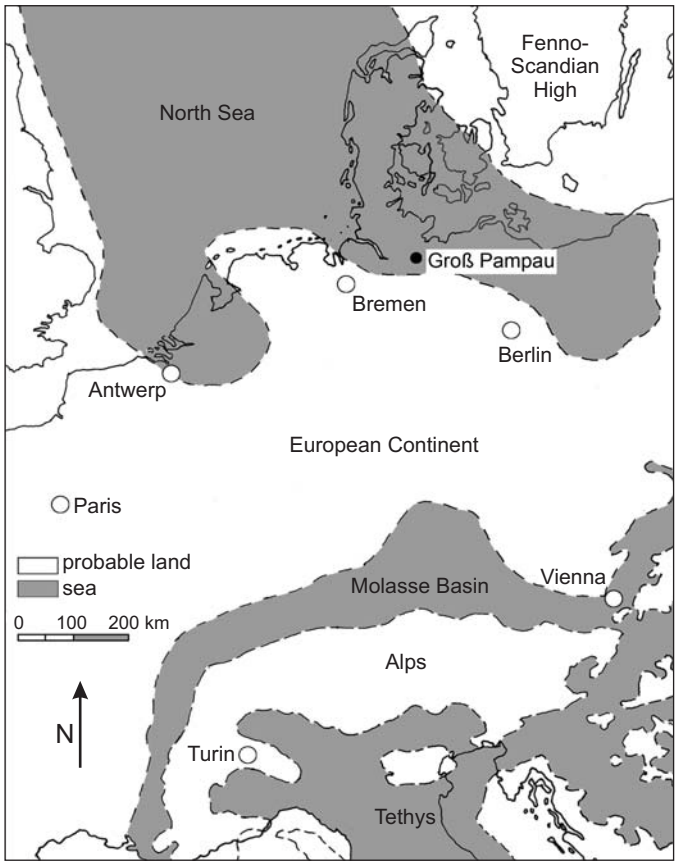


Fig. 1. Palaeogeographic map of mid-west Europe during the middle–late Miocene (compiled from Steininger et al. 1985; Huuse 2002; Rasmussen 2005) showing the locality Groß Pampau in a bay of the North Sea where the partial skeleton was recovered.

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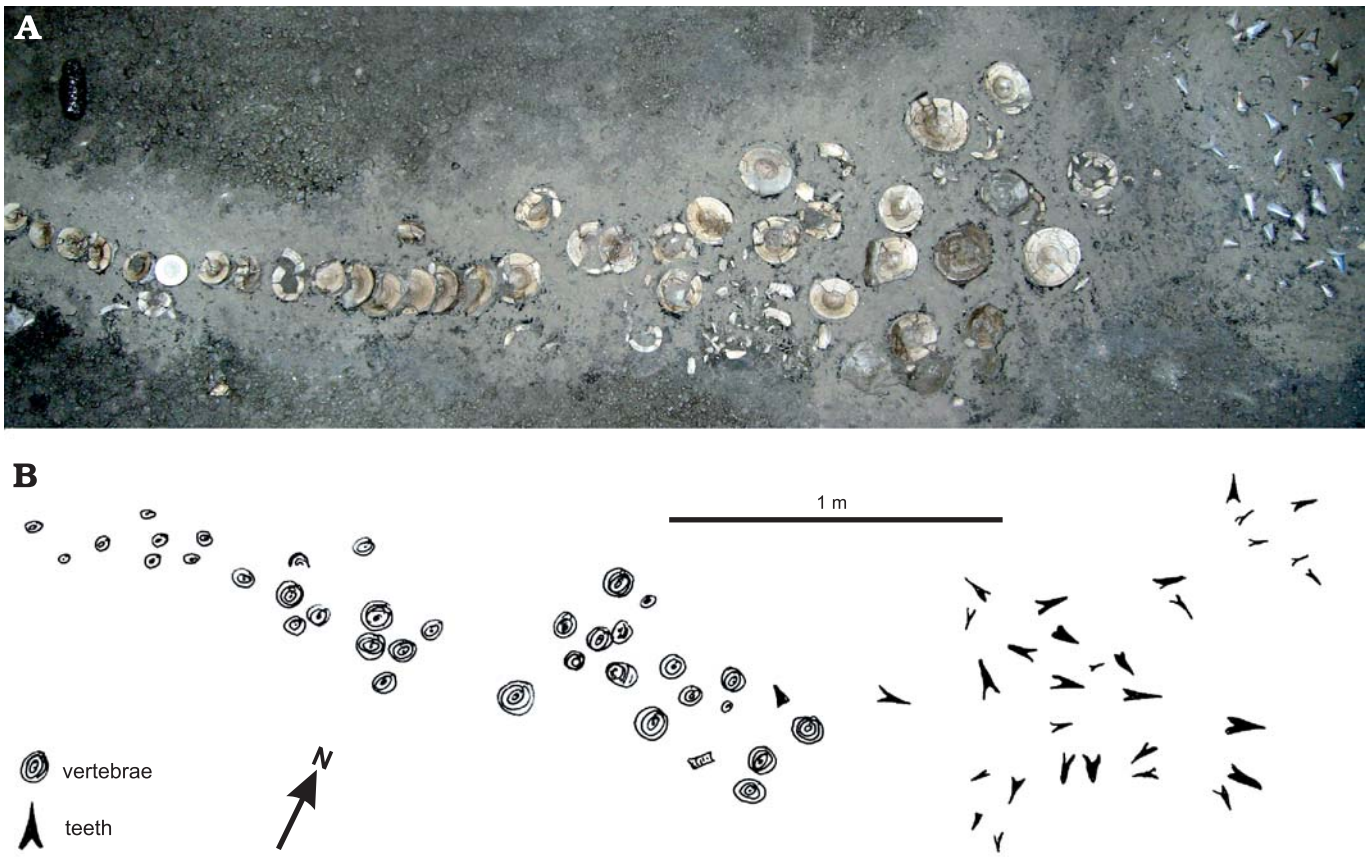


Fig. 2. Photograph (**A**) of mounted specimen MNU 071-20 of the mackerel shark *Carcharomodus escheri* (Agassiz,1843) in the museum and drawing (**B**) of its in situ finding position, in Groß Pampau, the middle–late Miocene, depicting preserved teeth and vertebral centra. The large anterior vertebrae were recovered from the sediment after the in situ drawing during the excavation was produced.

Terminology, material, and methods

A total of 42 oral teeth and 49 vertebrae belonging to a single, slightly disarticulated individual were collected at the Groß Pampau site in 1989 and deposited in the Museum für Natur und Umwelt in Lübeck, Germany (Fig. 2). Unfortunately, all material originally was glued into sediment for exhibition purposes and only 24 teeth and 18 vertebral centra could be removed from the sediment for this study without risking further damage. The remaining 18 teeth and 31 vertebrae were carefully measured and documented by preparing high-resolution digital images directly in the exhibition. Extracted material was cleaned from clay remains with H_2O_2 and Rewoquat® before being measured and documented. High-resolution digital images were prepared of every tooth in labial, lingual, mesial, and/or distal views and of all vertebrae. Teeth were coated with magnesium oxide in order to minimize reflections and increase contrasts prior to photography. X-ray radiographs of two vertebrae of different sizes were prepared for examining their internal structure and also to identify concentric growth band pairs for age estimates of the specimen.

Lamniform sharks possess a number of different types of teeth, depending on the position in the jaws and tooth morphology (Applegate 1965; Shimada 2002a). We employ Shimada's (2002a, b) terminology based on the identification of homologous teeth across extant macrophagous lamniform sharks. Accordingly, four tooth morphotypes within each jaw quadrant, symphyseals, anteriors, intermediates and laterals, respectively, are distinguished constituting the so-called "lamnoid tooth pattern". Shimada's (2002a) scheme does not distinguish "posterior teeth" as does Applegate's (1965), because this differentiation is quite subjective. Consequently, teeth close to mouth corner are included in the lateral series here. Nevertheless, we refer to antero- and posterolateral teeth for depicting the relative position of lateral teeth.

Each dentition can be divided into two major groups of tooth families—intrabullar and extrabullar. The intrabullar teeth are those supported by a dental bulla, whereas the extrabullar teeth are any teeth supported by a jaw cartilage distal to the dental bulla. The upper and lower dental bullae support teeth of the anterior rows, which are the largest teeth within their respective dental series. These two anterior upper and lower tooth rows, respectively, are always present in macrophagous lamniform sharks. Intermediate teeth, which generally are reduced in size, are present between anterior and lateral teeth. These teeth form on the intermediate bar of Siverson (1999) separating the anterior and posterior bullae (= extrabullar teeth of Shimada 2002a). This scheme

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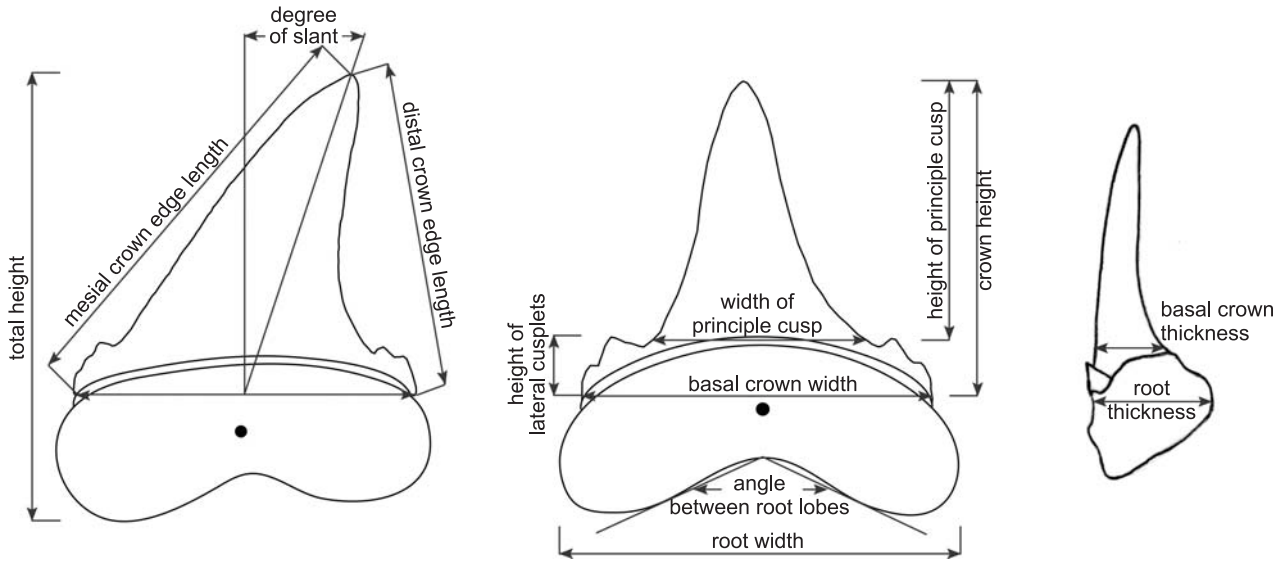


Fig. 3. Tooth measurements used in this study.

assumes the presence of two anterior and at least one intermediate tooth row in the upper jaws, whereas the number of symphyseal and lateral tooth rows may vary inter- and intra-specifically. The recognition of an intermediate tooth row in the lower jaw is a matter of convention, and we follow Shimada (2002a) in considering this tooth a third lower anterior tooth row because it is supported by the dental bulla.

Thirteen measurements of each tooth were taken (Fig. 3). These measurements were used to provide additional support for identification of the position of the disarticulated teeth analysed in this study and to provide a database for comparative studies.

The total body size of the lamnid taxon described herein is estimated employing the methods of Gottfried et al. (1996) and Shimada (2002c, d), which use individual skeletal elements (see these papers for detailed information about the methods). Gottfried et al. (1996) calculated a linear regression using the maximum vertebral widths (MVWs) from the vertebral columns of 16 extant Great White Sharks, using the formula: TL = a + b MVW, where "a" is the constant of the regression line equalling -0.22 and "b" represents the slope of the regression line equalling 0.096. Conversely to Gottfried et al.'s (1996) approach, Shimada (2002c, d) examined the relationship between the crown height (CH) for every tooth position and the total body length in the extant *Carcharodon carcharias* and *Isurus oxyrinchus*. For every tooth position, he established a simple formula for inferring the total body length. This is for the A2, which is easily identifiable and which is preserved in the studied specimen: TL = 2.160 + 12.103 CH in *Carcharodon* and TL = 3.693 + 11.463 CH in *Isurus*, respectively (the first number (a) in the formula represents the constant, the second number (b) the slope of the regression line). We consider the new taxon to be closely related to both the *Carcharodon* and *Isurus* lineages and thus feel confident in using these methods for reconstructing its body size.

Systematic palaeontology

Chondrichthyes Huxley, 1880

Elasmobranchii Bonaparte, 1838

Euselachii Hay, 1902

Neoselachii Compagno, 1977

Lamniformes Berg, 1958

Lamnidae Müller and Henle, 1838

Genus *Carcharomodus* nov.

Etymology: From Greek όμοιος (*omoios*), similar, and δόντι (*donti*), tooth; in combination with the name *Carcharodon*, in reference to the dental similarities with the living Great White Shark, *Carcharodon carcharias*.

Type species: *Carcharodon escheri* Agassiz, 1843 from the Mio-Pliocene of Europe; monotypic.

Diagnosis.—Extinct lamnid shark characterised by the following combination of dental and vertebral characters: (i) dignathic and monognathic heterodonty patterns with upper teeth superficially resembling those of *Cosmopolitodus*, whereas lowers resemble those of *Isurus* to some extend; (ii) main cusp with crenulated cutting edges in all tooth positions; (iii) upper anterior teeth large and not compressed labio-lingually with distally inclined triangular main cusp; (iv) root of upper anteriors massive with sub-vertical to obliquely oriented edges in labial and lingual views and salient lingual protuberance; (v) intermediate tooth small, massive and hook-like; (vi) upper lateral teeth more or less labio-lingually compressed with sub-triangular distally directed cusps with straight cutting edges; (vii) tips of cusps curved labially in upper lateral teeth of juveniles and additionally curved distally in adults; (viii) labial face of crown more or less overhanging labial face of root; (ix) anterior lower teeth with weakly mesially flexed main cusp; (x) main cusp of third lower anterior (= lower intermediate) tooth up-

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right with slightly longer mesial than distal cutting edge and with lingual curvature; (xi) main cusp height more than its width in lower anterolateral files; (xii) main cusp height is more than its width in lower posterolateral files; (xiii) lateral cusplets accompanying the main cusp present in all ontogenetic stages; (xiv) more than one pair of lateral cusplets might be developed in lateral teeth with second one being very incipient; (xv) lateral cusplets usually minute, broad, without crenulations and not distinctively separated from principal cusp; (xvi) lateral cusplets differently shaped in upper and lower teeth.

Differential diagnosis.—Teeth of *Carcharomodus* gen. nov. resemble teeth of *Isurus*, *Cosmopolitodus*, and *Carcharodon* to some extent. The combination of (i) a marked dignathic heterodonty pattern comprising upper teeth similar to those of *Cosmopolitodus*, but with more slender and generally more distally inclined or curved main cusps and lower teeth resembling those of *Isurus*; (ii) marked monognathic heterodonty; (iii) massive and hook-like upper intermediate tooth; (iv) main cusps with crenulated (not serrated) cutting edges in all teeth; (v) presence of lateral cusplets in teeth of all ontogenetic stages; and (vi) presence of an additional pair of incipient cusplets in lateral positions readily distinguishes the new taxon from all other lamniform sharks.

More specifically, teeth of *Carcharomodus* gen. nov. distinctly differ from teeth of *Carcharodon* by the following characters: (i) main cusp of anterior teeth distally inclined with mesial cutting edge being longer than distal one; (ii) less dorso-ventrally flattened tooth crown; (iii) lateral edges of root lobes in lateral tooth positions rounded rather than being subvertical as in *Carcharodon*; (iv) presence of lateral cusplets in all tooth positions throughout ontogeny; (v) intermediate upper tooth hook-like and not reversed; (vi) larger crown height/basal crown width ratio in lateral teeth; (vii) cusp tips of lateral teeth less curved distally; and (viii) basal crown margin in labial view less regularly arched being almost horizontal with only shallow medial concavity.

Teeth of the new genus most significantly differ from teeth of *Cosmopolitodus* in (i) having lateral cusplets; (ii) crenulated rather than smooth cutting edges; (iii) more slender main cusps in upper lateral teeth; (iv) more rounded lateral root edges in upper and lower lateral teeth; and (v) less pronounced and concavity of the basal root face in upper lateral teeth. The most significant differences to teeth of *Isurus* are (i) the serrated cutting edges and (ii) the presence of lateral cusplets also in adults. These differences unambiguously support the separation of the northern European from all other extinct and extant lamniform sharks.

Stratigraphic and geographic range.—Late early Miocene–Pliocene, Western and Central Europe.

Carcharomodus escheri (Agassiz, 1843) comb. nov.

Figs. 2, 5–11.

1843 *Carcharodon escheri*; Agassiz 1843: 260, pl. 36: 16–21.
1926 *Oxyrhina hastalis* Agassiz var. *escheri* Agassiz; Leriche 1926: 409, pl. 33: 1–8.

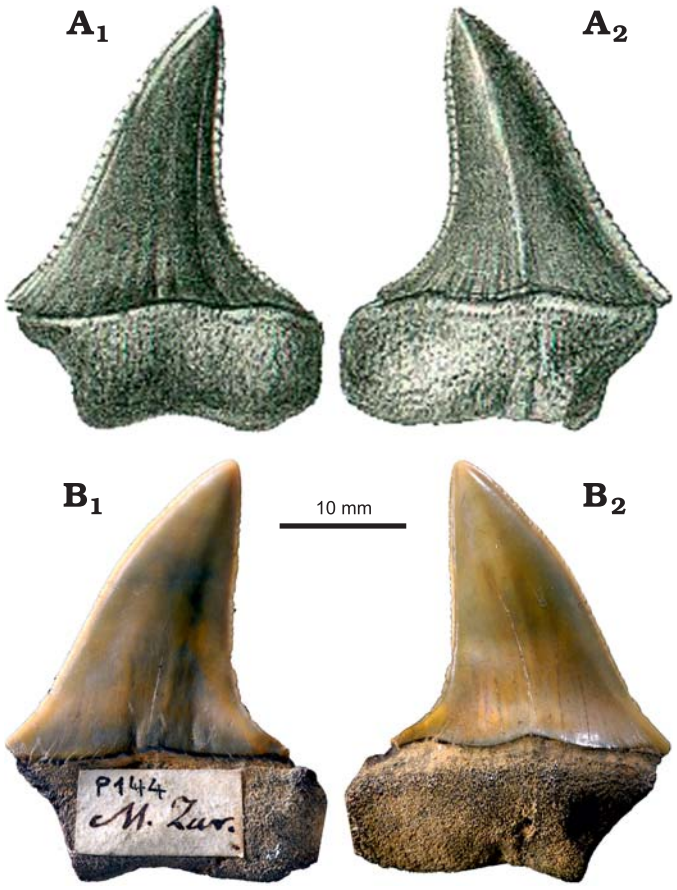


Fig. 4. Holotype of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843) from the Upper Marine Molasse (Burdigalian-Ottnagian, early Miocene) of Switzerland. **A**. Original drawings of Agassiz (1843: pl. 36: 16–18), in labial (A_1) and lingual (A_3) views. **B**. Photographs of holotype (ETZ 0000000001750), in labial (B_1) and lingual (B_2) views.

1927 *Oxyrhina hastalis* Agassiz var. *escheri* Agassiz; Leriche 1927: 74.
1961 *Isurus hastalis escheri* (Agassiz); Kruckow 1961: 44, table 1 (name only).
1969 *Isurus* (*Oxyrhina*) *escheri* (Agassiz); van den Bosch 1969: 30, figs. 27–39, 53, 55, 58–59.
1975 *Isurus escheri* (Agassiz); Bosch et al. 1975: 99, pl. 23, figs. 5–7.
1983 *Isurus escheri*; Bendix-Almgreen 1983: 2, 22 (name only).
1987 *Isurus escheri* Agassiz; Cappetta 1987: 96.
1988 *Isurus escheri* (Agassiz, 1843); Nolf 1988: 34, 162.
2006 *Carcharodon escheri* (Agassiz, 1843); Cappetta 2006: 78.
2008 *Cosmopolitodus escheri*; Wijnker et al. 2008: 174 (name only).
2010 "*Carcharodon*" *escheri* (Agassiz, 1844); Mollen 2010: 66, 67.
2012 *Isurus escheri*; Ehret et al. 2012: 1144, 1145, 1150.

Holotype: ETZ 0000000001750 (barcode number, previous collection number is ETZ P144), upper lateral tooth (Fig. 4).

Type locality: Switzerland (exact locality unknown).

Type horizon: "Kalkschiefer", Upper Marine Molasse, Burdigalian–Ottnangian, early Miocene.

Material.—Single incomplete and disarticulates specimen, MNU 071-20.

Diagnosis.—Same as for genus.

Description.—The skeleton of sharks is primarily cartilaginous but in certain places where strength is particularly im-

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portant, shark cartilage secondarily ossifies, forming calcified hydroxyapatite bone (Ridewood 1921; Goodrich 1930; Applegate 1967; Moss 1977; Compagno 1999). In particular, the jaws and the vertebral centra undergo secondary calcification during ontogeny, as the spinal column has to resist the powerful compressional forces of the surrounding water (e.g., Ridewood 1921; Dean and Summer 2006; Porter et al. 2014). Additionally, shark vertebrae grow through the incremental addition of calcified concentric rings (annuli). Centra are much more often preserved than other parts of the skeleton, but are most often found disassociated from the dentitions.

The partial skeleton presented herein comprises disarticulated teeth of all jaw quadrants and vertebral centra (Fig. 2). Unfortunately, no remains of the jaws and fin skeleton are preserved or were recovered during excavation. Along with the dentition, 49 calcified vertebral centra (Figs. 5–7) of *Carcharomodus escheri* are more or less well preserved. Most are damaged or only partly preserved; some were too imperfect for study or even being measured. When possible, three measurements were taken: height, width, and depth (Table 1). The recovered vertebral centra range from 1.26 to 7.77 cm in width. Although the vertebral centra were all disarticulated, their gradual decrease in size proves evidence that they once belonged to one vertebral column of a single individual (Fig. 8).

Table 1. Measurements (in cm) of preserved vertebral centra of *Carcharomodus escheri* (Agassiz, 1843). Numbers refer to individual vertebral centra.

Number	Width	Depth	Height
3	7.77		6.31
4	5.33		5.12
5	6.86		6.44
6	6.73		5.76
8	5.32	2.12	5.15
9	5.56	2.11	4.92
10	6.04		5.27
11	5.95	2.1	5.24
14	5.37	2.13	4.73
15	6.15		5.02
21			6.16
22			5.75
23		1.86	5.18
24			5.2
25			5.21
26		2.05	5.01
27	4.1	1.47	3.83
29		1.49	
30		1.62	3.84
31	3.67	1.66	3.57
33	3.81	1.43	3.63
35	3.56	1.5	
36		1.02	
37		1.21	3.15
40	2.88	1.24	2.23
41		1.22	
42	2.73	1.22	2.65
45	2.1	1.09	2
46		0.86	
47	1.98	1	1.97
48	1.46	0.86	1.48
49	1.26	0.72	1.21

The amphicoelous centra are of typical lamniform appearance, being slightly compressed dorso-ventrally and with deeply concave anterior and posterior faces. The largest vertebral centra are situated close to unidentifiable cranial remains decreasing continuously posteriorly in diameter size. The centra bear distinctive small circular perforations running through their centres representing the passage for the notochord. The better-preserved vertebral centra still show prominent paired dorsal and ventral depressions for articulation with the corresponding neural (basidorsal) and haemal (basiventral) arches. It is possible to determine the orientation of the vertebrae with the help of the distance of these depressions, because the basidorsal depressions are placed closer together than the basiventrals. Unfortunately, it was impossible to identify the attachment depressions for ribs because the larger centra, which are considered thoracic vertebrae, are less well preserved, being crushed. The calcification pattern of the vertebral centra of *Carcharomodus escheri* corresponds to the radial asterospondylic type (Hasse 1879), which is characteristic for lamniform sharks (Fig. 9).

Contrary to the vertebrae, fossil shark teeth possess high potential to provide information about taxonomic identities, phylogenetic relationships, life-history traits (e.g., ontogenetic changes, sexual variations, etc.) and diet preferences. The preserved tooth set of the specimen studied here thus is of major interest. It consists of 42 associated teeth from all four jaw quadrants (Fig. 2) ranging in size from ca. 1.5 to 4.2 cm in total height (Table 2). The marked dignathic and monognathic heterodonty patterns simplify the determination of each tooth position within the jaws. The 13 dental measurements taken from each tooth, which assisted in reconstructing the dental pattern of the studied sharks, are depicted in Table 2.

In addition to fully mineralised teeth with crown and root, some teeth are preserved only as thin enamel shells, which are often broken basally and which lack roots. These incomplete teeth represent replacement teeth, some of which are probably separated by two or more teeth from the functional tooth position of their corresponding file.

The symmetry of the principal cusp was used to divide teeth into two groups. The first sample comprises highly asymmetrical teeth with a distally inclined cusp with less well marked lateral cusplets of the upper jaw (Fig. 10), whereas the second sample consists of more or less symmetrical teeth with small but distinct lateral cusplets of the lower jaw (Fig. 11**)**. Teeth of the upper and lower jaws were divided into right and left teeth after measuring the length of the mesial and distal cutting edges. The mesial cutting edges are always longer than the distal ones giving the teeth

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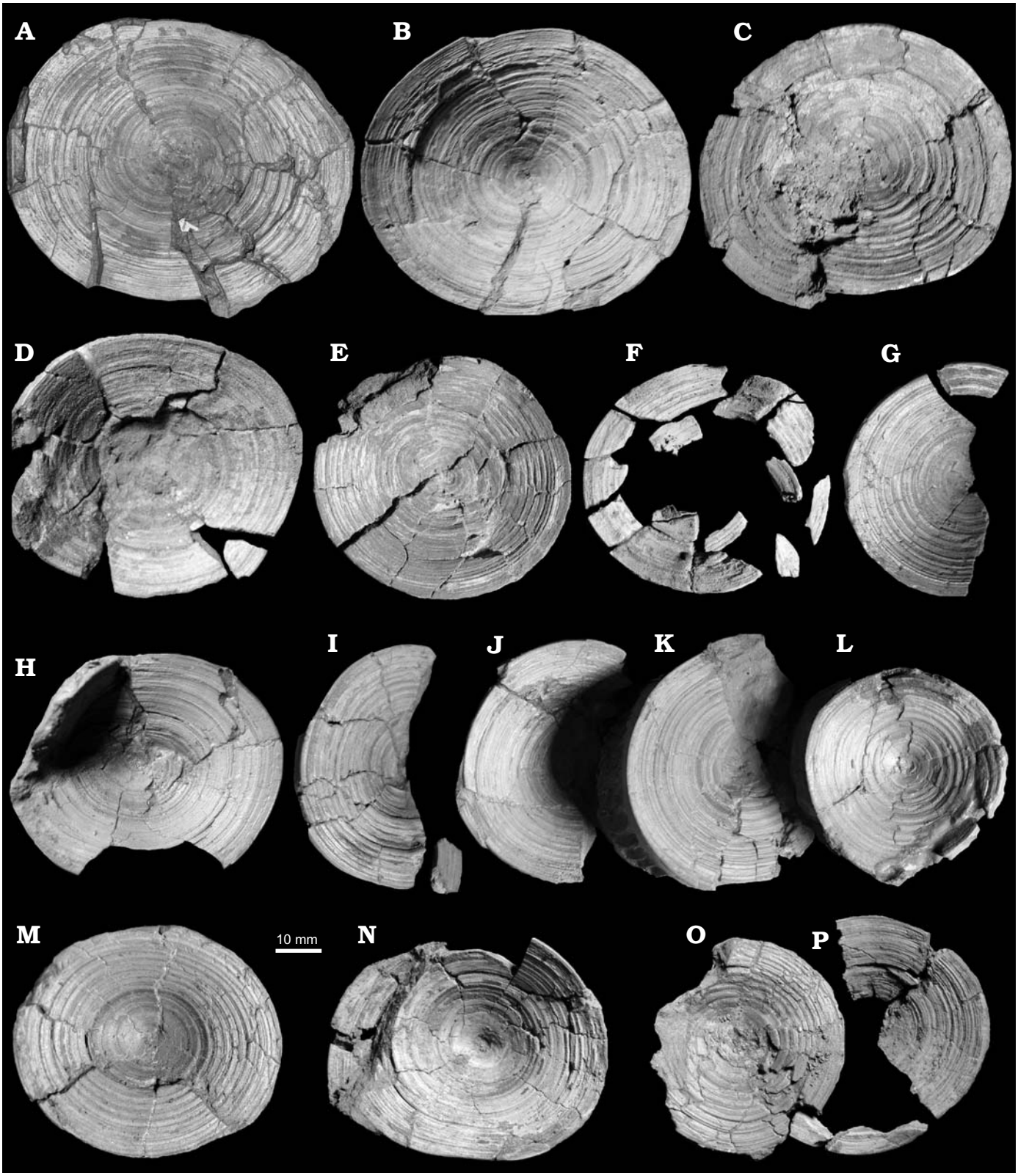


Fig. 5. Trunk vertebrae of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene, displaying the characteristic lamniform morphology and concentric growth bands from anterior (**A**) to posterior (**P**).

an asymmetric appearance in upper teeth. Teeth that are virtually identical in size and shape, and which provide similar measurements, are interpreted to come from the same tooth row and are thus lumped together. Furthermore, teeth of each identified jaw quadrant were sequentially assembled from larger, more erect principal cusps to smaller, more

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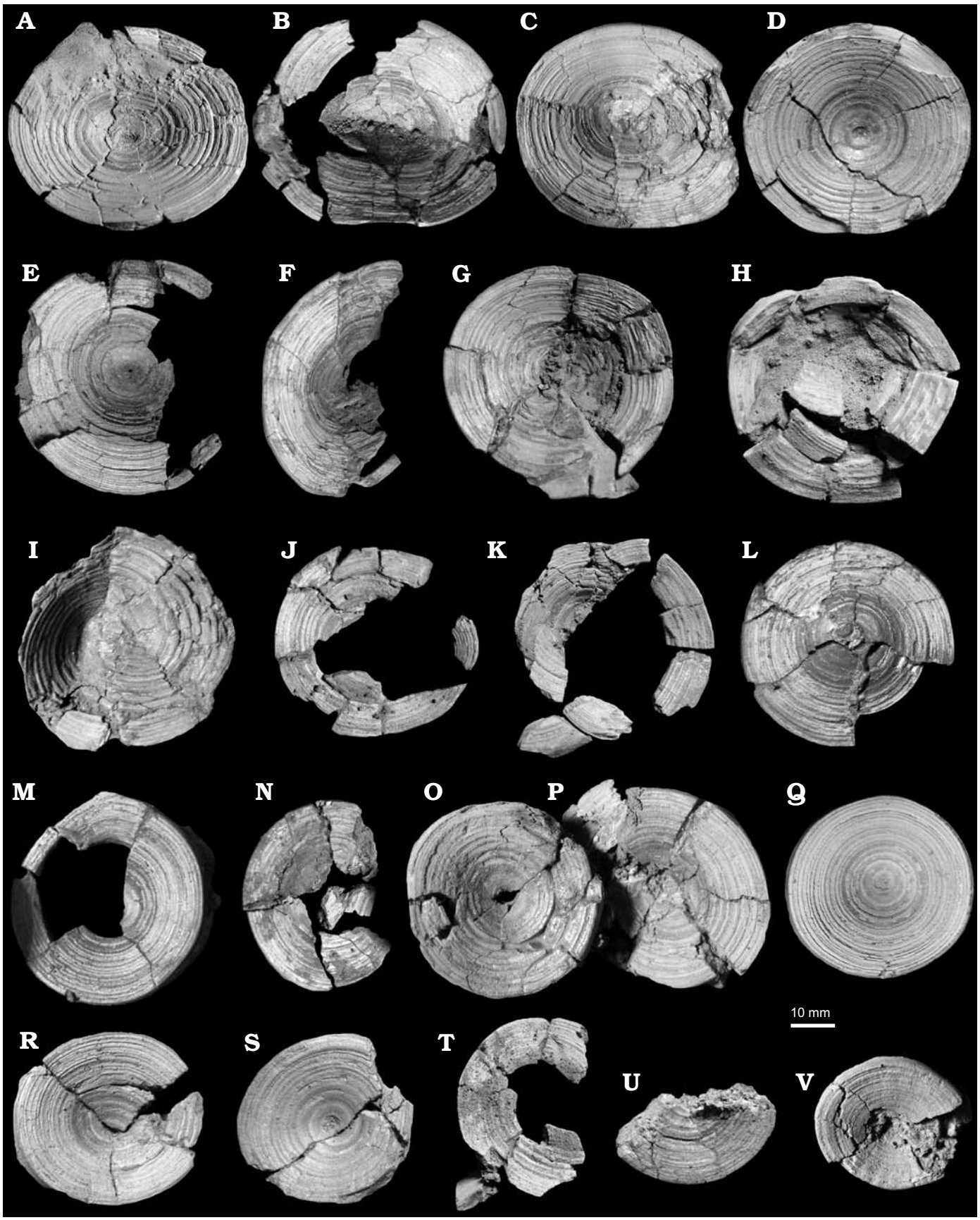


Fig. 6. Trunk and precaudal vertebrae of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene, from anterior (**A**) to posterior (**V**).

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inclined principal cusps. All fully developed teeth present a more or less labio-lingually flattened crown, a triangular principal cusp, and most teeth have at least one pair of small, triangular lateral cusplets.

The lingual neck separating the crown and the root is rather narrow and almost horizontal with only a faint medial concavity. The bilobed root is well developed but rather low, with generally one, rarely two small nutritive foramina on the salient lingual root protuberance. The root lobes are separated by a broad and shallow concavity, which is slightly more pronounced in anterior lower teeth. The principal cusp generally possesses a razor-like, irregularly crenulated cutting edge, whereas the lateral cusplets are devoid of any crenulations or serrations. This crenulation is stronger than the weak crenulation found in some teeth from the late Miocene Pacific, which previously were associated with *Cosmopolitodus hastalis*, but which certainly represents a different taxon. It is, however, not as strong as the saw-like serration of the cutting edges of *Carcharodon carcharias* teeth, which show clearly developed sharp points. The cutting edges of the teeth of *Carcharomodus escheri* are comparable

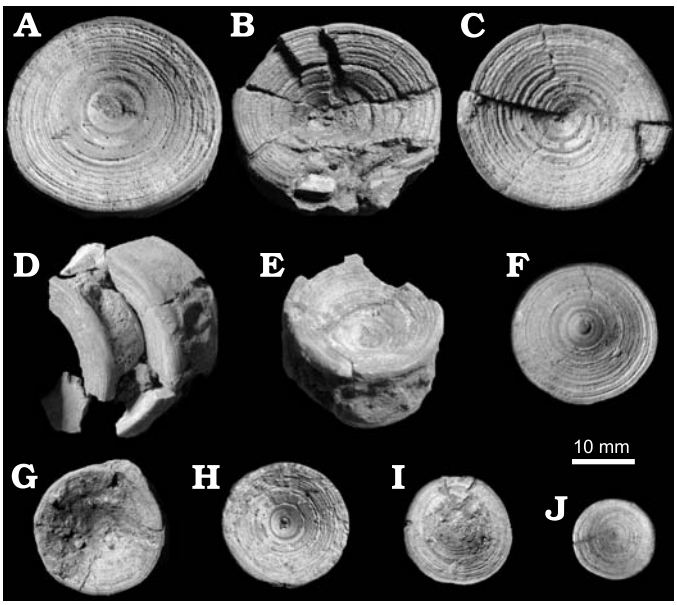


Fig. 7. Posteriormost precaudal and caudal vertebrae of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene, from anterior (**A**) to posterior (**J**).

Table 2. Tooth measurements (in cm) of *Carcharomodus escheri* (Agassiz, 1843). Abbrevations: BCT, basal crown thickness; BCW, basal crown width: maximum crown width at the base of the crown; CH, crown height: maximum vertical enameloid height; DCL, distal crown edge length: straight line between the crown tip and distalmost point of the crown; DS, degree of slant: the angle between a line drawn perpendicular to a straight line touching the lower extensions of the enameloid and beginning at the midpoint of the crown width and a line beginning at the same point and passing through the tip of the enameloid; LCH, height of lateral cusplets: if they are multiple, the height of the tallest of the lateral cusplets has been measured; MCL, mesial crown edge length: straight line between the crown tip and mesialmost point of the crown; PCH, height of principle cusp; PCW, width of principle cusp; RA, angle between root lobes; RT, root thickness; RW, root width; TH, total height of tooth. Numbers in first row refer to teeth depicted in Figs. 10 and 11, respectively.

	TH	BCW	CH	PCH	PCW	DCL	MCL	BCT	DS	LCH	RW	RA	RT
10A	4.2		3.171	3.143	2.471	3.29	4.09		19°				0.844
10B	3.5	2.191	2.821	2.554	1.976	2.78	3.3	0.74	14°		2.47	130°	0.9
10C	3.49	2.24	2.807	2.472	1.914	2.74	3.29	0.68	18°		2.442	135°	0.66
10D	3.1	2.337	2.44	2.146	1.811	2.57	2.98	0.61	14°	0.17	2.7	125°	0.601
10E	2.95	2.2	2.33	2.13	1.831	2.49	2.95	0.5	17.1°	0.2	2.69	150°	0.582
10F	2.76	1.93	2.141	1.887		2.15	2.39	0.53	13°	0.21		135°	
10G	1.94	1.636	1.45	1.251	1.2	1.44	2.04	0.46	20°	0.12	1.81	136°	0.45
10H		1.862	2.69			2.73	3.02	0.61	11°				
10I	3.68	2.08	2.89	2.694	1.872	2.95	3.2	0.73	17°		2.5	135°	0.682
10J	3.15	2.11	2.432	2.234	1.922	2.42	2.85	0.59	17°		2.43	135°	0.565
10K	3.01		2.322	2.045		2.33	2.63	0.61	13°	0.18		140°	0.55
10L	2.37	2	1.846	1.69	1.696	1.94	2.35	0.48	12.2°	0.15	2.04	160°	0.535
10M		2.189	3.088			3.16	3.67	0.65	17°				
11A	3.49	1.797	2.733	2.419	1.407	2.81	3	0.81	7.2°	0.18	2.20	110°	
11B	2.64	1.706	1.982	1.746	1.215	2.17	2.18	0.71	2.8°	0.24	2.07	115°	
11C	3.02	2.265	2.123	2.123	2.265	2.45	2.47	0.6	3°	0.27	2.55	145°	
11D	2.35	1.943	1.782	1.481	1.496	2.03	2.08	0.58	1°	0.3	2.22	130°	
11E	2.3	2.015	1.7	1.472	1.14	1.95	2.1	0.56	1°	0.31	2.01	125°	
11F	2.2	1.761	1.645	1.401	1.2	1.93	1.97	0.54	2°	0.3	1.95	125°	
11G	1.84	1.52	1.344	1.188	1.05	1.5	1.62	0.44	3°	0.28	1.61	137°	
11H	1.48	1.234	1.083	0.951	0.73	1.17	1.34	0.42	3°	0.22	1.26	140°	
11J		1.61	2.465			2.46	2.5	0.59					
11K								0.79					
11L		1.65	1.53	1.339	1.27	1.65	1.71	0.47		0.21			

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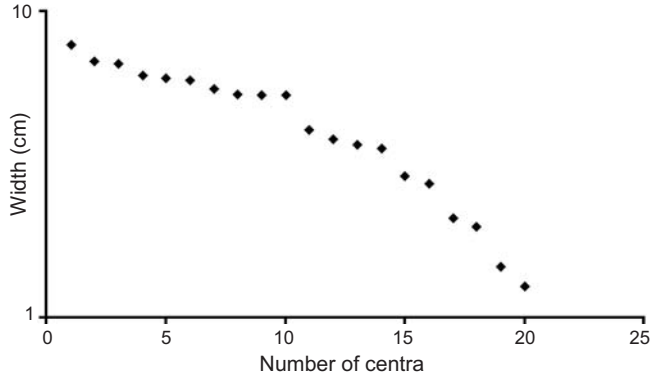


Fig. 8. Graphic representation of vertebral size decrease in *Carcharomodus escheri* (Agassiz, 1843) from anterior to posterior. Steps at positions 10-11, 14-15 and 18-19 indicate missing portions due to collecting and/or taphonomic artefacts.

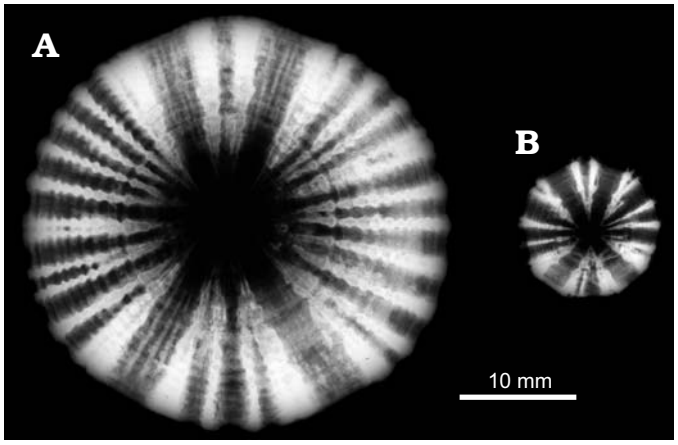


Fig. 9. Radiographs of vertebrae of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene. **A**. Precaudal vertebra, same as in Fig. 6Q. **B**. Caudal abdominal/caudal vertebra, same as in Fig. 7J.

to emery paper, which consists of tiny little grains that produce an irregular serration.

Teeth of the upper jaw (Fig. 10) are broader than the teeth of the lower jaw with distally inclined or curved main cusps, whereas the main cusps of lower jaw teeth are nearly erect. The lateral cusplets are less developed and greatly reduced at least in anterior and anterolateral files, and generally become slightly more distinct in posterolateral files. However, these lateral cusplets are never as distinct as those of lateral teeth. In all upper teeth, the principal cusp height is greater than its basal width.

The specimen preserves only two teeth referable to upper anterior positions (Fig. 10A), which are also the largest of all preserved teeth. Both are identical in shape and probably come from the same tooth row. The root of the slightly larger tooth is better mineralised than the root of the other one, but it is broken and not completely preserved, similar to the condition found in replacement teeth. The labial face base of the crown very slightly overhangs the root. The root is low with sub-vertical, slightly converging lateral edges in labial and lingual views. The root lobes are not distinctly separated but broadly united forming an obtuse angle with a very broad and shallow median concavity. The lingual protuberance is weak. A nutritive foramen cannot be observed due to the state of preservation. Very diminutive lateral cusplets are preserved mesially and distally, which are not well separated from the main cusp. Their size is not more than 6.3% of the size of the main cusp. The main cusp is broad and shows a complete but irregularly crenulated cutting edge and is inclined distally forming an angle of about 19°. Both mesial and distal cutting edges are slightly concave in their lower half with the mesial cutting edge being significantly longer than the distal one. The tip of the crown points labially.

One of the preserved teeth could be identified as an intermediate tooth because it is differently shaped in comparison to all other upper lateral teeth (Fig. 10B). The angle between its root lobes is 160°, whereas the root lobes of the other upper lateral teeth of similar size form a more obtuse angle of 135° on average. As in the anterior teeth, the base of the labial face of the crown very slightly overhangs the root, and the lingual protuberance is weak. The lingual face of the root shows two nutritive foramina, with one of them being slightly smaller than the other. A multiple pair of lateral cusplets accompanies the main cusp with its irregularly crenulated cutting edges. The lateral cusplets are not symmetrical on both sides, but the mesial one is divided forming two incipient tips, whereas the distal one is divided into three very small tips. Though the lateral cusplets are minute in size (7.85% of the total crown height), they are more distinct than those of the anterior teeth. The principal cusp is almost hook-like with a quite long and in its upper part convexly curved mesial but distinctly concavely curved distal cutting edge forming an angle of about 12° with the basal face of the root. It is reduced in size with its crown height being only about 58% of the crown height of the second anterior tooth, and about 79% of the crown height of the first lateral tooth. The root of the upper intermediate tooth is almost rectangular with broadly united root lobes separated only by a very shallow concavity, massive and with subvertical, converging lateral edges similar to the condition seen in the second anterior upper tooth. Following Shimada's (2002a) terminology, this tooth corresponds to the intrabullar intermediate tooth (or third upper anterior tooth).

Thirteen preserved teeth represent upper laterals (Fig. 10C–L). None of the lateral teeth has lateral cusplets that are equal in size on both mesial and distal sides but the presence of lateral cusplets in upper teeth seems to be very variable. The distal lateral cusplets generally are better developed and show more tips than those of the mesial side, but all are very minute. Even in the smallest preserved lateral tooth the height of the lateral cusplets does not exceed 8.28% of the total crown height. All teeth possess a main cusp that is distally inclined, with its tip being curved labially. The lingual protuberance is salient in all upper lateral teeth, and the lingual face of the root reveals one to two nutritive foramina, with one being smaller than the other.

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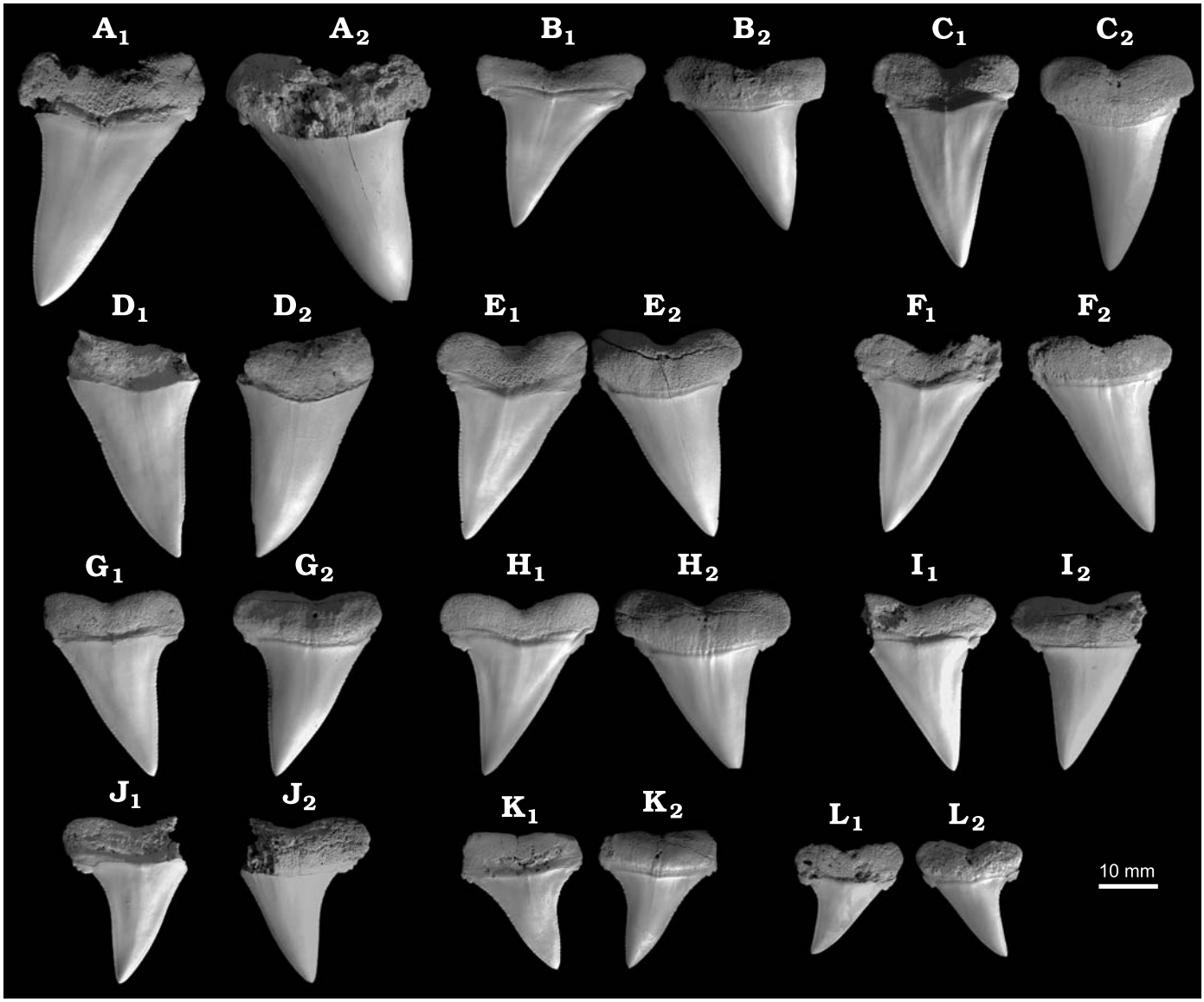


Fig. 10. Upper teeth of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene. **A**. Second upper right anterior tooth. **B**. Right upper first lateral tooth. **C**–**L**. Left (C, D, G, I, K) and right (E, F, H, J, L) upper teeth. Labial (A_1–L_1) and lingual (A_2–L_2) views. For positions of lateral teeth within jaw see Fig. 12.

One of the fully mineralised and best preserved teeth differs significantly from the others in having seemingly smooth cutting edges and a finer, more angular root with lobes forming an angle of about 150°, whereas the root lobes of the other lateral teeth form an angle of 135° on average (Fig. 10B). The mesial cutting edge is significantly concave, whereas the distal one is convex, giving the apex an anteriorly twisted appearance. Conversely, the mesial cutting edge is convex and the distal one more concave in all other teeth identified as upper laterals. The root is very low, with lobes that extend laterally more than 20% from the base of the crown, which is also distinct from other upper laterals. Only the mesial side shows a small heel that can be regarded as a very reduced lateral cusplet. It is also remarkable that this is the only tooth in the upper jaw where the base of the labial face of the crown does not overhang the labial face of the root. Nevertheless, based on its general size and appearance, we identify this tooth as being the first upper lateral tooth. This tooth clearly separates the new taxon from all other similar lamnid sharks. However, we refrain here from including this tooth in the diagnosis, because of its quite distinct morphology and hypothesised jaw position pending further studies of associated or completely articulated dentitions of this taxon.

Teeth of the lower jaw (Fig. 11) are characterised by lateral cusplets that are more or less equal in size on both sides of the nearly erect and less blade-like main cusp. In almost all the teeth of the lower jaw the principal cusp height is only slightly greater than its width.

Five teeth represent lower anteriors in comparison with extant lamnid taxa. Three of the teeth are badly preserved and lack their roots. The two others are identical in size

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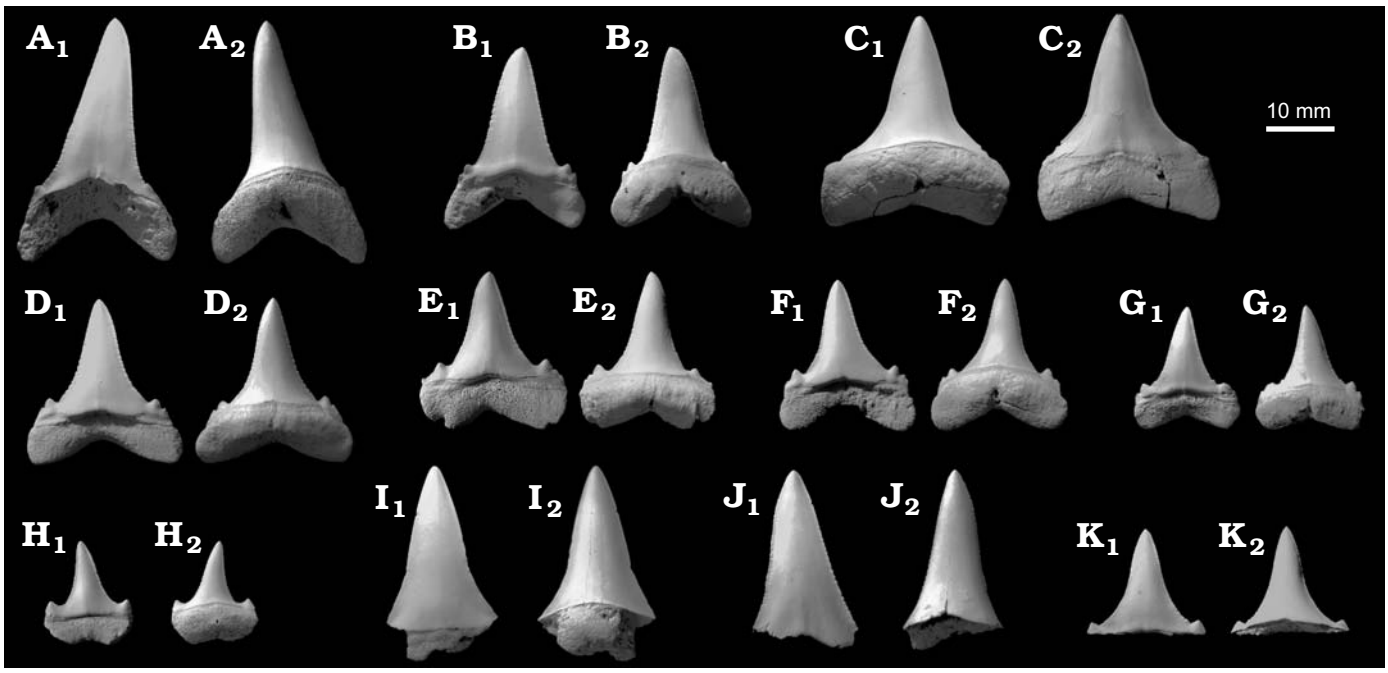


Fig. 11. Lower jaw teeth of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), MNU 071-20, from Groß Pampau, the middle–late Miocene. **A**. Lower left anterior tooth. **B**. Lower left intermediate tooth. **C**–**H**. Lower lateral teeth. Labial (A_1–H_1) and lingual (A_2–H_2) views. **I**. Incomplete anterior lower lateral tooth. **J**, **K**. Incompletely mineralized lower replacement teeth.

and shape, with one being completely developed with fully mineralised cusp and root, whereas the other is preserved as a thin enamel shell only, representing a replacement tooth. They thus represent two rearward positions and belong to the same tooth row and possess a slightly distally curved cusp with an anteriorly twisted apex. Labially, the main cusp distinctly juts out over the root. Lower anterior teeth are more slender than upper anteriors and superficially resemble those found in *Isurus*. Their roots are more massive, with one nutritive foramen, and display a more developed lingual protuberance. The asymmetrical root lobes are elongate and form an obtuse angle of 110° with the anterior root lobe, being more slender and longer than the distal one. Differences from *Isurus* and *Cosmopolitodus* include crenulated cutting edges and very incipient multiplied lateral cusplets with their height being only 6.4% of the total crown height.

The crown height of the third lower anterior, which also could be considered a lower intrabullar intermediate, is only 72.5% of that of the largest and most completely preserved lower anterior tooth. It is nevertheless larger than the following, first lateral tooth. It displays two symmetrical pairs of well-developed lateral cusplets, whose height is nearly 12% of the total crown height, escorting a nearly erect and straight main cusp with completely crenulated cutting edges. The main cusp reveals a lingual re-curvature and the apex point labially. The root shows a lingual protuberance and one nutritive foramen. The elongated root lobes are not symmetrical in shape, with the mesial one being more slender and elongated than the distal one similar to the condition found in lower anteriors. They form an obtuse angle and a V-shaped notch.

Thirteen teeth are identified as belonging to lower lateral files. Apart from the posterolateral teeth that display a slight inclination, the main cusps of lower lateral teeth are nearly vertical. All lateral teeth show two to three pairs of well developed, symmetrical lateral cusplets with heights between 14.3% and 23.8% of the total crown height, increasing from anterolateral to posterolateral files.

Body size estimates.—Only two teeth can be referred to upper anterior tooth rows, most probably from the second row. A definite, completely preserved first upper anterior is not available, as used in the work of Gottfried et al. (1996) to estimate the total body length. Gottfried et al. (1996) use a different terminology than Shimada (2002a). What Gottfried et al. (1996) call the second upper anterior [UA2] is the first upper anterior tooth [UA1] of Shimada (2002a). However, comparing the measurements of the tooth heights in extant Great White Sharks (Hubbell 1996), the two upper anterior teeth hardly differ in size or are even of nearly the same height, and therefore the same is assumed for the two upper anterior teeth of *Carcharomodus escheri*. The total height (crown + root) of the inferred second upper anterior tooth of this taxon measures almost exactly 42 mm. Applying the formula of Gottfried et al. (1996), a total body length of 3.81 m is established.

To validate this body size estimate, we also used Shimada's (2002d) method based on the second upper anterior tooth. The crown height of the second upper anterior is 31.76 mm, resulting in a total body length of 3.82 m, which is almost the same as derived from Gottfried et al's (1996) equation. For comparison, we also used the equation for body size estimation of *Isurus* spp. established by Shimada (2002c)

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assuming that the new taxon represents a lamnid shark with similar dental patterns to living lamnid sharks. Based on this equation and using the second upper anterior, the body size amounts to 3.67 m, which is slightly smaller than those derived from comparisons with the living Great White Shark. It is important to note that the teeth of the specimen described herein are not the largest ever found of this species. Others can reach a height of up to 50 mm, which would imply a body length of almost 5.00 m.

For comparison, we also calculated the total body length of our specimen using the size of vertebral centra and employing Gottfried et al.'s (1996) method. Extant Great White Shark, *Carcharodon carcharias*, has a total of 172 to 187 vertebrae, with the largest in the mid-body region (Gottfried et al. 1996), and very small ones that extend to the posterior tip of the caudal fin. Assuming that *Carcharodon carcharias* is closely related to *Carcharomodus*, it is likely that only 36% of the vertebrae are preserved in this specimen. Although the vertebral column thus is far from complete, it is still useful to estimate the total body size of this shark.

The largest preserved vertebral centrum has a diameter of 77.7 mm. This measure thus equals ca. 4.50 m total body length, which is significantly larger than the estimates derived from the teeth. This discrepancy might be related to the fact that the lamnid described here represents a different taxon. It is, however, reasonable to assume a total body length of this specimen of about 4.0 m based on all available evidence.

Age estimates.—Vertebral centra accumulate calcified growth material as they age, producing concentric layers, which can be used for age estimates of sharks both living and extinct (Cailliet et al. 2006; MacFadden et al. 2004). These concentric layers include opaque and translucent bands, which are generally assumed to have been deposited seasonally (Cailliet and Goldman 2004), and a pair of these layers forms a "ring" deposited annually (e.g., Gruber and Stout 1983; Natanson et al. 2002). However, various exceptions were documented for different sharks that cast some doubt on this model of annual ring periodicity (e.g., Stevens 1975; Natanson 1984; Cailliet et al. 1985; Branstetter and Musick 1994; Casey and Natanson 1992; Natanson 1993; Hamady et al. 2014). Nevertheless, the majority of studies indicate annual ring formation for most sharks, including lamniforms (e.g., Smith and Aseltine-Neilsen 2001; Campana et al. 2002). Although a detailed age analysis of the fossil lamniform shark using sophisticated methods such as bomb radiocarbon dating (Campana 2001) is beyond the scope of this paper, it is important to provide a rough age determination for assessing whether it is a juvenile or already has reached maturity. Ring count was executed on the X-ray images and all additional preserved vertebral centra starting at the birth-mark. Accordingly, all vertebrae display more than 10 (12–14) pairs of rings (Fig. 9). It is not possible to establish the exact number of bands because no thin sections of vertebral centra could be prepared. Nevertheless, our results suggest that this specimen of *Carcharomodus escheri* was more than 10 years old representing a late subadult to adult individual in comparison to living lamnid sharks (compare, e.g., Fowler et al. 2005; Goldman and Musick 2006; Cassoff et al. 2007).

Remarks.—Agassiz (1843) erected the species "*Carcharodon escheri*" for isolated teeth from the early-middle Miocene (Upper Marine Molasse) of Switzerland and southern Germany, respectively. These are the only definite findings from the Miocene Molasse basins. The holotype is the first tooth figured by Agassiz (1843: pl. 36: 16–18) from Switzerland. The exact locality of this specimen is unknown. The second figured tooth from southern Germany represents the paratype (Agassiz 1843, pl. 36: 19–21). Lateral cusplets are not preserved in both teeth because the basal parts of the cutting edges and the mesial root lobe in the holotype are damaged. In their general morphology, nevertheless, both teeth represent upper laterals. The synonymy list given above is far from being complete and only lists the most important references. This species was assigned variously to the genera *Carcharodon*, *Isurus*, *Macrorhizodus*, and *Oxyrhina* (e.g., Glikman 1964; Cappetta 2012). Woodward (1889: 411) synonymised *Carcharodon escheri* with *Carcharodon subserratus* Agassiz, 1843 based on a single specimen from the Eocene of Sheppey. According to Ward in Cappetta (2012) the specimen on which Woodward (1889) based his assignment represents a heavily mineralized and slightly abraded specimen, which originated from the Antwerp area and was imported to Sheppey, where it was sold with local fossils in the 19th century leading to the misinterpretation by Woodward (1889). *Carcharodon subserratus* represents a member of a distinct evolutionary lineage of very large macrophageous lamniforms of *Carcharocles*.

Stratigraphic and geographic range.—This species is quite common in the Mio-Pliocene of Europe (e.g., Leriche 1926; Kruckow 1960, 1965; Ceuster 1976; Bosch 1969, 1978, 1980; Bosch et al. 1975; Bendix-Almgreen 1983; Moths 1998). Its teeth, however, are very rare in the late early Miocene but become more abundant in the middle to late Miocene of the boreal realm (e.g., Priem 1912; Leriche 1926; Kruckow 1965; Brzobohatý and Schultz 1973; Cappetta 2012). The stratigraphic youngest remains are from the Zanclean–early Piacenzian (Pliocene) of, for instance, the Netherlands (Wijnker et al. 2008). Teeth identified as *Oxyrhina hastalis* var. *escheri* from the early Miocene of the Antwerp region by Leriche (1926) were transferred to *Isurus xiphodon* and *Isurus hastalis*, respectively, by Purdy et al. (2001). *Carcharomodus escheri* seems to be extremely rare in the Miocene Molasse Basin with the two teeth described by Agassiz (1843) being the only definite records. So far, we were not able to identify any other unambiguous specimen of this peculiar species in any Miocene locality of the Miocene Molasse Basin.

The taxonomic assignments of teeth from the Miocene of Portugal and Spain identified to this species (Antunes and Jonet 1970; Serralheiro 1954; García et al. 2009) are ambiguous and we currently consider these as belonging to

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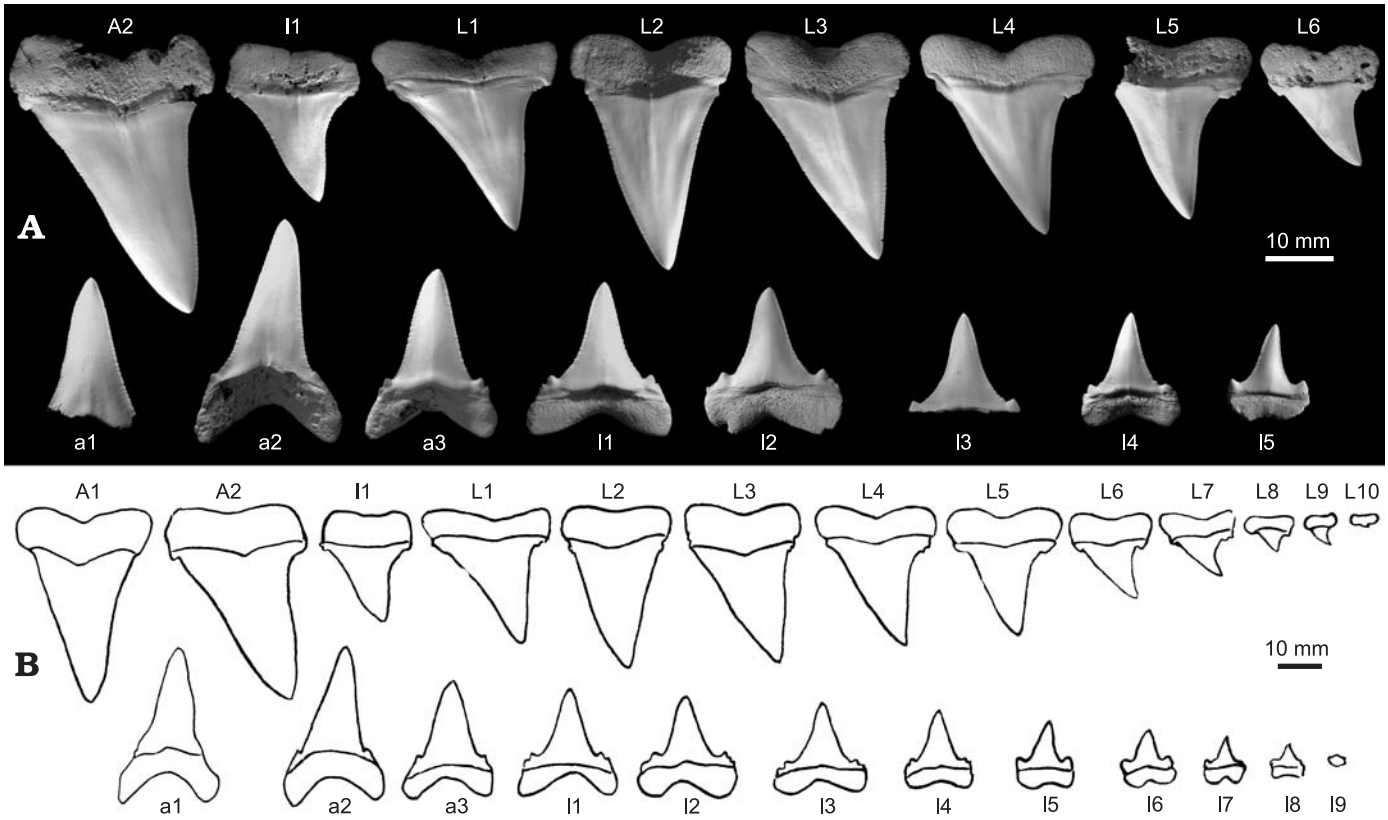


Fig. 12. Reconstructed left upper and lower tooth rows of the mackerel shark *Carcharomodus escheri* (Agassiz, 1843), in lingual view. **A**. Reconstruction based on preserved teeth. **B**. Drawing of the completely reconstructed dentition based on preserved teeth and comparisons with living lamnid sharks.

another isurid species. Additional teeth assigned to "*Isurus escheri*" were reported from many Mio-Pliocene localities outside of Eurasia. For instance, Fitzgerald (2004) reported "*Isurus escheri*" from the early Pliocene of Australia and Muizon and DeVries (1985) from the late Pliocene of Peru. However, we agree with Nyberg et al. (2006) and restrict the lamnid species *Carcharomodus escheri* to specimens occurring along the Atlantic coastline of Europe. All other specimens recovered outside Europe assigned to this species need to be transferred to a different taxon (e.g., Ehret et al. 2012). Consequently, *Carcharomodus escheri* seems to be a predominant element of Western and Central European elasmobranch faunas during the Miocene.

Discussion

Carcharomodus is a macrophagous lamniform shark and thus possesses a distinct ("lamnoid") dental pattern (secondarily lost in microphagous lamniform sharks), characterised by well differentiated teeth along the jaws, consisting of defined anterior and lateral files and an additional "intermediate" row separating anterior from lateral teeth (Compagno 1984). Symphyseals, however, are not preserved in the specimen. In addition, macrophagous lamniforms are characterised by having anterior and posterior dental bullae (Carvalho 1996) supporting anterior and intermediate teeth and lateral to posterior teeth respectively. Although it is not possible to observe these dental bullae in the specimen because of its preservation, it is most parsimonious to assume that these bullae were present based on the reconstructed dentition.

The teeth of *Carcharomodus escheri* (Fig. 12) represent a nearly complete range of morphologies in graded sizes, from presumed upper and lower anteriors and laterals from all four jaw quadrants. Also, this assemblage displays a high degree of linear correlation between tooth height and tooth width, which would not be the case if the assemblage was derived from numerous individuals of dissimilar sizes, ages, and genders, as shown by Kent and Powell (1998).

Since the tooth set consists of only disarticulated teeth, with no remains of the corresponding jaw elements, the reconstruction is based on the assumption that *Carcharomodus* is a member of Lamnidae, which is verified by the morphology and architecture of teeth and vertebral centra. Having a living shark as a model simplifies the reconstruction of the dentition, but determining the number of tooth files in each jaw is still a problem. The dental formula of an extant adult *Carcharodon carcharias* is A2-I1-L7-11/a3, l7-11, whereas juveniles have nine upper laterals and ten lower laterals, respectively (e.g., Hubbell 1996; Shimada 2005a). We also used dentitions of *Isurus*, sister to *Carcharodon*, to reinforce the reconstruction. The fact that the preserved tooth set consists of only 42 teeth renders it statistically unlikely

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or even impossible that a full set of teeth of a functional row is preserved. The very small posterolateral teeth are not preserved as is the first anterior tooth. However, we assume that the first upper anterior is as tall as, or even slightly smaller than, the second one, making the second upper anterior most likely the largest tooth, as in the living *Carcharodon carcharias*.

The upper intermediate tooth seemingly is reduced, but not reversed, conversely to the condition in *Carcharodon carcharias* based on the morphology and orientation of the root lobes. It also differs significantly from the upper intermediate tooth seen in *Cosmopolitodus hastalis*. It is diagnosed as intermediate and separated from the smaller lateral teeth by the angle between its root lobes and the degree of inclination of its principal cusp. The angle between the root lobes is about 160°. All lateral teeth of similar size show an angle of about 135°. Also, the angle of cusp inclination is much larger than in lateral teeth. Furthermore, the lateral cusplets of the upper intermediate tooth are smaller relative to the height of the principal cusp.

The first lateral tooth does not reveal marked serrations and the angle between its root lobes is intermediate between those of the intermediate and the second lateral tooth, supporting its inferred jaw position. The second lateral tooth is the largest and most upright of all lateral teeth, followed by lateral teeth that gradually decrease in size and gradually increase their angle of inclination.

The first lower anterior tooth is preserved, but not fully mineralised, probably representing a replacement tooth. As in other lamnid sharks, its crown height is smaller than that of the second one. The third lower anterior is intermediate in size between the second anterior and the first lateral tooth. The root of this tooth resembles that of anteriors, similar to the condition found in *Carcharodon* and *Cosmopolitodus*. A consistent pattern distinguishing teeth of *Carcharomodus* from other lamnids such as *Carcharodon* and *Cosmopolitodus*, however, is the more or less horizontal and narrow tooth neck separating the crown from the root.

The tooth arrangement of *Carcharomodus escheri* as reconstructed here is very characteristic of lamnid sharks (Fig. 12). Consequently, all living lamnids and *Carcharomodus* show similar dental patterns based on upper and lower tooth sizes within the jaws from anterior to posterior (Fig. 13). The upper jaw contains two enlarged anterior teeth, and a reduced upper intermediate tooth followed by one or two files of lateral teeth that are of transitional size between the intermediate tooth and the largest lateral tooth. The lower dentition is similar, but lacks a reduced intermediate tooth and the first lateral tooth is usually the highest of the lateral teeth. The dentition of *Carcharomodus* follows the general trend seen in living lamnids and is intermediate between that of *Carcharodon carcharias* and *Isurus* spp.

There is, however, an obvious difference in the relation of the largest lateral tooth to the largest anterior tooth in the upper jaw within lamnid sharks, with the ratio being significantly smaller in *Carcharodon* and *Carcharomodus*

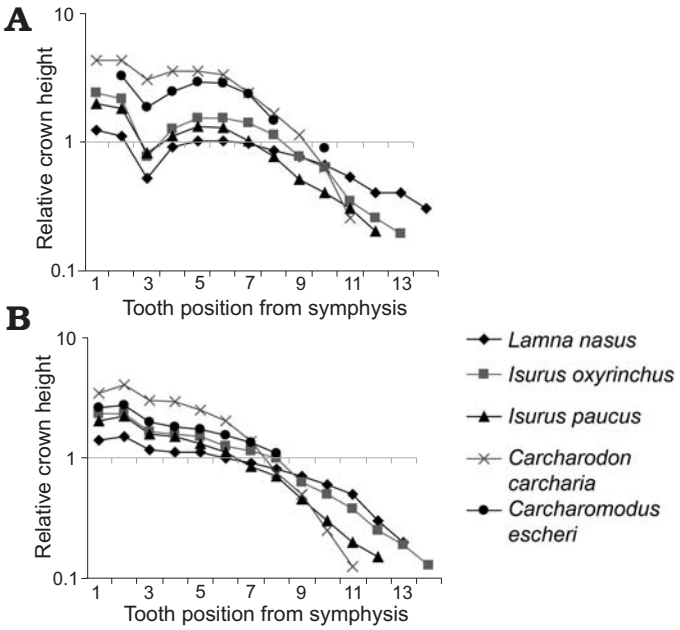


Fig. 13. Relative crown heights of the reconstructed dentition of *Carcharomodus escheri* (Agassiz, 1843) in comparison to living lamnids. Upper (**A**) and lower (**B**) jaw. Scaled logarithmically.

than in *Isurus*. The ratio between the height of the upper intermediate tooth and its neighbours also is significantly larger in *Carcharodon* and *Carcharomodus*. Teeth of *Carcharomodus* reveal an astonishing similarity to the tooth morphology of juvenile *Carcharodon carcharias*. This is particularly true of the first upper anteriors, which are more distally inclined than the largest of the lateral teeth, also the most upright in both species. In juvenile *Carcharodon carcharias* the third upper lateral tooth is the tallest of the lateral teeth, and the second lateral looks very similar to the first one, which would be highly hypothetical, though possible, to assume for *Carcharomodus*. In juvenile *Carcharodon carcharias,* the second upper lateral teeth possess only rudimentary lateral cusplets, as in the first upper lateral tooth of the reconstructed dentition of *Carcharomodus escheri*. It is possible that this latter tooth (Fig. 12) actually represents the second lateral tooth and that the first one is not preserved. This, however, only can be confirmed from a complete and articulated dentition. Also, in both juvenile *Carcharodon carcharias* and *Carcharomodus escheri* the lateral cusplets are more distinct in teeth of the lower jaw than those of the upper jaw.

Within monophyletic Lamnidae, a paedomorphic relationship of the dentition seemingly is present, with *Carcharodon* being paedomorphic in comparison to *Cosmopolitodus* and *Isurus*, and with *Carcharomodus* being paedomorphic in comparison to *Carcharodon carcharias*. The doublet rule (Wiley et al. 1991) states that if the sister group and the first two consecutive outgroups have the same character, then that character is decisive for the outgroup node. Regarding *Carcharodon* as the ingroup and *Cosmopolitodus* and *Isurus* as the two outgroups, the following pattern is evident. *Isurus* and *Cosmopolitodus* do

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not possess lateral cusplets, whereas *Carcharodon carcharias* possesses lateral cusplets in free-swimming juveniles up to a body length of 214 cm (Shimada 2002b), and teeth of *Carcharomodus* reveal lateral cusplets in all known ontogenetic stages, based on its fossil record of abundant isolated teeth of a wide array of sizes. Shimada (2002c) described a 61 cm long embryo of *Isurus oxyrinchus* possessing small distal lateral cusplets or at least distal heels, which might be similar in *Isurus paucus*. No embryonic teeth of *Cosmopolitodus hastalis* and *Carcharomodus escheri* are known, but they presumably follow this pattern. In *Carcharodon carcharias*, development is delayed and its teeth still show lateral cusplets in free-swimming juveniles, while teeth of *Carcharomodus* never reach the adult pattern of its living relatives, as exemplified by the specimen in this study, which already had, or almost had, reached maturity (see above).

The calculated body length of ca. 4 m, based on measurements of the second upper anterior teeth is more or less the same for both formulas. Using the maximum vertebral width, a significantly larger body length was calculated. As already mentioned, teeth of this specimen of *Carcharomodus escheri* are not the largest ever found, which implies that this specimen was not yet fully mature when it died. Consequently it is possible that proportions between teeth and vertebrae are not yet fully developed resulting in the discrepancies in body size estimates. There are also significant differences when using Shimada's (2002c, d) formula for different tooth positions. This could indicate, on the other hand, that the crown heights of *Carcharomodus* have not the same relations to the total body length as in *Carcharodon* and *Isurus*, and consequently that the formula calculated for one species cannot be used in the same way for other species, even if they are close relatives. At least this would be true for all files except the upper anterior files. The upper anterior teeth appear to be more appropriate for estimating the total body length, because two different formulas led to more or less the same result, and crown height and root height appear to have the same relations in *Carcharomodus escheri* and *Carcharodon carcharias*. More data, however, is needed to test the relationships between tooth measurements and total body lengths and their interspecific correlations.

Nevertheless, our results suggest that this specimen of *Carcharomodus escheri* was at least 10 years old with a body length between 3.8 and 4.5 m. The living Great White Shark, *Carcharodon carcharias*, which is considered here as a close relative of *Carcharomodus*, reaches maturity at 9–10 (males) and 12–14 (females) years, respectively (Kock and Johnson 2006). The estimated body size range also agrees more or less with the expected body size range at maturity of the extant Great White Shark, which is 4.5–5.0 m in females and 3.5–4.1 m in males (Kock and Johnson 2006). We thus assume that our specimen might already have reached maturity, although it is not possible to identify its gender since no pelvic fin skeletal remains, which could have included the pterygopods (clasper organs), were recovered.

Conclusions

The specimen of the lamnid shark *Carcharomodus escheri* (Agassiz, 1843), described in this study is the most complete fossil of this species known to date. Although not completely preserved, it enables a detailed morphological description of its dentition and a clear differentiation of this taxon from other lamnids. The new taxon seemingly is closely related to *Cosmopolitodus* and *Carcharodon* based on dental structures. However, detailed phylogenetic analyses are necessary to identify its relationships within Lamnidae. The standing diversity (raw number of genera) of lamnid sharks increases from the Palaeogene (one genus in the Palaeocene and three genera in the Eocene) to five genera in the Oligocene and Miocene, respectively (data from Cappetta 2012 and this study). Reasons for this diversity increase are varied and likely related to climatic (end-Oligocene to middle Miocene warm period), palaeogeographic and co-evolutionary patterns. Contemporaneous lamniforms also include the megatooth shark, *Megaselachus megalodon*, as well as an extinct species of *Carcharodon*, *C. hubelli*. Nevertheless, the standing diversity of lamniform sharks as a total group was highest in the Eocene (26 genera) during the Eocene climatic optimum.

Teeth of *Carcharomodus* and early *Carcharodon carcharias* are very common in late Miocene to Pliocene Atlantic coastal deposits of Europe, while teeth of *Megaselachus megalodon* seemingly are more abundant in the deposits of the Atlantic coastal plain of North America (Purdy 1996). The transitional forms from the Mio-Pliocene of the Pacific area, e.g., Peru (Muizon and DeVries 1985), represent another lineage of lamnid sharks indicating an even larger lamnid diversity during the Miocene. The taxonomic assignment and systematic position of this shark, however, remain momentarily unresolved.

The results presented here also indicate that the dental evolution of lamnid sharks might be related to paedomorphic processes. *Carcharodon* is paedomorphic in comparison to *Cosmopolitodus* and *Isurus*, while *Carcharomodus* is paedomorphic in comparison to *Carcharodon carcharias*.

The dentition of *Carcharodon carcharias* with its regularly triangular and serrated teeth is perfectly adapted to cut and gouge large, thick-skinned mammalian prey, whereas the teeth of *Carcharomodus escheri* are characterised by a dignathic heterodonty pattern consisting of pointed and narrow lower teeth suitable for grasping prey and blade-like upper teeth suitable for cutting through flesh. We thus assume that its feeding style of adults at least was intermediate between *Isurus* on the one hand and *Carcharodon* and *Cosmopolitodus* on the other. The disappearance of *Carcharomodus* and *Megaselachus megalodon* in the Pliocene, however, remains arguable. After both and the other large-toothed *Cosmopolitodus* spp. vanished, *Carcharodon carcharias* became the top marine predator, even though it never reached the enormous body size of *Megaselachus megalodon*.

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