

# An identification key to elasmobranch species based on dental morphological characters. Part B: extant Lamniform sharks (Superorder Galeomorphii: Order Lamniformes)

Ein auf zahnmorphologischen Merkmalen basierender Bestimmungsschlüssel für Elasmobranchierarten. Teil B: rezente Lamniforme Haie (Überordnung Galeomorphii: Ordnung Lamniformes)

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**Summary:** Apart from wet-collection specimens, shark and ray (Neoselachii) museum collection specimens are often represented as articulated jaws or single teeth. In many cases, detailed information on locality, species identification and data on the specimen's body are lacking. The identification key for jaws and teeth presented herein is part B of a planned series of dental identification keys. Herein, lamniform sharks are in focus. Today, the order Lamniformes comprises 15 species in 10 genera and 7 families. All of these large active pelagic sharks have a worldwide geographic distribution. The key is essentially based on the following characters: dental formula, presence/absence of specific categories of teeth ((para-)symphyseal, intermediate teeth), form of crown, number of cusplets, and dentition type. The key allows the identification to genus and species level, if adequate specimens are available. It is further supplemented by a detailed species account. The glossary presented in part A of this series extended by some terms that are specific for lamniform sharks.

**Key words:** Mackerel sharks, dentition, Elasmobranchii, single-access identification key, teeth

**Zusammenfassung:** In zahlreichen wissenschaftlichen Sammlungen befinden sich neben formaldehyd- bzw. alkoholkonservierten Ganzkörper- und anatomischen Präparaten oftmals Kiefer und Zähne von Haien und Rochen. Bei diesen Exemplaren fehlen häufig detaillierte Informationen über die Art, das Geschlecht oder die geografische Herkunft. Mit der vorliegenden Arbeit wird ein weiterer Teil eines Bestimmungsschlüssels für Kiefer und Zähne von lamniformen Haien vorgestellt (Teil B der geplanten Reihe). Diese Ordnung beinhaltet derzeit 15, meist großwüchsige, weltweit verbreitete pelagische Arten in zehn Gattungen und sieben Familien. Zur Identifizierung wird dabei im Wesentlichen auf folgende Merkmale zurückgegriffen: Zahnformel, An- oder Abwesenheit bestimmter Zahngruppen ((Para-) Symphysenzähne, Intermediärzähne), Form der Krone, Anzahl der Zahnspitzen und Art der Bezahnung. Der Schlüssel ermöglicht die Bestimmung bis auf Artebene. Ergänzt wird er durch eine detaillierte Artbeschreibung in Bezug auf zahnmorphologische Merkmale. Das im ersten Teil vorgestellte Glossar wird um einige Begriffe, die für diese lamniformen Haie von Bedeutung sind, erweitert.

**Schlüsselwörter:** Makrelenhaiartige, Bezahnung, Elasmobranchii, dichotomer Bestimmungsschlüssel, Zähne

## 1. Introduction

In contrast to other groups of sharks such as Carcharhiniformes and Squaliformes for example, the mackerel sharks (Lamniformes) did not experience a large number of new species

descriptions recently. While in Carcharhiniformes and Squaliformes 184 new species were described since 1983, only a single lamniform shark was described: *Megachasma pelagios*, the megamouth shark, so far the second known filter-feeding lamniform. In total there are 15 lamniform shark

species, representing 2,76% of the overall shark diversity (543 species, POLLERSPÖCK & STRAUBE 2020a). All of them are characterized by large body sizes compared to other shark taxa. Further, lamniform sharks are pelagic and dominated by fast-swimming predators including the white shark *Carcharodon carcharias*, one of the most studied shark species (POLLERSPÖCK & STRAUBE 2020b). Their dentitions are adapted to their feeding habits. As active hunters, a larger part of lamniform dentitions is adapted to capture fast swimming prey, while others show serrated teeth for sawing purposes. Their characteristic large teeth are well represented in the fossil record and therefore, Lamniformes are considered to have the most complete fossil record of sharks (PIMIEN-

TO & BENTON 2020). The phylogeny of Lamniformes based on mitochondrial DNA sequence data support monophyly of the order, however, intraordinal relationships are not fully resolved and understood. Families Mitsukurinidae, Lamnidae, Pseudocharcharhinidae and Megachasmidae are supported as clades while Alopiidae, Cetorhinidae and Odontaspidae appear paraphyletic (NAYLOR et al. 2012). STONE & SHIMADA (2019) excluded the genus *Carcharias* from Odontaspidae and established the family Carchariidae for the genus.

Here, we present a morphological identification key with focus on jaw and tooth morphologies of lamniform sharks allowing for genus and, if adequate material is available, species level identification.

**Tab. 1:** Overview of Lamniformes (POLLERSPÖCK & STRAUBE 2020).

**Tab. 1:** Taxonomie der Ordnung Lamniformes (POLLERSPÖCK & STRAUBE 2020).

Species/Common name	Family	Tooth formula	TL in cm (born)	TL in cm (max)
<i>Alopias pelagicus</i> Nakamura, 1935/ Pelagic thresher	Alopiidae	41-45/37-38	130-160	365
<i>Alopias superciliosus</i> (Lowe, 1841)/ Bigeye thresher	Alopiidae	19-27/20-24	100-140	480
<i>Alopias vulpinus</i> (Bonnaterre, 1788)/ Thintail thresher	Alopiidae	32-52/25-50	120-150	575
<i>Cetorhinus maximus</i> (Gunnerus, 1765)/ Basking shark	Cetorhinidae	100->200/ 100-200	150-170	>1000
<i>Carcharodon carcharias</i> (Linnaeus, 1758)/ Great white shark	Lamnidae	23-28/21-25	110-160	600
<i>Isurus paucus</i> Rafinesque, 1810/ Shortfin mako	Lamnidae	24-26/24-29	60-70	400
<i>Isurus paucus</i> Guitart Manday, 1966/ Longfin mako	Lamnidae	24-26/22-26	92-97	430
<i>Lamna ditropis</i> Hubbs & Follett, 1947/ Salmon shark	Lamnidae	22/22	65-80	305
<i>Lamna nasus</i> (Bonnaterre, 1788)/ Porbeagle	Lamnidae	22-31/24-29	60-80	355
<i>Megachasma pelagius</i> Taylor, Compagno & Struhsaker, 1983/Megamouth shark	Megachasmidae	55-115/75- 121	<170	>550
<i>Mitsukurina owstoni</i> Jordan, 1898/ Goblin shark	Mitsukurinidae	38-52/34-50	80-90	550
<i>Carcharias taurus</i> Rafinesque, 1810/ Sand tiger shark	Carchariidae (previously Odontaspidae)	36-54/32-46	85-105	320
<i>Odontaspis ferax</i> (Risso, 1810)/ Smalltooth sand tiger	Odontaspidae	46-56/34-48	100-105	450
<i>Odontaspis noronhai</i> (Maul, 1955)/ Bigeye sand tiger	Odontaspidae	40/44	?	427
<i>Pseudocarcharias kamoharai</i> (Matsubara, 1936)/ Crocodile shark	Pseudocarchariidae	26-29/19-26	41	122

## 2. Material and Methods

The identification key is primarily based on information from scientific literature. The information on dental formula in the paragraph “species accounts” is mainly derived from SHIMADA (1999, 2002). The data obtained by SHIMADA (1999) were reviewed on the basis of exemplary publications published after 1999 and the investigated references are added in the material part of the species accounts. The row counts of tooth types (para-/symphyseal, anterior, intermediate, lateral) are based on the right side of the jaws only. In the dental formula given in the species description by SHIMADA (2002), the first upper jaw tooth in the genera *Mitsukurina* and *Carcharias* is defined as symphyseal tooth. Other authors (e.g. TANIUCHI 1970, APPLIGATE & ESPINOSA-ARRUBARRENA, 1996) refer to this tooth as the first anterior tooth due to its size. Used “?” in dental formulas mark missing or doubtful data. The most recent accepted taxonomy of the order Lamniformes based on current literature is shown in table 1. The added tooth formulae show the total count (range) of

teeth in the upper and lower jaw, the total length (TL) data in cm of newborn specimens and the maximum reported size. All data were taken from EBERT et al. (2013) (Tab. 1).

CAPPETTA (1986, 2012) grouped the dentitions of elasmobranchs in the following dental types: clutching, tearing, cutting, crushing, grinding, clutching-grinding, cutting-grinding and crushing-grinding types. In lamniform sharks only three types are present, the cutting, tearing and clutching type (Tab. 2).

## 3. Morphological identification key to teeth of lamniform sharks

The following key has been developed for identification at species level for complete specimens or isolated jaws, but can be used in many cases for isolated teeth as well. When selecting the morphological characters of teeth, we focused on using characters that can be identified without removing teeth from the jaws. In particular, no lingual root features were used. The presence/absence or the number of specific

**Tab. 2:** Summary of the most important morphological tooth characters in lamniform sharks.

**Tab. 2:** Zusammenstellung der wichtigsten zahnmorphologischen Merkmale bei lamniformen Haie.

Species	usually one upper intermediate present	usually four upper intermediate present	usually upper or lower (para) symphyseal present	one pair of cusplets present	usually more than one pairs of cusplets present	upper/lower teeth serrated	root belobed	dental type	number of rows upper jaw, minimum	number of rows upper jaw, maximum	number of rows lower jaw, minimum	number of rows lower jaw, maximum	Crown height (A1 in mm) range
<i>Alopias pelagicus</i>	yes	no	yes	no	no	no	yes	cutting	19	28	18	23	2.1-4.2
<i>Alopias superciliosus</i>	no	no	yes	no	no	no	yes	cutting	11	13	10	13	10.1-15.5
<i>Alopias rubripinus</i>	yes	no	yes	no	no	no	yes	cutting	19	28	16	27	1.5-8.2
<i>Cetorhinus maximus</i>	yes	no	no	no	no	no	no	clutching	100	131	100	139	1.6-6.4
<i>Carcharodon carcharias</i>	yes	no	no	no	no	yes	yes	cutting	11	14	11	14	11.4-48.9
<i>Isurus paucus</i>	yes	no	no	no	no	no	yes	cutting	10	14	10	14	7.7-38.0
<i>Isurus paucus</i>	yes	no	no	no	no	no	yes	cutting	10	14	11	13	20.5-35.0
<i>Lamna ditropis</i>	yes	no	no	yes	no	no	yes	cutting	12	16	13	15	8.4-12.3
<i>Lamna nasus</i>	yes	no	no	yes	no	no	yes	cutting	12	16	11	16	7.8-15.0
<i>Megachasma pelagius</i>	yes	no	no	possible	no	no	yes	clutching	42	56	43	69	-
<i>Mitsukurina owstoni</i>	no	no	yes	no	no	no	yes	tearing	22	32	23	29	10.1-21.5
<i>Carcharias taurus</i>	yes	no	yes	yes	no	no	yes	tearing	16	36	15	25	7.8-29.7
<i>Odontaspis ferox</i>	no	yes	yes	yes	yes	no	yes	tearing	19	30	17	25	9.5-25.5
<i>Odontaspis noronhai</i>	yes	no	yes	yes	no	no	yes	tearing	17	22	17	24	13.0
<i>Pseudocarcharias kamoharui</i>	yes	no	no	no	no	no	yes	tearing	12	17	9	14	6.5-11.1

groups of teeth, such as symphyseal teeth or intermediate teeth, are important characters for lamniform shark identification. A summary of characters is shown in Table 2.

Lateral tooth: smaller teeth, continuously decreasing in size, toward the commissure region of the jaw (Fig. 1).

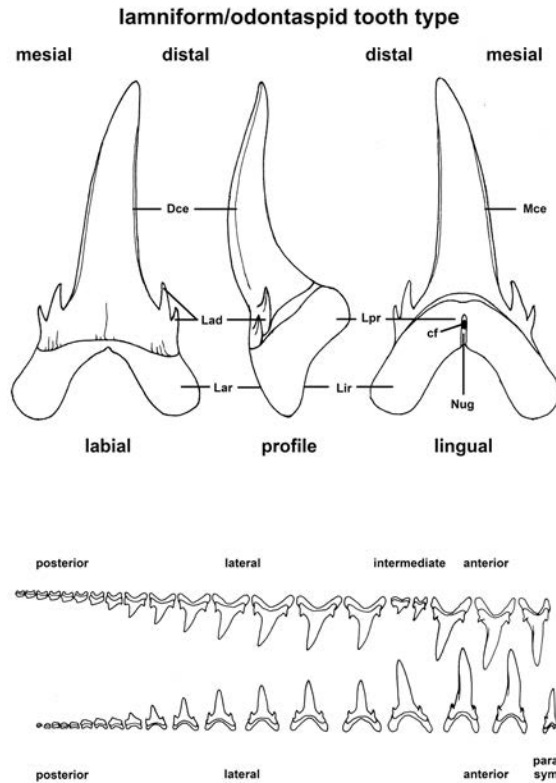
### 3.1. Glossary (tooth morphological characters, after CAPPETTA 2012)

Remark: The following terms complements the glossary published in POLLERSPÖCK & STRAUBE (2019).

Intermediate tooth: reduced tooth in lamniform sharks between upper anterior and upper lateral teeth, sometimes distorted cusps (Fig. 1).

### 3.2. Morphological identification key

- 1a: more than 80 rows of teeth in the upper and lower jaw, teeth small (in relation to meckelian/palatoquadrate cartilage).....2
- 1b: less than 80 rows of teeth in the upper and lower jaw, medium or large teeth (in relation to meckelian/palatoquadrate cartilage) .....3
- 2a: teeth in upper and lower jaw erected, hook like, and labial face with ornamentation, root



**Fig. 1:** Lamniform/odontaspid tooth forms; abbreviations: Dce (distal cutting edge), Mce (mesial cutting edge), Lad (lateral cusplets), Lar (labial face of the root), Lpr (lingual protuberance of the root), Lir (lingual face of the root), cf (central foramen), Nug (nutritive or basal groove). © drawings: Helmut Bracher, Altdorf  
**Abb. 1:** Lamniforme/odontaspide Zahnformen; Abkürzungen: Dce (distale Schneide), Mce (mesiale Schneide), Lad (laterale Seitenspitzen), Lar (labiale Wurzelfläche), Lpr (linguale Wurzelprotuberanz), Lir (linguale Wurzelfläche), cf (zentrales Foramen), Nug (Basalfurche). © Zeichnungen: Helmut Bracher, Altdorf

monolobed, more than 200 rows of teeth in the upper and lower jaws .....*Cetorhinus maximus*  
 2b: teeth in upper and lower jaws in anterior teeth weakly, in lateral teeth moderately distally bent, labial face without ornamentation, root bilobed, significantly less than 200 rows of teeth in the upper and lower jaws .....*Megachasma pelagios*  
 3a: all teeth broad, triangular and with strongly serrated cutting edges .....*Carcharodon carcharias*  
 3b: teeth without serrated cutting edges .....4  
 4a: usually three anterior teeth in the upper jaw present .....5  
 4b: usually two anterior teeth in the upper jaw present .....6  
 5a: no intermediate tooth/teeth in the upper jaw, crown with clearly visible lingually parallel folds .....*Mitsukurina owstoni*  
 5b: intermediate tooth/teeth in the upper jaw usually present, crown lingually smooth or only with weakly developed irregularly folds .....*Carcharias taurus*  
 6a: usually one pair or more than one pairs of lateral cusplets in anterior and lateral tooth rows present .....7  
 6b: lateral cusplets absent or only rudimentary cusplets in anterior tooth present .....10  
 7a: usually one pair of thin lateral cusplets present .....8  
 7b: usually two or three pairs of thin lateral cusplets present .....*Odontaspis ferox*  
 8a: usually one pair of thin, hooklike cusplets present, upper and lower lateral teeth with slender cusps .....*Odontaspis noronhai*  
 8b: usually one pair of broad, triangular cusplets present, upper and lower lateral teeth with broad, triangular cusps .....9 (genus *Lamna*)  
 9a: strongly distally bent upper intermediate tooth, triangular, at the base of the crown very broad lower lateral teeth .....*Lamna ditropis*  
 9b: erected upper intermediate tooth, triangular, more slender lower lateral teeth .....*Lamna nasus*  
 10a: needle-like upper anterior teeth, slender lateral teeth, lingual basal groove present .....*Pseudocarcharias kamoharui*  
 10b: slender or triangular upper anterior teeth, triangular lateral teeth, lingual basal groove absent .....11

11a: slender upper anterior teeth, genus *Isurus* .....12  
 11b: triangular upper anterior teeth, genus *Alopias* .....13  
 12a: robust and broad two upper anterior teeth, cutting edges of anterior teeth reach to the basis of the crown, intermediate tooth below lateral margin of palatine process of palatopterygoquadrate cartilage .....*Isurus paucus*  
 12b: slender upper lateral teeth, cutting edges of anterior teeth don't reach the basis of the crown, intermediate tooth usually below upper two-thirds of lateral margin of palatine process .....*Isurus oxyrinchus*  
 13a: usually less than 13 rows in upper/lower jaw .....*Alopias superciliosus*  
 13b: usually more than 20 rows in upper/lower jaw, very broad and triangular upper and lower teeth .....*Alopias vulpinus*  
 13c: usually more than 20 rows in upper/lower jaw, significantly slender upper and lower teeth .....*Alopias pelagicus*

### 3.3. Species accounts (ordered as in Tab. 2)

Family Alopiidae Bonaparte, 1835

Genus *Alopias* Rafinesque, 1810

Type species: *Alopias macrourus* Rafinesque, 1810

#### ***Alopias pelagicus* Nakamura, 1935 (Fig. 2A)**

Synonymy: None.

Distribution: Oceanic and wide-ranging in the Indo-Pacific (COMPAGNO 2001).

Size: TL (max): 3650 mm, TL (born): 1300-1600 mm (EBERT et al. 2013).

Dental formula (most common/age): 0-2-1-18/1-20; (0-2)-(2)-(1-2)-(16-22)/(0-1)-(18-22) (SHIMADA 2002).

Crown height (A1 in mm/TL): 2.1 mm/1700 mm TL; 3.9 mm/2410 mm TL (SHIMADA 1999).

Material: OKADA (1955) (OKADA 1955) (n=1); BASS et al. (1975) (n=1); CASTRO (1983) (n>1); ITOIGAWA et al. (1985) (n=1); SAINSBURY et al. (1985) (n>1); RANDALL (1986) (n>1); LAST & STEVENS (1994) (n>1); COMPAGNO et al. (1995) (n>1); SHIMADA (1999) (n=11); COMPAGNO (2001) (n>1); HERMAN et al. (2004) (n=2).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2d+4d/CITES annex: II (04.10.2017) (REARDON et al. 2009).

Description (after HERMAN et al. 2004, SHIMADA 1999, 2002; BASS et al. 1975): Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism and ontogenetic heterodonty absent; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; anterior and intermediate teeth always higher than broad, lateral and posterior teeth always broader than high; no serration, no ornamentation, no pairs of cusplets.

Upper jaw (most common: 21 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; upper teeth slightly larger than lower teeth, triangular and erected cusp of the first anterior tooth, the second one and all following teeth are strongly bent distally; straight or weakly convex curved mesial cutting edge, the labial face of the crown is slightly, the lingual face strongly convex; low and a small distal heel, blunt cusplet-like humps can be present; lingual face of root shows one or two foramina in basal groove, no other lingual foramina present, labial side with numerous scattered foramina.

Lower jaw (most common: 21 rows): usually 1 (para-)symphyseal tooth, no intermediate tooth, small parasymphyseal tooth, parasymphyseal tooth and first lateral tooth erected, all following teeth strongly bent distally; straight or weakly convex curved mesial cutting edge, labial face of crown slightly, lingual face strongly convex; low and small distal heel, blunt cusplet-like hump can be present; lingual face of root shows one or two foramina in basal groove, no other lingual

foramina present, labial side with numerous scattered foramina.

### ***Alopias superciliosus* (Lowe, 1841) (Fig. 2B)**

Synonymy: *Alopias profundus* Nakamura, 1935.

Distribution: Oceanic and coastal, virtually circumglobal in tropical and temperate seas (EBERT & STEHMANN 2013).

Size: TL (max): 4800 mm, TL (born): 1000-1400 mm (EBERT et al. 2013).

Dental formula (most common/rage): 0-2-0-10/0-11; (0)-(2)-(0-1?)-(9-11)/(0-1)-(10-12) (SHIMADA 2002).

Crown height (A1 in mm/TL): 10.1 mm/2870 mm TL; 15.5 mm/3720 mm TL (SHIMADA 1999).

Material: KATO et al. (1967) (n>1); ANTUNES (1970) (n=2); BLACHE et al. (1970) (n>1); FITCH (1974) (n>1); GUITART (1974) (n=2); BASS et al. (1975) (n=2); FIGUEIREDO (1977) (n>1); TANIUCHI (1979) (n>1); CADENAT & BLACHE (1981) (n>1); GRUBER & COMPAGNO (1981) (n=8); CASTRO (1983) (n>1); CIGALA-FULGOSI (1983) (n=5); ESCHMEYER & HERALD (1983) (n>1); QUERO (1984) (n>1); ITOIGAWA et al. (1985) (n=2); SAINSBURY et al. (1985) (n>1); IVANOV (1986) (n=2); ROBINS & RAY (1986) (n>1); LAST & STEVENS (1994) (n>1); COMPAGNO et al. (1995) (n>1); SHIMADA (1999) (n=25); COMPAGNO (2001) (n>1); GADIG (2001) (n>1); HERMAN et al. (2004) (n=8); KABASAKAL & KARHAN (2008) (n=2); CORSINI-FOKA & SIOULAS (2009) (n=2); GOMES et al. (2010) (n>1); KABASAKAL et al. (2011) (n=3); DUFFY & STEWART (2015) (n>1); LANTERI et al. (2017) (n=1).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2bd/CITES annex: II (04.10.2017) (AMORIM et al. 2009).

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**Fig. 2: A** *Alopias pelagicus* Nakamura, 1935: male, 282 cm TL, Gulf of California, coll. 29.01.2001, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Alopias superciliosus* (Lowe, 1841): male, 442 cm TL, Sydney, Australia, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 2: A** *Alopias pelagicus* Nakamura, 1935: männliches Exemplar, 282 cm Gesamtlänge, Golf von Kalifornien, coll. 29.01.2001, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Alopias superciliosus* (Lowe, 1841): männliches Exemplar, 442 cm Gesamtlänge, Sydney, Australien, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.



Description (after HERMAN et al. 2004, SHIMADA 1999, 2002; BASS et al. 1975): Gradient monognathic heterodonty present; gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism and ontogenetic heterodonty absent; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; anterior teeth always higher than broad, lateral and posterior teeth always broader than high; no serration, no ornamentation, no pairs of cusplets.

Upper jaw (most common: 12 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, no intermediate tooth; upper teeth slightly larger than lower teeth, triangular and erected cusp of first two anterior teeth, the third and all sequential teeth strongly bent distally; weakly convex curved mesial cutting edge, labial face of crown slightly, lingual face strongly convex; low and small distal heel present, blunt cusplet-like hump can be present in posterior teeth; mesial with blade-like lobate extension; lingual face of root shows one or two foramina in basal groove, no other lingual foramina present, labial side with numerous scattered foramina.

Lower jaw (most common: 11 rows): usually no (para-)symphyseal tooth, no intermediate tooth, erected first lateral tooth, all following teeth less erect, strongly bent distally teeth in more posterior positions; weakly convex curved mesial cutting edge, labial face of crown slightly, lingual face strongly convex; low and small distal heel present, blunt cus-

plet-like hump can be present in posterior teeth only; mesial with blade-like lobate extension; lingual face of root shows one or two foramina in basal groove, no other lingual foramina present, labial side with numerous scattered foramina.

### ***Alopias vulpinus* (Bonnaterre, 1788) (Fig. 3A)**

Synonymy: *Vulpecula marina* Garman, 1913; *Squalus vulpes* Gmelin, 1789; *Squalus vulpes* Berkenhout, 1789 [described independent from *Squalus vulpes* Gmelin, 1789, earliest publication not established, FRICKE et al. 2019]; *Alopias macrourus* Rafinesque, 1810; *Galeus vulpecula* Rafinesque, 1810; *Squalus alopecias* Gronow, 1854; *Alopecias barrae* Perez Canto, 1886; *Alopecias chilensis* Philippi, 1902; *Alopecias longimana* Philippi, 1902; *Vulpecula marina* Garman, 1913; *Alopias caudatus* Phillipps, 1932; *Alopias greyi* Whitley, 1937.

Distribution: Oceanic and coastal, virtually circumglobal in tropical and temperate seas (EBERT & STEHMANN 2013).

Size: TL (max): 5750 mm, TL (born): 1200-1500 mm (EBERT et al. 2013).

Dental formula (most common/rage): 0-2-1-20/1-18; (0-2)-(2)-(1-2)-(16-22)/(0-2?)-(16-25) (SHIMADA 2002).

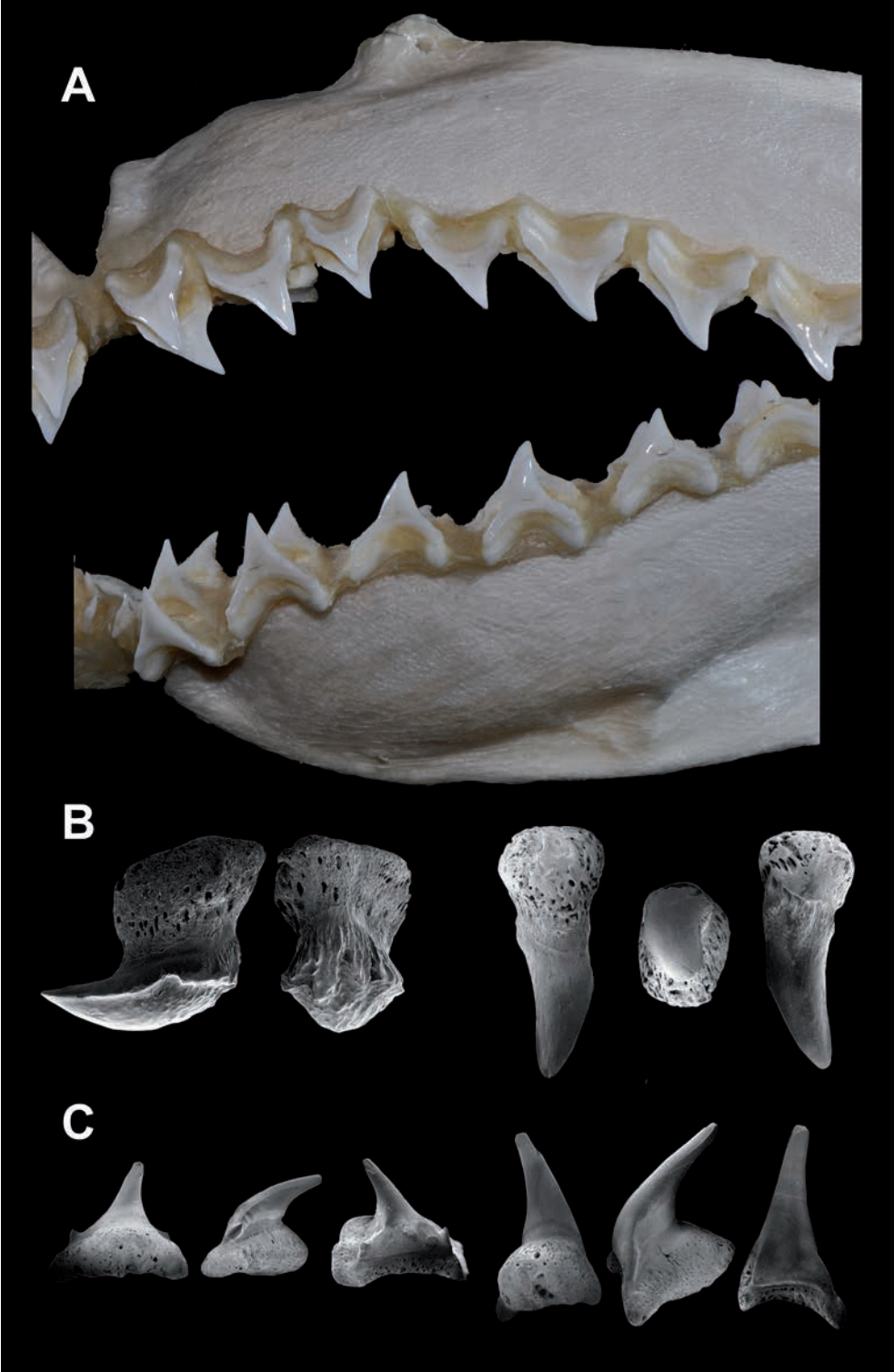
Crown height (A1 in mm/TL): 2.3 mm/1520 mm TL; 7.7 mm/3980 mm TL (SHIMADA 1999).

Material: DAY 1880-1884 (n=1); MOREAU (1881) (n=1); DAY (1889) (n=1); JORDAN & FOWLER (1903) (n=1); GARMAN (1913) (n=1); RAY 1928 (n=1); WHITLEY (1940) (n=2); FOW-

**Fig. 3: A** *Alopias vulpinus* (Bonnaterre, 1788): male, 396 cm TL, Cornwall, UK, coll. 03.06.1993, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Cetorhinus maximus* (Gunnerus, 1765): left: male, juvenile, 320 cm TL, Port Arcachon, France, right: female, adult, 800 cm TL, off Concarneau, France, images by JACQUES HERMAN, Belgium. **C** *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983: male, 489 cm TL, Santa Catalina Island, Mexico, images by JACQUES HERMAN, Belgium.

**Abb. 3: A** *Alopias vulpinus* (Bonnaterre, 1788): männliches Exemplar, 396 cm Gesamtlänge, Cornwall, Vereinigtes Königreich, coll. 03.06.1993, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Cetorhinus maximus* (Gunnerus, 1765): links: juveniles, männliches Exemplar, 320 cm Gesamtlänge, Port Arcachon, Frankreich, rechts: erwachsenes, weibliches Exemplar, 800 cm Gesamtlänge, vor Concarneau, Frankreich, Fotos von JACQUES HERMAN, Belgien. **C** *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983: männliches Exemplar, 489 cm Gesamtlänge, Santa Catalina Island, Mexico, Fotos von JACQUES HERMAN, Belgien.





LER (1941) (n>1); DARTEVELLE & CASIER (1943) (n=1); BAUGHMAN & SPRINGER (1950) (n>1); TORTONESE (1956) (n>1); BEAUMONT (1959) (n>1); CHEN (1963) (n>1); STEAD (1963) (n=1); GOHAR & MAZHAR (1964) (n=1); KATO et al. (1967) (n>1); MISRA (1969) (n=1); BLACHE et al. (1970) (n>1); MUNDUS & WISNER (1971) (n>1); GUBANOV (1972) (n=22); FITCH (1974) (n>1); BASS et al. (1975) (n=1); CADENAT & BLACHE (1981) (n>1); CASTRO (1983) (n>1); QUERO (1984) (n>1); GOMON et al. (1994) (n>1); LAST & STEVENS (1994) (n>1); COMPAGNO et al. (1995) (n>1); SHIMADA (1999) (n=55); COMPAGNO (2001) (n>1); GADIG (2001) (n>1); HERMAN et al. (2004) (n=23); GOMES et al. (2010) (n>1); ERGÜDEN et al. (2015) (n=1); DUFFY & STEWART (2015) (n>1).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2bd/CITES annex: II (04.10.2017) (GOLDMAN et al. 2009).

Description (after HERMAN et al. 2004, SHIMADA 1999, 2002; BASS et al. 1975): Gradient monognathic heterodonty present; disjunct monognathic heterodonty weakly present (only upper jaw); sexual dimorphism and ontogenetic heterodonty absent; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; no serration, no ornamentation, no pairs of cusplets.

Upper jaw (most common: 23 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; upper teeth slightly larger than lower teeth, triangular and nearly erect cusp of the first three anterior teeth, all subsequent teeth show increasing inclination of cusps distally; weakly convex curved mesial cutting edge, slightly labial face of the crown, strongly convex lingual face of the crown; mesial/distal heel absent; lingual face of root shows one or two foramina in basal groove, no other lingual foramina present, labial side with numerous scattered foramina.

Lower jaw (most common: 19 rows): usually single (para-)symphyseal tooth, no intermediate tooth, very small parasymphyseal tooth with erected cusp and thick root; erected first three lateral teeth, all following teeth are weakly bent distally, all subsequent teeth show an increasing

inclination of cusps distally; straight to weakly convex curved mesial cutting edge, the labial face of crown slightly, lingual face strongly convex; mesial/distal heel absent; lingual face of root shows one or two foramina in basal groove, no other lingual foramina present, labial side with numerous scattered foramina.

Family Cetorhinidae Gill, 1861

Genus *Cetorhinus* Blainville, 1816

Type species: *Squalus gunnerianus* Blainville, 1810

### ***Cetorhinus maximus* (Gunnerus, 1765) (Fig. 3B)**

Synonymy: *Tetroras angiova* Rafinesque, 1810; *Squalus gunnerianus* Blainville, 1810; *Squalus homianus* Blainville, 1810; *Squalus pelegrinus* Blainville, 1810; *Squalus peregrinus* Blainville, 1810; *Squalus (Cetorhinus) gunneri* Blainville, 1816; *Squalus (Cetorhinus) sbavianus* Blainville, 1816; *Halsydrus pontoppidani* Fleming, 1817; *Squalus isodus* Macri, 1819; *Squalus rostratus* Macri, 1819; *Squalus elephas* Lesueur, 1822; *Squalus rasbleighanus* Couch, 1838; *Squalus rhinoceros* Mitchell in DeKay, 1842; *Squalus cetaceus* Gronow, 1854; *Polyprosopus macer* Couch, 1862; *Cetorhinus blainvillei* Brito Capello, 1869; *Selachus pennantii* Cornish, 1885; *Tetroras maccoyi* Barrett, 1933; *Cetorhinus maximus infanuncula* van Deinste & Adriani, 1953; *Cetorhinus normani* Siccardi 1961.

Distribution: Circumglobal in temperate and boreal oceans (EBERT & STEHMANN 2013).

Size: TL (max): > 10000 mm, TL (born): 1500-1700 mm (EBERT et al. 2013).

Dental formula (most common/rage): ?; (?100-131)/(?100-139) (SHIMADA 2002).

Crown height (A1 in mm/TL): 1.6 mm/4110 mm TL; 6.4 mm/6410 mm TL (SHIMADA 1999).

Material: GOODE & BEAN (1895) (n=1); JORDAN & EVERMANN (1896) (n=1); STARKS (1917) (n=1); PHILLIPPS (1924) (n=1); FANG & WANG (1932) (n=1); BIGELOW & SCHROEDER (1948) (n=2); GUDGER (1948) (n=1); TORTONESE (1956) (n=1); TENG (1958) (n=1); SICCARDI (1961) (n=1); CHEN (1963) (n=1); SADOWSKY (1973) (n=1); SPRINGER & GILBERT (1976) (n=1); COMPAGNO (1982) (n=1); CASTRO (1983) (n=1); ESCHMEYER & HERALD

(1983) (n=1); BOSCH (1984) (n=1); KUNZLIK (1988) (n=1); TOMAS & GOMES (1989) (n=1); COMPAGNO (1990) (n=1); LAST & STEVENS (1994) (n=1); SHIMADA (1999) (n=4); HERMAN et al. (2004) (n=6); WELTON (2013) (n=4); DUFFY (2015) (n>1).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2ad+3d/CITES annex: II (13.02.2003, previously annex III since 13.09.2000) (FOWLER 2009).

Description (after HERMAN et al. 1993, WELTON 2013): Gradient monognathic heterodonty present; disjunct monognathic heterodonty absent; sexual dimorphism not observed, strongly ontogenetic heterodonty in both sexes present; anaulacorhizid root vascularizations stage present; root monolobed; lingual basal groove absent; no serration, strongly labial ornamentation only in juveniles, weakly in adult specimen, no pairs of cusplets, no morphological difference between upper and lower jaw teeth.

Upper/lower jaw (most common: >100 rows): usually no (para-)symphyseal tooth, no anterior teeth, no intermediate tooth; teeth very small, maximum tooth size <10 mm, crown height usually equals root height, hook like erected to strongly lingually declined crown, labial and lingual face of crown strongly convex, mesial and distal cutting edges present, in adults, cutting edges elongated reaching to almost half of crown, in juveniles near crown base; strongly labial ornamentation of crown in juveniles; in adult vertical enameloid folds originate at the crown basis and never reach the apex of the crown, no cusplets, monolobed, massive root, nearly circular in mesial view; numerous small foramina labially, lingually and basally.

Family Lamnidae Bonaparte, 1835

Genus *Carcharodon* Smith in Müller & Henle, 1838

Type species: *Squalus carcharias* Linnaeus, 1758

### ***Carcharodon carcharias* (Linnaeus, 1758) (Fig. 4)**

Synonymy: *Carcharias lamia* Rafinesque, 1810; *Carcharias verus* Cloquet, 1817; *Squalus (Carcharias) vulgaris* Richardson, 1836; *Carcharodon smithii*

Müller & Henle in Agassiz, 1838; *Carcharodon capensis* Smith, 1839; *Carcharodon rondeletii* Müller & Henle, 1839; *Carcharias atwoodi* Storer, 1848; *Carcharias vorax* Owen, 1853; *Carcharias maso* Morris, 1898; *Carcharodon albimors* Whitley, 1939.

Distribution: Cosmopolitan range throughout most seas and oceans with concentrations in temperate coastal seas (EBERT et al. 2013).

Size: TL (max): 6000 mm, TL (born): 1100-1600 mm (EBERT et al. 2013).

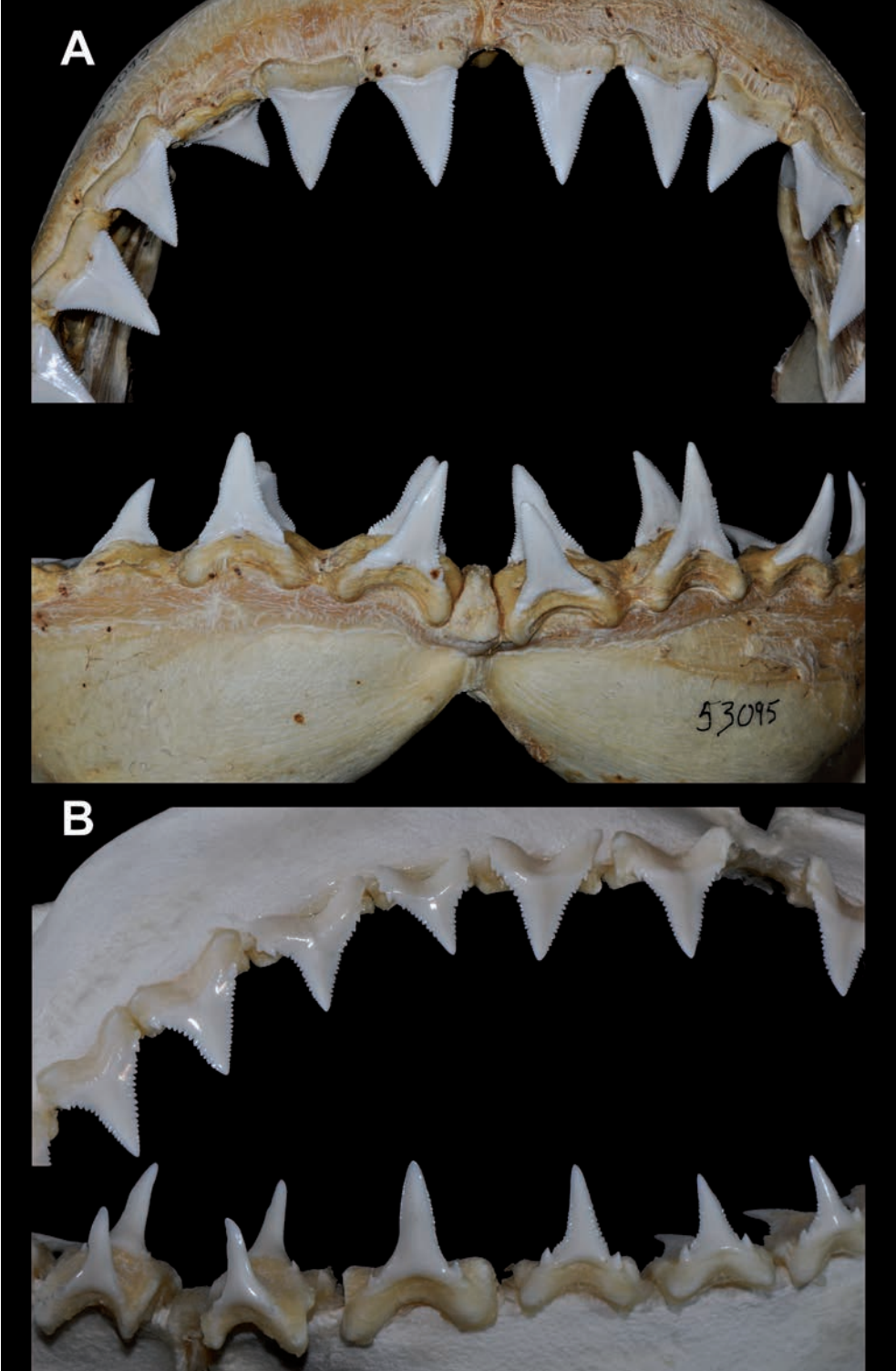
Dental formula (most common/range): 0-2-1-10/0-11; (0)-(2)-(1)-(8?-11)/(0)-(11-14) (SHIMADA 2002).

Crown height (A1 in mm/TL): 11.4 mm/1350 mm TL; 48.9 mm/5630 mm TL (SHIMADA 1999).

Material: GÜNTHER (1870) (n=1); LAWLEY (1881) (n=1); FACCIOLA (1894) (n=1); JORDAN & EVERMANN (1896) (n=1); GARMAN (1913) (n=1); BARNARD (1925) (n=1); RAY (1928) (n=1); FOWLER (1936) (n=1); SPRINGER (1939) (n=1); BIGELOW & SCHROEDER (1948) (n=2); SMITH (1949) (n=?); BAUGHMAN & SPRINGER (1950) (n=1); SMITH (1951) (n=1); COPLEY (1952) (n=1); FOWLER (1956) (n>1); TORTONESE (1956) (n=1); TENG (1958) (n=1); CADENAT (1962) (n=1); CHEN (1963) (n=1); STEAD (1963) (n=1); TEMPLEMAN (1963) (n=1); KATO (1965) (n=1); FOLLETT (1966) (n>1); LINEWEAVER & BACKUS (1970) (n=1); MUNDUS & WISNER (1971) (n>1); RANDALL (1973) (n=1); BASS et al. (1975) (n>32); UYENO & MATSUSHIMA (1979) (n=2); SICCARDI et al. (1981) (n=3); ELST (1981) (n>1); CASTRO (1983) (n>1); GOTO et al. (1984) (n=1); BASS (1986) (n=1); ELLIS & McCOSKER (1991) (n=1); GOMON et al. (1994) (n>1); LAST & STEVENS (1994) (n>1); YABE 1995 (n=1); APPLGATE & ESPINOSA-ARRUBARRENA (1996) (n=1); FERGUSON (1996) (n=1); FRANCIS (1996) (n=3); GADIG & ROSA (1996) (n=1); HUBBELL (1996) (n=4); UCHIDA et al. (1996) (n=1); SHIMADA (1999) (n=44), MADDALENA (2006) (n=101).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2cd+3cd/CITES annex: II (12.01.2005), (FERGUSON et al. 2009).

Description: (after CAPPETTA 2012; BASS et al. 1975): Gradient monognathic and weakly



disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty present (Fig. 4B); holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove absent; cutting edge with serration, no labial/lingual ornamentation, no pairs of cusplets (in adults, Fig. 4A).

Upper jaw (most common: 13 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; upper teeth clearly broader and slightly larger than lower teeth, triangular, symmetrical and nearly erected cusps of the first two anterior teeth, all following teeth triangular, weakly bent distally; straight and strongly irregular serrated mesial and distal cutting edges; flat labial face of crown, slightly convex lingual face; mesial/distal heel absent; cusplets absent (in adults), juvenile specimens may show smooth-edged, lanceolate main cusps with pairs of denticles; low root with weakly developed flat root lobes, lingual face of root shows a single central foramen, basal groove absent, labial side with numerous scattered foramina.

Lower jaw (most common: 11 rows): usually no (para-)symphyseal, no intermediate tooth; triangular and nearly erected and symmetrical cusps; lower teeth differ from upper teeth in presence of slender cusps; straight and strongly irregular serrated mesial and distal cutting edges, flat labial face of the crown, slightly convex lingual face; mesial/distal heel absent; cusplets absent (in adults), juvenile specimens may have smooth-edged, lanceolate main cusps with pairs of denticles, root higher compared to upper teeth; well developed root lobes, length of lobes decreases towards commissure; lingual face of root shows a

single central foramen, basal groove absent, labial side with numerous scattered foramina.

Genus *Isurus* Rafinesque, 1810

Type species: *Isurus oxyrinchus* Rafinesque, 1810

***Isurus oxyrinchus* Rafinesque, 1810 (Fig. 5A, 6A)**

Synonymy: *Isurus spallanzanii* Rafinesque, 1810; *Squalus (Lamna) cepedii* Lesson, 1831; *Lamna oxyrhina* Cuvier & Valenciennes in Agassiz, 1835; *Oxyrhina gomphodon* Müller & Henle, 1839; *Oxyrhina glauca* Müller & Henle, 1839; *Lamna latro* Owen, 1853; *Isuropsis dekaayi* Gill, 1862; *Carcharias tigris* Atwood, 1869; *Lamna guentheri* Murray, 1884; *Lamna huidobrii* Philippi, 1887; *Isurus mako* Whitley, 1929; *Isurus bideni* Phillipps, 1932; *Isurus tigris africanus* Smith, 1957.

Distribution: Cosmopolitan range throughout tropical and warm-temperate seas but seldom occurring in waters below 16 °C (EBERT & STEHMANN 2013).

Size: TL (max): 5000 mm, TL (born): 600-700 mm (EBERT et al. 2013, LOPEZ-MIRONES et al. 2020).

Dental formula (most common/range): 0-2-1-10/0-2-11; (0)-(2)-(0?-1)-(8?-11)/(0)-(10-14) (SHIMADA 2002).

Crown height (A1 in mm/TL): 7.7 mm/760 mm TL; 33.0 mm/3510 mm TL (SHIMADA 1999).

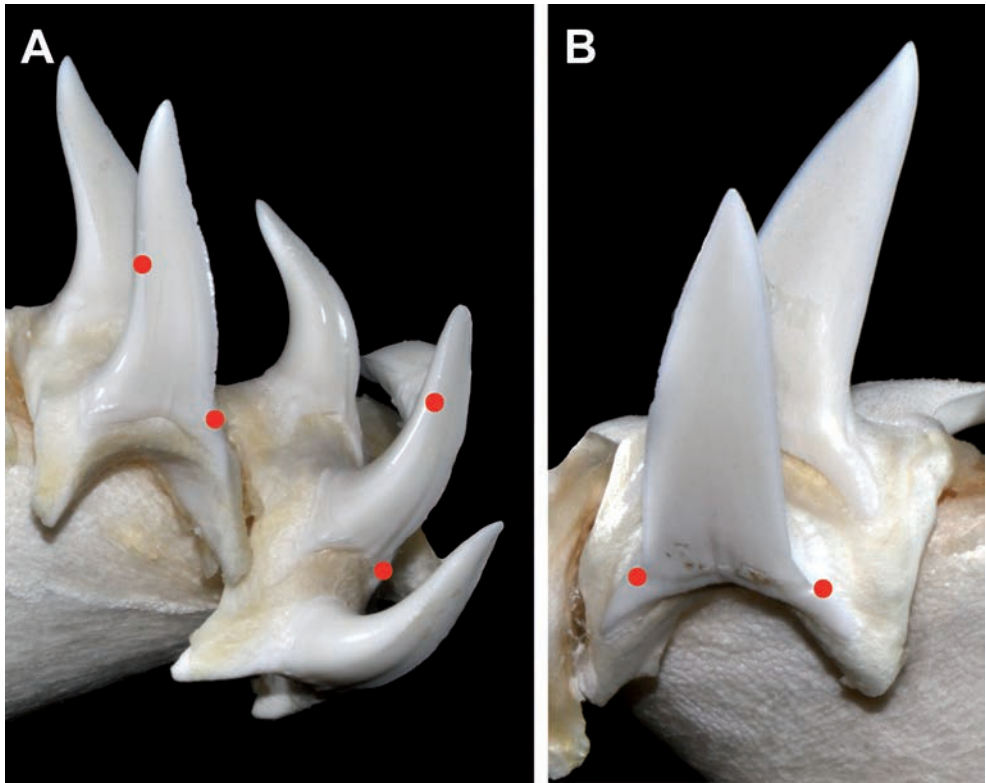
Material: GÜNTHER (1870) (n=1); LAWLEY (1881) (n=1); MOREAU (1881) (n=1); MURRAY (1884) (n=1); DAY (1889) (n=1); JORDAN & EVERMANN (1896) (n=1); GARMAN (1913) (n=?); PHILLIPPS (1926) (n>1), RAY (1928)

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**Fig. 4:** *Carcharodon carcharias* (Linnaeus, 1758): **A** sex unknown, TL unknown, off Hobart, Australia, coll. 06/1982, coll. by fishermen and P. LEWIS, American Museum of Natural History (AMNH) collection nr. I-53095, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** Male, juvenile, 157 cm TL, off Ventura, California, coll. 06/1996, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 4:** *Carcharodon carcharias* (Linnaeus, 1758): **A** Geschlecht und Gesamtlänge unbekannt, vor Hobart, Australien, coll. 06/1982, gesammelt von einem Fischer und P. LEWIS, American Museum of Natural History (AMNH), Sammlungs-Nr. I-53095, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** Juveniles, männliches Exemplar, 157 cm Gesamtlänge, vor Ventura, Kalifornien, coll. 06/1996, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

(n=1); WHITLEY (1934) (n=2); WHITLEY (1940) (n=1); DARTEVELLE & CASIER (1943) (n=1); BIGELOW & SCHROEDER (1948) (n>1); BAUGHMAN & SPRINGER (1950) (n>1); DEPPERMAN (1953) (n=1); SMITH (1953) (n=1); FOWLER (1956) (n>1); SMITH (1957) (n>1); TORTONESE (1956) (n>1); FOURMANOIR (1961) (n=1); CADENAT (1962) (n=1); STEAD (1963) (n=?); TIBBO et al. (1963) (n=1); TOMINAGA (1963a, b) (n>1); D'AUBREY (1964a) (n=1); GOHAR & MAZHAR (1964) (n=1); APPLGATE (1966) (n=1); GARRICK (1967) (n=65); LINDBERG & LEGEZA (1967) (n=1); MISRA (1969) (n=1); ANTUNES & JONET (1970) (n=1); GOTO (1970) (n=1); LINEWEAVER & BACKUS (1970) (n=1); GUBANOV (1974) (n=1); BASS et al. (1975) (n=15); GLICKMAN (1980) (n=1); JONES & KUMARAN (1980) (n>1); SICCARDI et al. (1981) (n=3); CASTRO (1983) (n>1); RANDALL (1986) (n>1); ESPINOSA-ARRUBARRENA (1987) (n=2); MORENO & MORON (1992) (n=103); FRANCIS & RANDALL (1993) (n=1); GOMON et al. (1994) (n>1); LAST & STEVENS (1994) (n>1); SHIMADA (1999) (n=84); COMPAGNO (2001) (n>1); CELONA et al. (2004) (n=2); IUCN Red List Category and Criteria/CITES status: Endangered A2bd/CITES annex: II (28.09.2019) (RIGBY et al. 2019a).



**Fig. 5:** Lower anterior teeth of **A** *Isurus oxyrinchus* Rafinesque, 1810, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Isurus paucus* Guitart Manday, 1966, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama; the red dots shows the ends of the cutting edges.  
**Abb. 5:** Unterer anteriorer Zahn von **A** *Isurus oxyrinchus* Rafinesque 1810, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Isurus paucus* Guitart Manday, 1966, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama; die roten Punkte bezeichnen das Ende der Schneidekanten.

Description (after BIGELOW & SCHROEDER 1948; GARRICK 1967; COMPAGNO 2001)

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty present; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove absent; cutting edge smooth, no labial/lingual ornamentation, no pairs of cusplets.

Upper jaw (most common: 13 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; upper teeth and lower teeth of same row about same width and height, first two teeth are much larger than sequential teeth, cusps of the first two anterior teeth slender with labially curved crown apex; intermediate tooth usually positioned below upper two-thirds of lateral margin of palatine process (GARRICK 1967); triangular, weakly bent distally sequential teeth; straight and smooth mesial and distal cutting edges, first two anterior teeth with incomplete cutting edges on lateral margin (excepting largest adults), flat labial face of crown, strongly convex lingual face of crown; mesial/distal heel absent; cusplets absent, root low with strongly developed root lobes in anterior and intermediate teeth; weakly developed in lateral teeth; lingual face of root shows a single central foramen, basal groove absent, labial side without scattered foramina.

Lower jaw (most common: 13 rows): usually no (para-)symphyseal, no intermediate tooth; first two anterior teeth larger than sequential teeth, slender, labially curved crown apex of cusps of first two anterior teeth, all sequential teeth triangular, the third one bent distally, sequential teeth erected; straight and smooth mesial and distal cutting edges, first two anterior teeth with incomplete cutting edges on lateral margin (excepting largest adults), flat labial face of crown, strongly convex lingual face of crown; mesial/distal heel absent; cusplets absent, root low with strongly developed root lobes in anterior teeth, weakly developed in lateral teeth, lingual face of root shows a single central foramen, basal groove absent, labial side without scattered foramina.

***Isurus paucus* Guitart Manday, 1966 (Fig. 5B, 6B)**

Synonymy: *Isurus alatus* Garrick, 1967.

Distribution: Widespread in tropical and warm temperate waters, and likely occurring globally, although its distribution is poorly recorded (EBERT et al. 2013).

Size: TL (max): 4300 mm, TL (born): 920-970 mm (EBERT et al. 2013).

Dental formula (most common/range): 0-2-1-10/0-2-10; (0)-(2)-(1)-(7-11)/(0)-(11-13) (SHIMADA 2002).

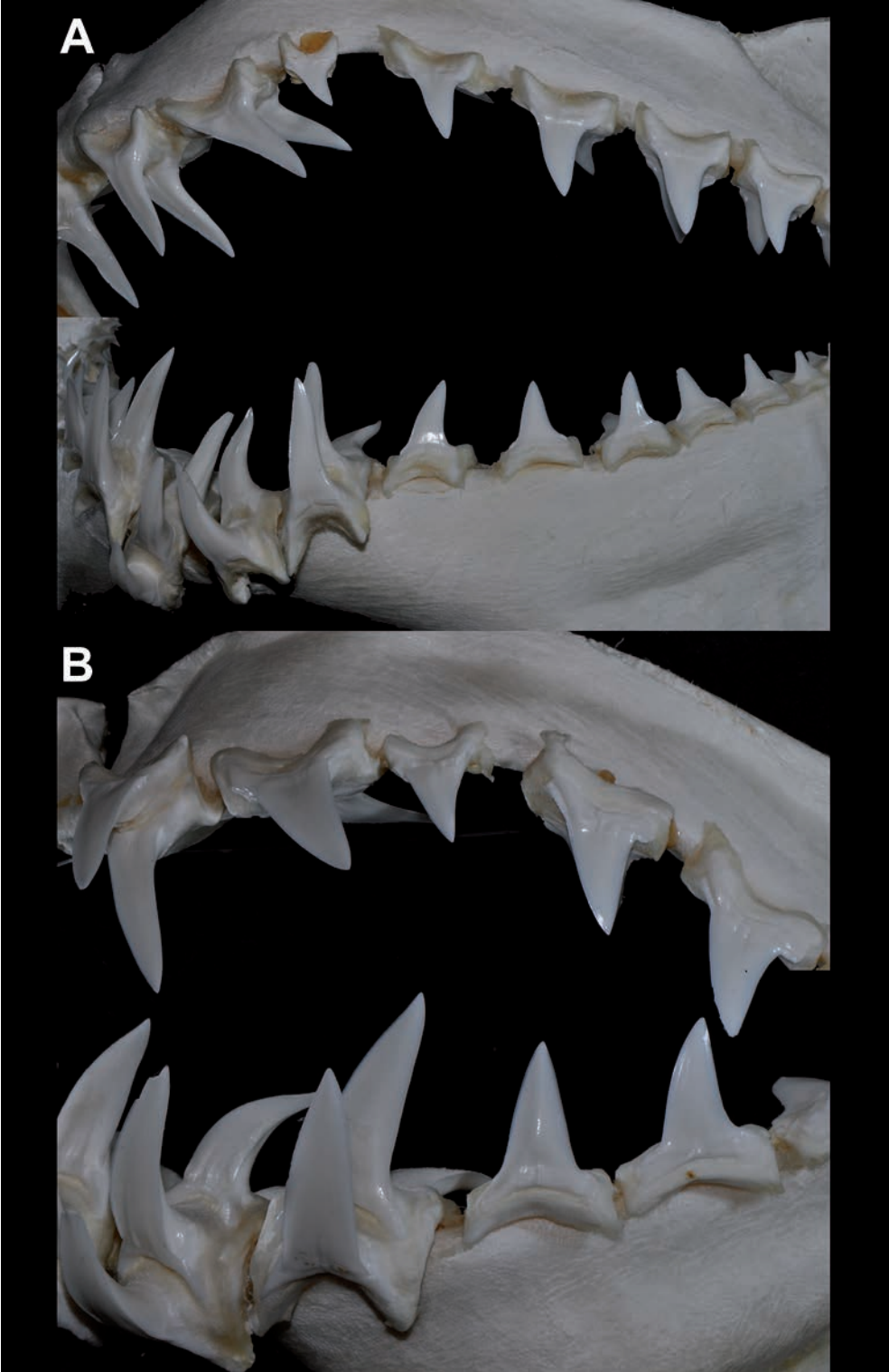
Crown height (A1 in mm/TL): 24.9 mm/1980 mm TL; 36.5 mm/4270 mm TL (SHIMADA 1999).

Material: GUITART-MANDAY (1966) (n=3); GARRICK (1967) (n=4); DODRILL & GILMORE (1979) (n=1); CASTRO (1983) (n>1); ESPINOSA-ARRUBARENA (1987) (n=1); MORENO & MORON (1992) (n=9); SHIMADA (1999) (n=23); COMPAGNO (2001) (n>1); CELONA et al. (2004) (n=2); EBERT (2001) (n=1); HEMIDA & CAPAPÉ (2008) (n=2); IUCN Red List Category and Criteria/CITES status: Endangered A2d/CITES annex: II (28.09.2019) (RIGBY et al. 2019b).

Description (after GARRICK 1967; COMPAGNO 2001):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty present; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove absent; cutting edge smooth, no labial/lingual ornamentation, no pairs of cusplets.

Upper jaw (most common: 13 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; upper and lower teeth of same rows about same width and height, first two teeth are larger than others, first two anterior teeth with robust cusps, noticeably broader, less flexuous, and less oblique compared to *I. oxyrinchus* teeth; intermediate tooth below lateral margin of palatine process of the palatopterygoquadrate cartilage (GARRICK 1967); triangular, weakly bent distally sequential teeth; straight and smooth mesial and distal cutting edges, cutting edges of all teeth extend from apex to base of crown, labial face of the crown flat, lingual face of





crown strongly convex; mesial/distal heel absent; cusplets absent; low root with strongly developed root lobes in anterior and intermediate teeth and weakly developed in lateral teeth, lingual face of root shows a single central foramen, basal groove absent, labial side without scattered foramina.

Lower jaw (most common: 12 rows): usually no (para-)symphyseal tooth, 2 anterior teeth; upper and lower teeth of the same row about same width and height, first two teeth larger than sequential teeth, first 2 anterior teeth with robust cusps, noticeably broader, less flexuous, and less oblique compared to those of *I. oxyrinchus*; erected sequential teeth; straight and smooth mesial and distal cutting edges, all teeth with cutting edges extending from apex to base of crown, flat labial face of crown, strongly convex lingual face of crown; mesial/distal heel absent; cusplets absent, low root with strongly developed root lobes in anterior and intermediate teeth and weakly developed in lateral teeth; lingual face of root shows a single central foramen, basal groove absent, labial side without scattered foramina.

Genus *Lamna* Cuvier, 1816

Type species: *Squalus cornubicus* Gmelin, 1789

### ***Lamna ditropis* Hubbs & Follett, 1947 (Fig. 7A)**

Synonymy: None.

Distribution: North and central Pacific Ocean, ranging between 30°N-65°N (COMPAGNO 2001).

Size: TL (max): 3050 mm, TL (born): 650-800 mm (EBERT et al. 2013).

Dental formula (most common/range): 0-2-1-10/0-2-12; (0)-(2)-(1)-(9-13?)/(0)-(13-15) (SHIMADA 2002).

Crown height (A1 in mm/TL): 8.4 mm/920 mm TL; 12.3 mm/2140 mm TL (SHIMADA 1999).

Material: JORDAN & FOWLER (1903) (n>1); SANO (1960) (n=1); TOMINAGA (1963a, b) (n=1); OKADA & KOBAYASHI (1968) (n=5); NAKAYA (1971) (n=4); ABE et al. (1979) (n=1); CASTRO (1983) (n>1); KAKIZAWA (1984) (n=3); PAUST & SMITH (1986) (n=?); GLICKMAN (1988) (n=1); HOWORTH (1991) (n=1); SHIMADA (1999) (n=23).

IUCN Red List Category and Criteria/CITES status: Least Concern/no CITES listing (GOLDMAN et al. 2009).

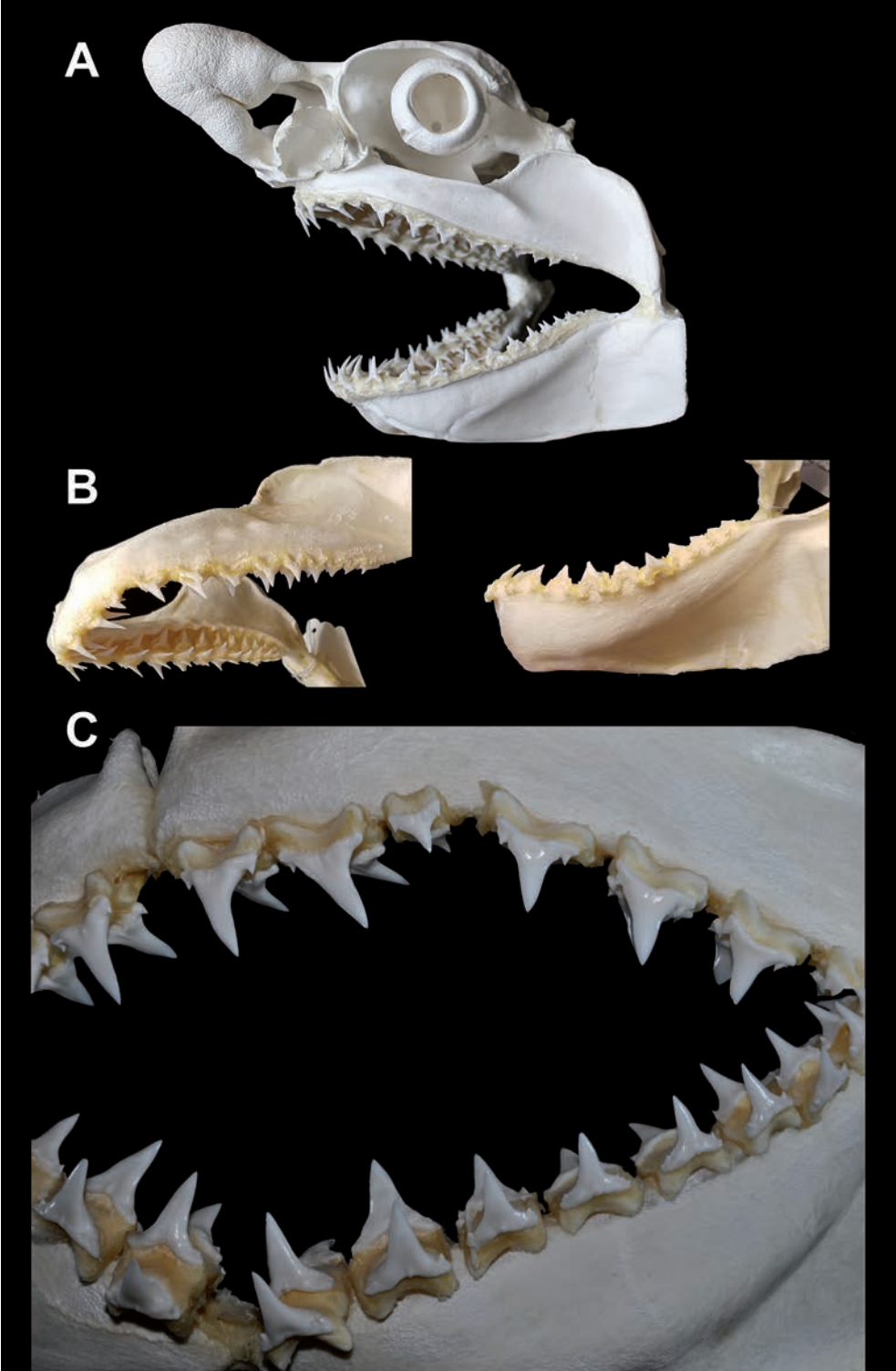
Description (after NAKAYA 1971):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty possible present (in *Lamna nasus*: teeth of embryos or juvenile specimens often without cusplets); holaulacorhizid root vascularizations stage present; root bilobed; lingual basal groove absent; cutting edge smooth, no labial/lingual ornamentation, usually one pair of cusplets.

Upper jaw (most common: 13 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; the first 2 teeth larger than sequential teeth, slender and erected cusps of the first 2 anterior teeth; triangular and erected intermediate tooth, strongly bent distally 4th tooth, sequential two teeth weakly bent distally, all other teeth erected; straight and smooth mesial and distal cutting edges, all cutting edges extend from apex to base of crowns, labial face of crown flat or weakly convex, lingual face of crown strongly convex; mesial/distal heel absent; low, broad and usually one pair of triangular cusplets present, in some teeth a third and/or a fourth weakly developed cusplet present, bilobed root, usually one, sometimes a

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**Fig. 6: A** *Isurus oxyrinchus* Rafinesque, 1810: sex unknown, 252 cm TL, coll. 12.11.1993, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Isurus paucus* Guitart Manday, 1966: sex unknown, 252 cm TL, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **Abb. 6: A** *Isurus oxyrinchus* Rafinesque, 1810: Geschlecht unbekannt, 252 cm Gesamtlänge, coll. 12.11.1993, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Isurus paucus* Guitart Manday, 1966: Geschlecht unbekannt, 252 cm Gesamtlänge, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.



second, central foramen on lingual face of root, basal groove absent.

Lower jaw (most common: 14 rows): usually no (para-)symphyseal, no intermediate tooth; the first two anterior teeth larger than sequential teeth, slender, erected, symmetrical and triangular cusps of the first 2 anterior teeth, all sequential teeth broader, erected, and triangular; straight and smooth mesial and distal cutting edges, all cutting edges extend from apex to base of crown, labial face of crown flat, lingual face of crown strongly convex; mesial/distal heel absent; low, broad and usually a single pair of triangular cusplets present, in some teeth a third and/or a fourth weakly developed cusplet present; root of the first anterior teeth root deeply arched and bilobed, root lobes of lateral teeth forming wide angles, usually one, sometimes a second, central foramen on lingual face of root, basal groove absent.

### ***Lamna nasus* (Bonnaterre, 1788) (Fig. 7B, C)**

Synonymy: *Squalus glaucus* Linnaeus, 1758; *Squalus cornubicus* Gmelin, 1789; *Squalus pennanti* Walbaum, 1792; *Squalus cambricus* Turton, 1800; *Squalus monensis* Shaw, 1804; *Squalus cornubiensis* Pennant, 1812; *Squalus selanonus* Leach, 1818; *Selanonius walkeri* Fleming, 1828; *Lamna punctata* Storer, 1839; *Oxyrhina daekayi* Gill, 1862; *Isuropsis dekeyi* Gill, 1862; *Lamna philippi* Perez Canto, 1886; *Lamna whitleyi* Phillips, 1935.

Distribution: Wide-ranging coastal and oceanic species found in temperate and cold-temperate waters worldwide (below 18°C) (EBERT & STEHMANN 2013).

Size: TL (max): 3550 mm, TL (born): 600-800 mm (EBERT et al. 2013).

Dental formula (most common/range): 0-2-1-11/0-2-11; (0)-(2)-(0-1)-(10-13?)/(0)-(11-16) (SHIMADA 2002).

Crown height (A1 in mm/TL): 7.8 mm/1040 mm TL; 14.8 mm/2440 mm TL (SHIMADA 1999).

Material: GÜNTHER (1870) (n>1); HAAST (1875) (n=1); DAY (1880-1884) (n>1); FRIES et al. (1895) (n>1); JORDAN & EVERMANN (1896) (n>1); LERICHE (1905) (n=1); GARMAN (1913) (n=1); PHILLIPPS (1924) (n=1); LAHILLE (1928) (n=1); RAY (1928) (n>2); GRIMPE (1929) (n>1); NOBRE (1935) (n>1); FOWLER (1936) (n=1); LUBBERT & EHRENBaum (1936) (n>1); DARTEVELLE & CASIER (1943) (n=1); BIGELOW & SCHROEDER (1948) (n>1); SMITH (1949) (n>1); GRAHAM (1953) (n=1); TORTONESE (1956) (n>1); TIBBO et al. (1963) (n>1); TEMPLEMAN (1963) (n=1); NAKAYA (1971) (n=1); SVETLOV (1978) (n=1); MENNI & GASZTONYI (1977) (n=1); CADENAT & BLACHE (1981) (n>1); STEVENS et al. (1983) (n=3); CASTRO (1983) (n>1); STEEL (1985) (n=1); ARQUEZ et al. (1986) (n=1); SCOTT & SCOTT (1988) (n>1); WELTON & FARISH (1993) (n=1); LAST & STEVENS (1994) (n>1); LUCIFORA & MENNI (1998) (n=1); SHIMADA (1999) (n=62); SHIMADA (2002) (n=1); CHAVEZ et al. (2012) (n=19);

IUCN Red List Category and Criteria/CITES status: Vulnerable A2bd+3d+4bd/CITES annex: II (14.09.2014, previously annex III since 13.09.2000) (STEVENS et al. 2006).

Description (after NAKAYA 1971, PURDY & FRANCIS 2007):

**Fig. 7: A** *Lamna ditropis* Hubbs & Follett, 1947: skull, female, 200 cm TL, off Japan, collection number SEC-SKU312, image by SEBASTIEN ÉNAULT, www.kraniata.com. **B** *Lamna nasus* (Bonnaterre, 1788): sex unknown, TL unknown, collection: Zoological Museum Hamburg (ZMH 25880), left side: upper lateral tooth, right side: lower lateral tooth. **C** *Lamna nasus* (Bonnaterre, 1788): female, 243 cm TL, coll. 01.12.1993, North Sea, landed at Aberdeen, Scotland, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 7: A** *Lamna ditropis* Hubbs & Follett, 1947: Schädel, weibliches Exemplar, 200 cm Gesamtlänge, Sammlungsnummer: SEC-SKU312, Foto von SEBASTIEN ÉNAULT, www.kraniata.com. **B** *Lamna nasus* (Bonnaterre, 1788): Geschlecht und Gesamtlänge unbekannt, Sammlung: Zoologisches Museum Hamburg (ZMH 25880), links: oberer lateraler Zahn, rechts: unterer lateraler Zahn. **C** *Lamna nasus* (Bonnaterre, 1788): weibliches Exemplar, 243 cm Gesamtlänge, coll. 01.12.1993, Nordsee, angelandet in Aberdeen, Schottland, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty present (teeth of embryos or juvenile specimens often without cusplets, PURDY & FRANCIS 2007); holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove absent; cutting edge smooth, no labial/lingual ornamentation, usually one (sometimes two) pair of cusplets.

Upper jaw (most common: 14 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; the first 2 teeth larger than sequential teeth, first two anterior teeth with slender and erected cusps; triangular and erected intermediate tooth, the next 2 to 3 teeth weakly bent distally, all sequential teeth erected and symmetrical; straight and smooth mesial and distal cutting edges, all cutting edges extend from apex to base of crowns, labial face of crown flat or weakly convex, lingual face of crown convex; mesial/distal heel absent; usually one pair of triangular, low cusplets present, in some teeth a third and/or a fourth weakly developed cusplet present, bilobed root, root lobes of lateral teeth obtuse to almost straight angles, usually one, sometimes a second, central foramen on lingual face of root, basal groove absent.

Lower jaw (most common: 13 rows): usually no (para-)symphyseal, no intermediate tooth; the first two anterior teeth larger than sequential teeth, of first two anterior teeth with broad, erected, symmetrical and triangular cusps and following lateral teeth; straight and smooth mesial and distal cutting edges, all cutting edges extend from apex to base of crown, labial face of crown flat, lingual face of crown strongly convex; mesial/distal heel absent; usually one pair of broad, triangular, low and outward facing cusplets present, in some teeth additionally a third and/or a fourth weakly developed cusplet present; root of the first anterior teeth deeply arched and bilobed, lobes of lateral teeth forming wide angles, usually one, sometimes a second, central foramen on lingual face of root, basal groove absent.

Family Megachasmidae Taylor, Compagno & Struhsaker, 1983

Genus *Megachasma* Taylor, Compagno & Struhsaker, 1983

Type species: *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983

***Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983 (Fig. 3C)**

Synonymy: None.

Distribution: Wide-ranging in tropical and temperate areas of all major oceans, although its full distribution remains poorly-known (EBERT et al. 2013).

Size: TL (max): >5500 mm, TL (born): <1700 mm (EBERT et al. 2013).

Dental formula (most common/range): 37-56/43?-74 (SHIMADA 2002; TANAKA et al. 2004; WANG et al. 2007).

Crown height: about 7.0-9.0 mm/4710 mm TL (female) (YABUMOTO et al. 1997).

Material: TAYLOR et al. (1983) (n=1); BERRA & HUTCHINS (1990) (n=1); LAVENBERG (1991) (n=1); YABUMOTO et al. (1997) (n=1); WHITE et al. (2004) (n=1); TANAKA et al. (2004) (n=3); WANG et al. (2007) (n=1).

IUCN Red List Category and Criteria/CITES status: Least Concern/no CITES listing (KYNE et al. 2019).

Description (after HERMAN et al. 1993; YABUMOTO et al. 1997):

Weakly dignathic heterodonty present, lower teeth sometimes with cusplets, upper teeth without cusplets (HERMAN et al. 1993); disjunct monognathic heterodonty absent; sexual dimorphism maybe present, number of teeth rows in females is fewer than in males (YABUMOTO et al. 1997: female: 83/97 rows; male (similar size): 108/128 rows); extremely large symphyseal interspace present; holaulacorhizid root vasculariations stage absent; root monolobed; lingual basal groove absent; strong lingual protuberance of the root; cutting edge short, smooth, no labial/lingual ornamentation, sometimes one pair of cusplets (only observed in lower teeth).

Upper jaw: usually no (para-)symphyseal tooth, no anterior teeth, no intermediate tooth; teeth

of upper jaw considerably smaller in the first few rows, in the following rows only slightly smaller; broad based, elongated and strongly lingual inclined cusps, short, straight and smooth mesial and distal cutting edges, all cutting edges extend from apex to about a third/a half of crowns; labial face of crown convex, lingual face of crown strongly convex; mesial/distal heel absent; cusplets absent, monolobed or bilobed root, with only weakly developed lobes, extremely lingual root protuberance present, randomly arranged numerous foramina present at all sides of root, single lingual central foramen present, basal groove absent. Lower jaw: usually no (para-)symphyseal, no intermediate tooth; teeth of lower jaw differs only in size and presence of lateral cusplets without cutting edges in some lower posterior teeth from upper jaw teeth.

Family Mitsukurinidae Jordan, 1898

Genus *Mitsukurina* Jordan, 1898

Type species: *Mitsukurina owstoni* Jordan, 1898

### ***Mitsukurina owstoni* Jordan, 1898 (Fig. 8A-B)**

Synonymy: *Odontaspis nasutus* de Bragança, 1904; *Scapanorhynchus jordani* Hussakof, 1909; *Scapanorhynchus doffeini* Engelhardt, 1912; *Scapanorhynchus mitsukurii* White, 1937.

Distribution: Widespread global distribution across the Atlantic and Indo-Pacific Oceans (EBERT et al. 2013).

Size: TL (max): 5500 mm, TL (born): 800-900 mm (EBERT et al. 2013).

Dental formula (most common/range): 1-2-0-23/1-2-22; (1)-(2)-(0-1)-(19-28?)/(1)-(22-29) (SHIMADA 2002, the parasymphyseal tooth in this dental formula is defined as the first anterior tooth by other authors, see material and methods); 18-25/17-25 (YANO et al. 2007; n=44).

Crown height (A1 in mm/TL): 21.5 mm/3350 mm TL; 10.0 mm/1100 mm TL (SHIMADA 1999).

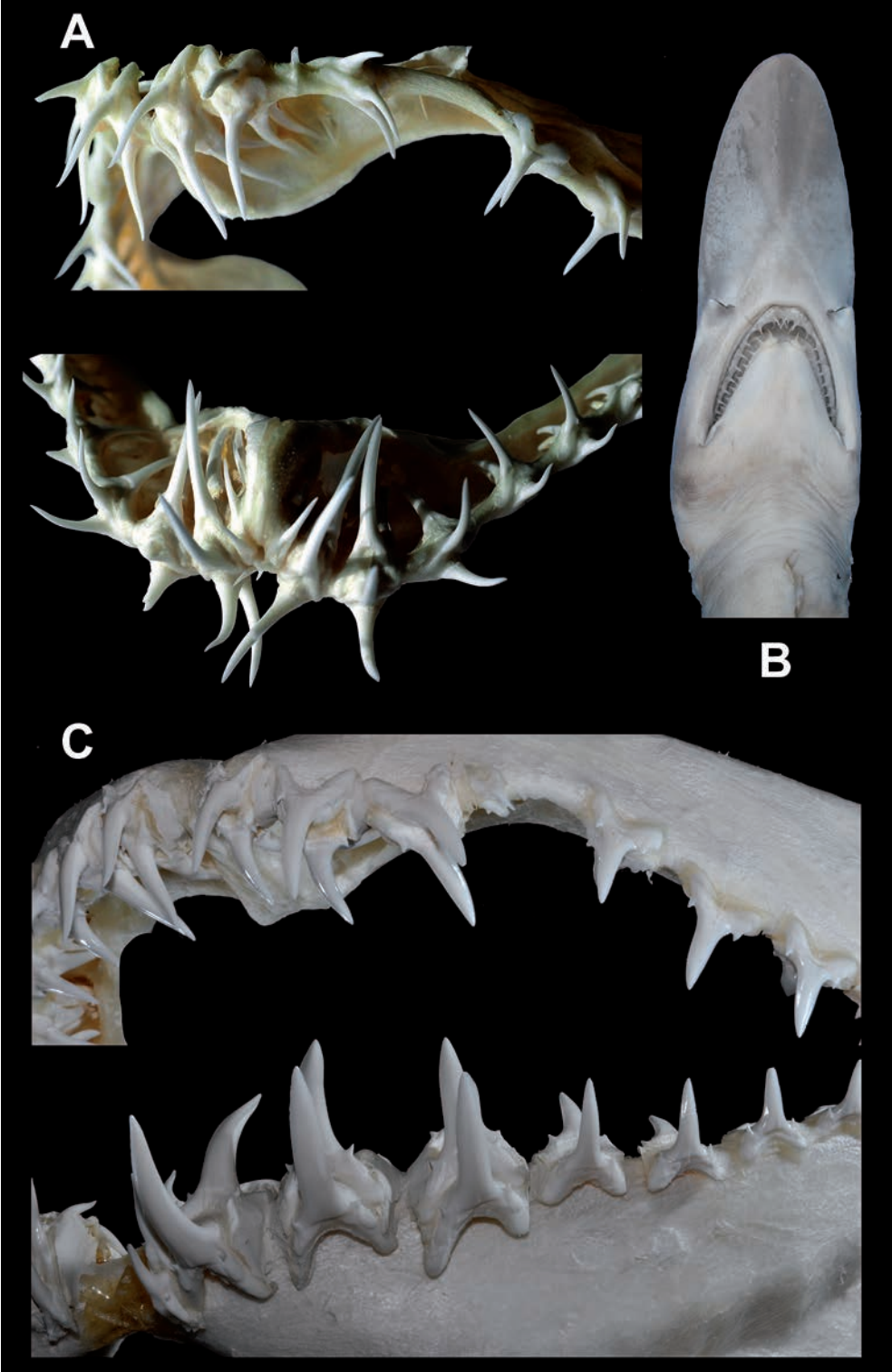
Material: JORDAN (1898) (n=1); GARMAN (1913) (n>1); RAY (1928) (n=1); NOBRE (1935) (n=1); BASS et al. (1975) (n=1); CAPPETTA (1980) (n=2); CADENAT & BLACHE (1981) (n=2); KOBAYASHI et al. (1982) (n=1); COMPAGNO (1982) (n>1); UYENO & SASAKI (1983) (n=1); STEVENS & PAXTON

(1985) (n=2); GOMON et al. (1994) (n>1); SHIMADA (1999) (n=4); YANO et al. (2007) (n=44); RINCON et al. (2012) (n=1); Natural History Museum Vienna, NMW-91241 (n=1); Tokai University Japan, Collection Sho Tanaka (n=1). IUCN Red List Category and Criteria/CITES status: Least Concern/no CITES listing (FINUCCI & DUFFY 2018).

Description (after BASS et al. 1975; CAPPETTA 1980):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty unknown; holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; cutting edge smooth, no labial ornamentation, lingual ornamentation (folds) usually present and well developed, usually no pairs of cusplets, sometimes a single or a pair of minute hook like cusplets.

Upper jaw (most common: 26 rows): usually 1 (para-)symphyseal tooth, 2 anterior teeth, no intermediate tooth; slender, needle like with an sigmoid profile first anterior tooth (labelled as symphyseal tooth in Shimada's dental formula); the following three anterior teeth larger than sequential teeth, cusps of the second and third anterior teeth straight or weakly distally declined; usually missing intermediate tooth, gap between second anterior and first lateral tooth. Sequential teeth broader at bases compared to anterior teeth, weakly bent distally; straight and smooth mesial and distal cutting edges, all teeth with cutting edges extending from apex to base of crowns, labial face of crown flat, lingual face of crown strongly convex with tight, marked folds; folds fairly regular (parallel) at base becoming flexible and more irregular towards apex; in anterior teeth folds extend almost to crown apex, in more laterally teeth not as extended; mesial/distal heel absent; cusplets usually absent, high root shows strongly developed root lobes, single central foramen in centre of strongly developed protuberance on lingual face of root; root lobes similar in length and symmetrical (except for lobes of the second anterior tooth) with flattened end; basal groove present, labial side without scattered foramina.



Lower jaw (most common: 12 rows): usually 1 (para-)symphyseal tooth, 2 anterior teeth; upper and lower teeth of same rows about same width and height, small parasymphyseal tooth with slender crown; laterally compressed root with shorter and narrower mesial lobe compared to distal root lobes; first two anterior teeth larger than sequential teeth; generally, lower jaw teeth morphologically similar to upper jaw teeth, only differences are vertically erected crowns.

Family Carchariidae Müller & Henle, 1838

Remark: The family Carchariidae was formally resurrected for the genus *Carcharias* by STONE & SHIMADA (2019), until then, the genus *Carcharias* was assigned to the family Odontaspidae.

Genus *Carcharias* Rafinesque, 1810

Type species: *Carcharias taurus* Rafinesque, 1810

### ***Carcharias taurus* Rafinesque, 1810 (Fig. 8C)**

Synonymy: *Squalus americanus* Mitchell, 1815; *Squalus littoralis* Lesueur, 1818; *Squalus littoralis* Mitchell, 1818; *Carcharias griseus* Ayres, 1843; *Carcharias tricuspidatus* Day, 1878; *Odontaspis cinerea* Ramsay, 1880; *Lamna ecarinata* Hemprich & Ehrenberg 1899; *Carcharias arenarius* Ogilby, 1911; *Carcharias owstoni* Garman, 1913; *Odontaspis platensis* Lahille, 1928.

Distribution: Wide-ranging in warm-temperate and tropical coastal waters of the Atlantic Ocean, Mediterranean Sea, and Indo-West Pacific Ocean; absent from the Central Pacific and eastern Pacific Oceans (EBERT & STEHMANN, 2013).

Size: TL (max): 3200 mm, TL (born): 850-1050 mm (EBERT et al. 2013).

Dental formula (most common/range): 1-2-1-16/1-2-22; (1-2)-(2)-(0-5)-(13-27)/(1)-(14-25) (SHIMADA 2002, the parasymphyseal tooth in this dental formula is defined as the first anterior tooth by other authors, see material and methods).

Crown height (A1 in mm/TL): 8.4 mm/1040 mm TL; 25.7 mm/2750 mm TL (SHIMADA 1999).

Material: OGIŁBY (1911) (n=1); GARMAN (1913) (n>1); LAHILLE (1928) (n>2); RAY (1928) (n>3); FOWLER (1936) (n>1); SPRINGER (1938) (n=3); BIGELOW & SCHROEDER (1948) (n>2); SMITH (1949) (n>2); FOWLER (1956) (n>1); TORTONESE (1956) (n>1); TENG (1958) (n=1); CHEN (1963) (n=1); SOLJAN (1963) (n=1); STEAD (1963) (n=1); APPLGATE (1965) (n=3); SMITH & SMITH (1966) (n=1); DAVIES (1966) (n=1); ABE et al. (1968) (n=1); TANIUCHI (1970) (n=24); SADOWSKY (1970) (n=528); BASS et al. (1975) (n=39); ELST (1981) (n>1); CADENAT & BLACHE (1981) (n>1); GILMORE et al. (1983) (n=3); CASTRO (1983) (n>2); BASS & COMPAGNO (1986) (n=1); RANDALL (1986) (n>1); GOMES & REIS (1990) (n>1); WELTON & FARISH (1993) (n=1); GOMON et al. (1994) (n>1); LAST & STEVENS (1994) (n>1); SHIMADA (1999) (n=87); LUCIFORA et al. (2003) (n>1).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2ab+3d/no CITES listing (POLLARD & SMITH 2009).

Description (after BASS et al. 1975; REINECKE et al. 2011):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty present: dentition of embryos or juvenile specimens under 100 cm TL lack the cusplets

**Fig. 8: A, B** *Mitsukurina owstoni* Jordan, 1898: A: upper and lower teeth, sex and TL unknown. B: Head of a juvenile specimen in ventral view, off the eastern side of Miho Peninsula (35°00'N, 138°29'E) near Shimizu city, Feb. 20, 2007, female, 119.8 cm TL. **C** *Carcharias taurus* Rafinesque, 1810: sex unknown, 335 cm TL, Philippines, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 8: A, B** *Mitsukurina owstoni* Jordan, 1898: A: Zähne des Ober- und Unterkiefers, Geschlecht und Gesamtlänge unbekannt. B: Schädel eines juvenilen Exemplares, ventrale Ansicht, gefangen vor der Ostseite von Halbinsel Miho (35°00'N, 138°29'E) nahe der Stadt Shimizu, 20.02.2007, Geschlecht weiblich, 119.8 cm Gesamtlänge. **C** *Carcharias taurus* Rafinesque, 1810: Geschlecht unbekannt, 335 cm TL, Philippinen, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

(TANIUCHI 1970; SADOWSKY 1970), holaulacohrizid root vasculariations stage present; root bilobed; lingual basal groove present; cutting edge smooth, no labial ornamentation, cusp lingually smooth or only with weakly developed irregularly folds.

Upper jaw (most common: 20 rows): usually no (para-)symphyseal tooth, 3 anterior teeth, 1 intermediate tooth; anterior teeth larger than sequential teeth, strait or weakly distally declined cusps of first three anterior teeth. Narrow and inclined or apically curved cusp in intermediate teeth, with asymmetrical root and cusp; lateral teeth with distally inclined cusps, triangular and low cusplets; straight and smooth mesial and distal cutting edges, all teeth with cutting edges which extending from apex to base of crowns, cutting edge at cusplets present; labial face of crown plane to weakly convex, lingual face of crown strongly convex, smooth or with weakly developed irregularly folds, mesial/distal heel absent; one pair of cusplets usually present, strongly developed long root lobes, one central foramen on lingual face of root in the centre of strongly developed protuberance, root lobes similar in length and symmetrical (except for the lobes of the third anterior tooth), basal groove present.

Lower jaw (most common: 25 rows): usually 1 (para-)symphyseal tooth, 2 to 3 anterior teeth; upper teeth and lower teeth of same rows about same width and height, small parasymphyseal tooth with slender crown; anterior teeth larger than sequential teeth; generally, lower jaw teeth morphologically similar to upper jaw teeth, only differences are lesser inclinations of main cusps.

Genus *Odontaspis* Agassiz, 1838

Type species: *Carcharinus ferox* Risso, 1827

### ***Odontaspis ferox* (Risso, 1810) (Fig. 9A)**

Synonymy: *Odontaspis herbsti* Whitley, 1950.

Distribution: Circumglobal, but patchily distributed in most temperate and tropical seas (EBERT & STEHMANN 2013).

Size: TL (max): 4500 mm, TL (born): 1000-1050 mm (EBERT et al. 2013).

Dental formula (most common/range): 1-2-4-18/1-3-18; (0-2)-(2)-(2-6)-(15-20)/(1-2?)-(16-23) (SHIMADA 2002).

Crown height (A1 in mm/TL): 9.5 mm/1100 mm TL; 22.7 mm/3140 mm TL (SHIMADA 1999).

Material: MOREAU (1881) (n=1); LERICHE (1905) (n=1); RAY (1928) (n=1); DESBROSSES (1930) (n=1); DARTEVELLE & CASIER (1943) (n=1); WHITLEY (1950) (n>3); MAUL (1955) (n=1); SOLJAN (1963) (n=1); DAUGHERTY (1964) (n=1); ABE et al. (1968) (n=1); GARRICK (1974) (n=2); BASS et al. (1975) (n=3); CADENAT & BLACHE (1981) (n=1); CASTRO (1983) (n>2); OTAKE (1984) (n=2); GUBANOV (1985) (n=2); SEIGEL & COMPAGNO (1986) (n=1); LAST & STEVENS (1994) (n>1); MENNI et al. (1995) (n=1); BONFIL (1995) (n=1); COMPAGNO et al. (1995) (n>1); VILLAVICENCIO-GARAYZAR (1996) (n=2); SHIMADA (1999) (n=7); KABASAKAL & BAYRI (2019) (n=1); TAVARES et al. (2019) (n=1).

IUCN Red List Category and Criteria/CITES status: Vulnerable A2bd/no CITES listing (GRAHAM et al. 2016).

Description (after BASS et al. 1975, CAPPETTA 2012):

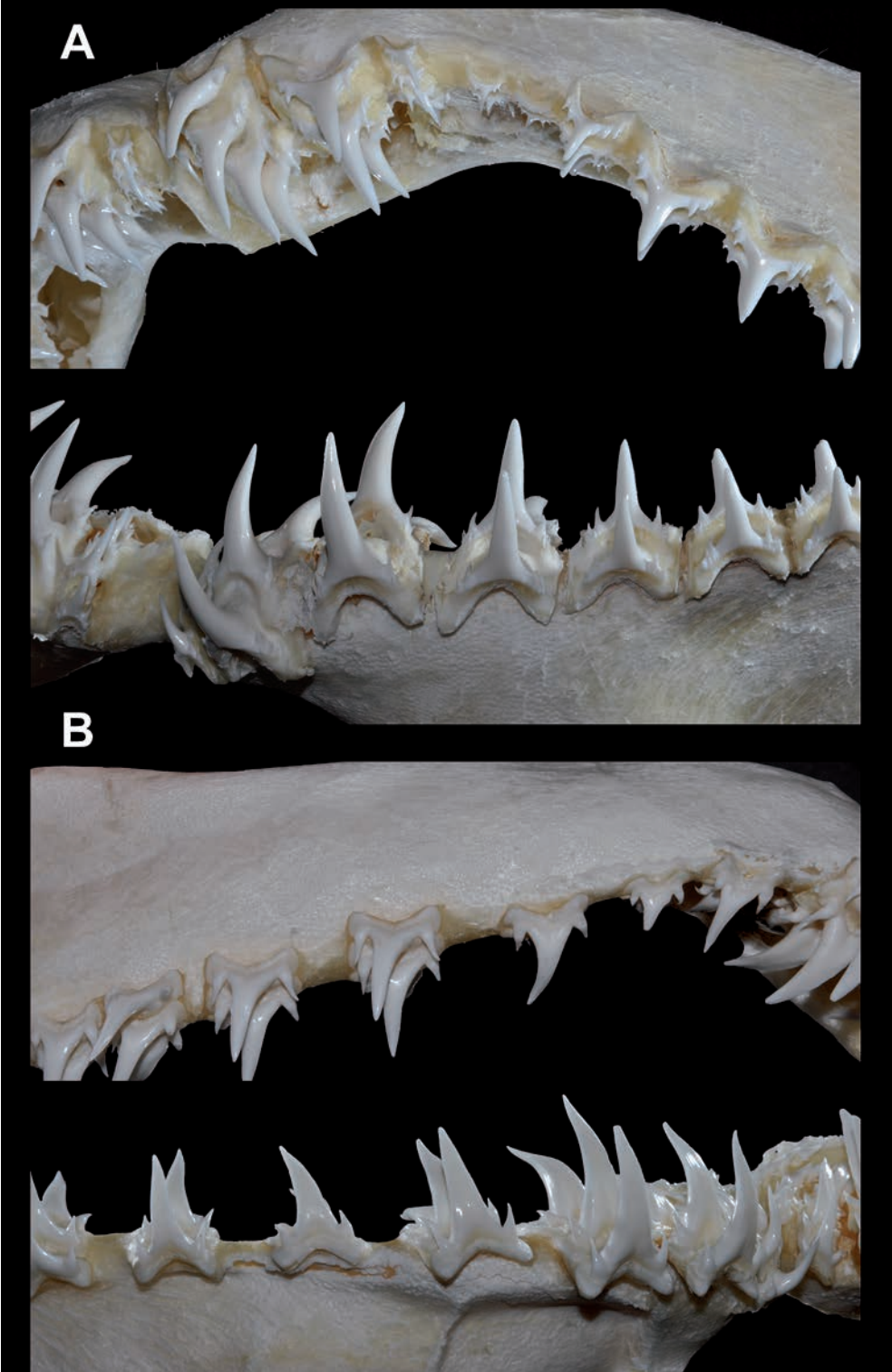
Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism

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**Fig. 9: A** *Odontaspis ferox* (Risso, 1810): sex unknown, 387 cm TL, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Odontaspis noronhai* (Maul, 1955): sex unknown, 479 cm TL, Taiwan, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 9: A** *Odontaspis ferox* (Risso, 1810): Geschlecht unbekannt, 387 cm Gesamtlänge, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** *Odontaspis noronhai* (Maul, 1955): Geschlecht unbekannt, 479 cm Gesamtlänge, Taiwan, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.





not observed, ontogenetic heterodonty not observed, holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; cutting edge smooth, no labial ornamentation, cusp lingually/labially smooth.

Upper jaw (most common: 25 rows): usually 1 (para-)symphyseal tooth, 2 anterior teeth, up to 4 intermediate teeth; anterior teeth much larger than sequential teeth, strait or weakly distally declined cusps of first two anterior teeth; intermediate teeth with narrow cusps; root and cusp asymmetrical, lateral teeth with distally inclined cusps, 2-3 pairs of sharp and high cusplets; straight and smooth mesial and distal cutting edges, cutting edges extend from apex to base of crown; cutting edge at cusplets present; plane to weakly convex labial face of crown, lingual face of crown strongly convex and smooth, mesial/distal heel absent; strongly developed root lobes, one central foramen in the centre of strongly developed protuberance on lingual face of root, root lobes of lateral teeth similar in length and symmetrical, basal groove present.

Lower jaw (most common: 22 rows): usually 1 (para-)symphyseal tooth, 3 anterior teeth; upper and lower teeth of same rows about same width and height, small parasymphyseal tooth with slender crown; t anterior teeth larger than sequential teeth; all lower jaw teeth generally morphologically similar to upper jaw teeth, lesser inclination of main cusp only difference.

### ***Odontaspis noronhai* (Maul, 1955) (Fig. 9B)**

Synonymy: None.

Distribution: Possibly circumglobal in all warm seas but as presently known sporadically distributed with very few records in the Atlantic and Indo-Pacific (EBERT et al. 2013).

Size: TL (max): 4270 mm, size at birth unknown (EBERT et al. 2013).

Dental formula (most common/range): 0-2-1-17/3-3-16; (0-1)-(2)-(1)-(14-18)/(1-4)-(16-20?) (SHIMADA 2002).

Crown height (A1 in mm/TL): 13.0 mm/? mm TL (SHIMADA 1999).

Material: MAUL 1955 (n=1); SADOWSKY et al. (1984) (n=4); BRANSTETTER & McEACHRAN (1986) (n=1); HUMPHREYS et al. (1989) (n=1); SHIMADA (1999) (n=1); KERSTETTER & TAYLOR (2008) (n=1).

IUCN Red List Category and Criteria/CITES status: Least Concern/no CITES listing (KYNE & EBERT 2019).

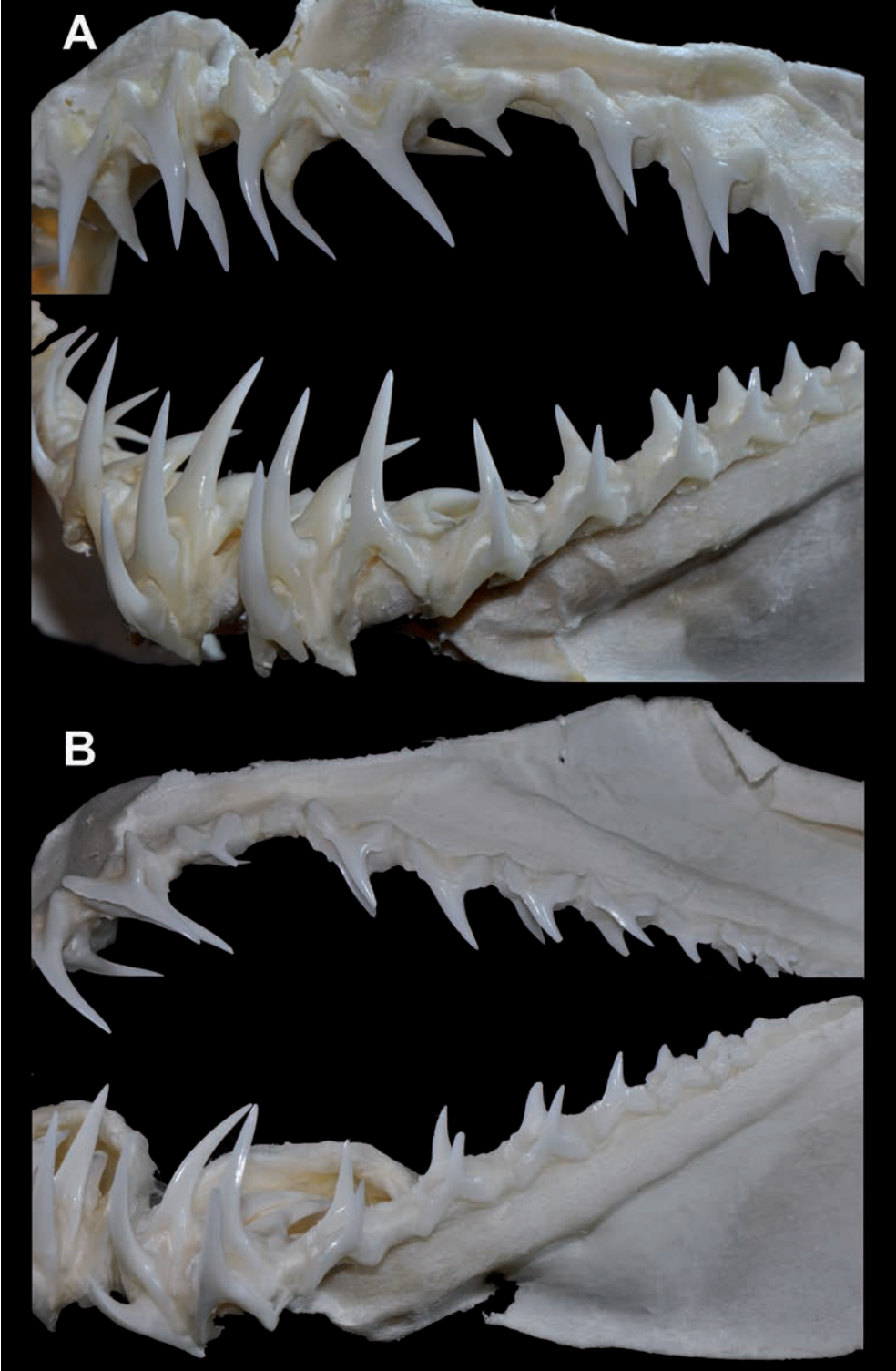
Description (after SHIMADA 2001; CAPPETTA 2012):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism not observed, ontogenetic heterodonty not observed, holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; cutting edge smooth, no labial ornamentation, cusp lingually/labially smooth.

Upper jaw (most common: 20 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; anterior teeth larger than sequential teeth, strait or weakly distally declined cusps of first two anterior teeth; intermediate tooth with narrow cusp in occlusal half broadening towards base, root and cusp asymmetrical; lateral teeth with distally inclined cusps, usually one pair of straight and high cusplets; cusplets tend to point away from central cusp, straight and smooth mesial and distal cutting edges, cutting edges extend from apex to base of crown, cutting edge at cusplets weakly developed; labial face of crown plane to weakly convex, lingual face of crown strongly convex and smooth, mesial/distal heel is absent; strongly developed long root lobes,

**Fig. 10:** *Pseudocarcharias kamoharui* (Matsubara, 1936): **A** female, 104 cm TL, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** male, 99 cm TL, coll. 29.06.1985, Caribbean, north of Venezuela, collection: Jaws International, GORDON HUBBELL, Florida, images by ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.

**Abb. 10:** *Pseudocarcharias kamoharui* (Matsubara, 1936): **A** weibliches Exemplar, 104 cm Gesamtlänge, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama. **B** Männliches Exemplar, 99 cm Gesamtlänge, coll. 29.06.1985, Karibik, nördlich von Venezuela, Sammlung: Jaws International, GORDON HUBBELL, Florida, Fotos von ROSS ROBERTSON, Smithsonian Tropical Research Institute, Panama.



single central foramen in centre of well developed protuberance on lingual face of root, root lobes of lateral teeth similar in length and symmetrical, basal groove present.

Lower jaw (most common: 22 rows): usually 3 (para-)symphyseal teeth, 3 anterior teeth; upper teeth and lower teeth of same row about same width and height, small parasymphyseal tooth with slender crown; the anterior teeth larger than sequential teeth; all teeth with similar morphological characters as upper jaw teeth, lesser inclination of main cusp only difference.

Family Pseudocarchariidae Taylor, Compagno & Struhsaker, 1983

Genus *Pseudocarcharias* Cadenat, 1963

Type species: *Carcharias (Pseudocarcharias) pelagicus* Cadenat, 1963

### ***Pseudocarcharias kamoharai* (Matsubara, 1936) (Fig. 10A, B)**

Synonymy: *Carcharias yangi* Teng, 1959; *Carcharias (Pseudocarcharias) pelagicus* Cadenat, 1963.

Distribution: Circumglobal in oceanic waters of the Indo-Pacific and Atlantic Oceans (EBERT et al. 2013).

Size: TL (max): 1220 mm, TL (born): 410 mm (EBERT et al. 2013).

Dental formula (most common/range): 0-2-1-10/0-3-9; (0)-(2)-(0-2)-(10-13)/(0)-(9?-14) (SHIMADA 2002).

Crown height (A1 in mm/TL): 6.5 mm/510 mm TL; 11.1 mm/870 mm TL (SHIMADA 1999).

Material: MATSUBARA (1936) (n=1); TENG (1959) (n=1); CADENAT (1963) (n=1); D'AUBREY (1964b) (n=1); ABE et al. (1969) (n=1); BASS et al. (1975) (n=3); FUJITA (1981) (n=6); COMPAGNO (1982) (n>1); SADOWSKY et al. (1989) (n=3); CIGALA-FULGOSI (1992) (n>3); ROMANOV & SAMOROV (1994) (n=1); LAST & STEVENS (1994) (n>1); SHIMADA (1999) (n=10); STEWART (2001) (n=1); MELÉNDEZ et al. (2006) (n=1); KANNAN et al. (2019) (n=1).

IUCN Red List Category and Criteria/CITES status: Least Concern/no CITES listing (KYNE et al. 2019).

Description (after CIGALA-FULGOSI 1992):

Gradient monognathic and disjunct monognathic heterodonty present; sexual dimorphism absent, ontogenetic heterodonty not present, holaulacorhizid root vasculariations stage present; root bilobed; lingual basal groove present; cutting edge smooth, no labial ornamentation, cusp linguallly/labially smooth.

Upper jaw (most common: 13 rows): usually no (para-)symphyseal tooth, 2 anterior teeth, 1 intermediate tooth; anterior teeth much larger than sequential teeth, relatively high, needle-like, strait or weakly distal declined cusps of first two anterior teeth; intermediate teeth with narrow, distally inclined cusps, root and cusp asymmetrical; lateral teeth with distally inclined cusps, no cusplets present; straight and smooth mesial and distal cutting edges, cutting edge extends from apex to base of crown, labial face of crown plane to weakly convex, strongly convex and smooth lingual face of crown, weakly mesial/distal heel present, strongly developed long root lobes, one central foramen in centre of strongly developed protuberance on lingual face of root, root lobes of lateral teeth similar in length and symmetrical, basal groove is present.

Lower jaw (most common: 11 rows): usually no (para-)symphyseal tooth, 3 anterior teeth; upper teeth and lower teeth of same row about same width and height, anterior teeth larger than sequential teeth; lower jaw teeth generally morphologically similar to upper jaw teeth, lesser inclination of main cusp only difference.

### **Acknowledgments**

Many thanks to HELMUT BRACHER (Altdorf) for the permission to use his drawings of lamnid shark teeth and to JASON SEITZ, ROSS ROBERTSON, SEBASTIEN ENAULT ([www.kraniata.com](http://www.kraniata.com)) and IRIS FEICHTINGER for providing images of jaws and SHO TANAKA for collection details on the *Mitsukurina* specimen. Our special thanks go to KENSHU SHIMADA for providing the data from his doctoral thesis.

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Received: 27.04.2020

Accepted: 31.07.2020

Published: