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An identification key to elasmobranch genera based on dental morphological characters Part A: Squalomorph sharks (Superorder Squalomorphii)

Ein auf zahnmorphologischen Merkmalen basierender Bestimmungsschlüssel für Elasmobranchiergattungen Teil A: Squalomorphe Haie (Überordnung Squalomorphii)

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Summary: In addition to articulated, mostly formaldehyde-fixed and ethanol-preserved, taxidermy or anatomical specimens, sharks and rays are represented in scientific collections by numerous jaws and isolated teeth. These specimens often source from historical collections where existing informations about species, sex or geographic origin in many cases are scarce, incomplete or incorrect. The identification key for jaws and teeth presented herein focuses on squalomorph sharks, which comprise almost 34 % of all sharks with 179 species in 31 genera and 11 families. The key is essentially based on the following characters: vascularisation stage, labial apron, number of cusplets, distal heel, lingual ornamentation, cutting edge, and dentition kind. The key allows the identification to genus level. It is further supplemented by a comprehensive glossary of tooth morphological terms as well as an updated checklist of all currently described squalomorph sharks with indication of the distribution and the dental formula.

Key words: Dentition, Elasmobranchii, single-access key, teeth

Zusammenfassung: In zahlreichen wissenschaftlichen Sammlungen befinden sich neben formaldehyd- oder alkoholkonservierten Ganzkörper- und anatomischen Präparaten oftmals Kiefer und Zähne von Haien und Rochen. Diese Exemplare stammen häufig aus historischen Sammlungen und die vorhandenen Informationen über die Art, das Geschlecht oder die geografische Herkunft sind oftmals lückenhaft oder falsch. Mit der vorliegenden Arbeit wird ein Bestimmungsschlüssel für Kiefer und Zähne von squalomorphen Haien vorgestellt. Diese Überordnung beinhaltet derzeit 179 Arten in 31 Gattungen und 11 Familien und stellt damit annähernd fast 34 % aller heute bekannten Haiarten dar. Zur Identifizierung wird dabei im Wesentlichen auf folgende Merkmale zurückgegriffen: Art des Vaskularisationssystems, labiales Apron, Anzahl der Zahnspitzen, Talon, linguale Ornamentik, Form der Schneide und Art der Bezahnung. Der Schlüssel ermöglicht die Bestimmung bis auf Gattungsebene. Ergänzt wird er durch ein umfangreiches Glossar der wichtigsten zahnmorphologischen Begriffe sowie eine aktualisierte Checkliste aller derzeit bekannten squalomorphen Haie mit Angabe der geographischen Verbreitung und der Zahnformel.

Schlüsselwörter: Bezahnung, Elasmobranchii, dichotomer Bestimmungsschlüssel, Zähne

1. Introduction

Besides numerous synapomorphies, sharks, skates and rays (Elasmobranchii) are characterized by the outstanding feature of being able to produce teeth only within the dental lamina and constantly replace jaw teeth throughout their lifetime (Reif 1978; Smith et al. 2013; Underwood et al. 2016). The elasmobranch dentition often reflects feeding habits and allows for tracing ecological characteristics of its bearer (Reif 1976; Motta 2004). Due to these specializations, dental morphological characters are further useful on numerous taxonomic levels, in many instances even for species level identification (Sáez & Pequeño 2010; Shimada 2002, 2005; Voigt & Weber 2011). Therefore, dental characters of extant species are also decisive for the identification of extinct species. The reason for that lies in the fact that the fossil record of elasmobranchs mainly comprises fossilized teeth. Contrasting a rather detailed record of fossil teeth, articulated fossils of elasmobranchs are rather scarce, as Elasmobranchii have a cartilaginous skeleton, which is less prone for fossilization. Therefore, numerous fossil taxa are described based on dental characters only (e.g. Cappetta & Case 2016; Ebersole & Ehret 2018; Pollerspöck & Straube 2017; Shimada et al. 2017; Welton 2016).

Recently, Guinot et al. (2018) and Mollen (2019) pointed out the importance of morphological descriptions of teeth in newly described extant elasmobranch species as references for the fossil record. Today, in most descriptions of extant species, the dental formula and images of upper and lower teeth are reported (e.g. Kawauchi et al. 2014; Straube et al. 2011; Weigmann & Kaschner 2017; White et al. 2017). Apart from few exceptions (e.g. Gutteridge & Bennett 2014; Psomadakis et al. 2009; Rangel et al. 2016; Straube et al. 2007), ontogenetic and sexual variation of dental characters mostly remain unknown.

Living squalomorph sharks are characterized by numerous distinct specializations of dentitions allowing for a species-level identification in several examples such as *Trigonognathus kabeyai* or *Chlamydoselachus anguineus* (Cappetta & Adnet 2001; Pfeil 1983). Apart from the highly diverse angel sharks (Squatiniformes), many squalomorphs are deep-water inhabitants (Kyne & Simpfendorfer 2007), a habitat supporting the development of specialized dentitions (Adnet & Cappetta 2001). Their distinctive dental features further allow clear identification of the fossil record (e.g. Maisey 2012).

As scientific collections of both extant and extinct elasmobranchs often hold jaws and/or teeth only, in this study we aim for providing dental morphological characters of the superorder Squalomorphii as a first step to summarize known dental characters used for identification of taxa.

2. Material and Methods

The identification key is based primarily on the information in the scientific literature and was supplemented in part by research of Pollerspöck et al. (2018). The valid species and the classification listed in the checklist (tab. 1) were downloaded from the database www.shark-references.com (Pollerspöck & Straube 2019). The information on dental formula and distribution contained in the checklist is derived from the first descriptions of the species or from the references listed in table 1 (column "remarks"). Distribution data were encoded using data from the Food and Agriculture Organization (FAO) Fisheries and Aquaculture Department (http://www.fao.org/fishery/area/search/en) (fig. 1, tab. 2).

The taxonomy of the superorder Squalomorphii is following Pollerspöck & Straube, 2019 and is shown in table 3. In addition, the maximum total length of the specimens derived from Ebert et al. (2013) was rounded to the nearest full 10 cm to have an approximate size. This can be useful for excluding specimens beforehand or double-check, if a specimen falls into a size range known from literature. Further, we specified for each genus an approximate maximum width of the jaws. For this, the values for the mouth width were determined from available publications listed below and the following average values as percentage of standard length were used. These data should be used as reference values only: family Pristiophoridae: 5% (Weigmann et al. 2014: 4,3%-5,9%TL, Ebert & Wilms, 2013: 3,6%-4,0%TL; Yearsley et al. 2008: 4,4%-4,9%TL); family Squatinidae: 12% (Vaz & De Carvalho, 2013: 10.8%-15.6%TL, 9.9%-15.1%TL, 13.7%-15.4%TL); all other families: 10% (e.g. Straube et al. 2011 for *Etmopterus* spp.: 10,23%TL, Last et al. 2007a,b for *Squalus* spp.: 6.9%-7.7%TL, 7.8%-8.6%TL, 8.1%-8.4%TL; White et al. 2013 for *Centrophorus* spp.: 6,8%-10,4%TL, Yano et al. 2004 for *Somniosus* spp.: 7.2%-13.9%TL, 7.9%-10.9%TL, 6.5%-11.3%TL).

Tab. 1: Checklist of sharks of the superorder Squalomorphii (status as of 01. January 2019).
Tab. 1: Checkliste der Haie der Überordnung Squalomorphii (Stand: 01. Januar 2019).
Remarks: All data have been extracted from the original descriptions of the species, except in cases where the column „Remarks" shows a different reference. The geographical distribution is indicated by the FAO fishing areas (http://www.fao.org/fishery/area/search/en). This list is included here to allow for narrowing down the number of possible species, if the collection locality is known. Further, including geographic information may allow a more detailed identification compared to the identification based on jaws and teeth alone.

#	Scientific name	Species authorship	Dental formula (upper/lower)	Remarks	Geographic distribution (FAO areas)
			Hexanchiformes: Chlamydoselachidae		
1	*Chlamydoselachus africana*	Ebert & Compagno, 2009	28-30/24-27		47
2	*Chlamydoselachus anguineus*	Garman, 1884	19-30/21-29	Last & Stevens 2009	27, 34, 31, 87, 77, 61, 71, 81, 57
			Hexanchiformes: Hexanchidae		
3	*Heptranchias perlo*	Bonnaterre, 1788	18-24/11-13	Last & Stevens 2009	37, 27, 34, 47, 41, 31, 21, 87, 61, 71, 81, 57, 51
4	*Hexanchus griseus*	Bonnaterre, 1788	18-20/13	Last & Stevens 2009	37, 27, 34, 47, 41, 31, 21, 67, 77, 87, 81, 71, 61, 57, 51
5	*Hexanchus nakamurai*	Teng, 1962	18/11	Last & Stevens 2009	27, 37, 31, 81, 71, 61, 57, 51
6	*Hexanchus vitulus*	Springer & Waller, 1969	?		31
7	*Notorynchus cepedianus*	Péron, 1807	15-16/13	Last & Stevens 2009	47, 41, 87, 77, 67, 61, 71, 81, 57, 51
			Pristiophoriformes: Pristiophoridae		
8	*Pliotrema warreni*	Regan, 1906	?	Ebert et al. 2013	47, 51
9	*Pristiophorus cirratus*	Latham, 1794	33-40/36	Ebert et al. 2013	57, 81
10	*Pristiophorus delicatus*	Yearsley et al., 2008	42/37		71
11	*Pristiophorus japonicus*	Günther, 1870	35-58/48	Ebert et al. 2013	61
12	*Pristiophorus lanae*	Ebert & Wilms, 2013	36–48/32–40		71
13	*Pristiophorus nancyae*	Ebert & Cailliet, 2011	31–35/29–34	Jabado & Ebert 2015	51
14	*Pristiophorus nudipinnis*	Günther, 1870	32-37/?	Ebert et al. 2013	57, 81
15	*Pristiophorus schroederi*	Springer & Bullis, 1960	36/32		31
			Squatiniformes: Squatinidae		
16	*Squatina aculeata*	Cuvier, 1829	19-24/19-23	Ebert et al. 2013	27, 37, 34, 47
17	*Squatina africana*	Regan, 1908	20-22/18-20	Ebert et al. 2013	47, 51
18	*Squatina albipunctata*	Last & White, 2008	18/14-18		71, 81
19	*Squatina argentina*	Marini, 1930	24/24	Vaz & De Carvalho 2013	41
20	*Squatina armata*	Philippi, 1887	?	Ebert et al. 2013	87
21	*Squatina australis*	Regan, 1906	20/18	Ebert et al. 2013	57, 81
22	*Squatina caillieti*	Walsh et al., 2011	20/18		71
23	*Squatina californica*	Ayres, 1859	14-19/14-20	Ebert et al. 2013	67, 77, 87
24	*Squatina david*	Acero et al., 2016	20/20		31
25	*Squatina dumeril*	Lesueur, 1818	20/18-20	Ebert et al. 2013	31
26	*Squatina formosa*	Shen & Ting, 1972	18-20/20	Walsh & Ebert 2007	61
27	*Squatina guggenheim*	Marini, 1936	18-22/18-22	Vaz & De Carvalho 2013	41
28	*Squatina heteroptera*	Castro-Aguirre et al., 2007	16/16		31

Tab. 1: Continued.
Tab. 1: Fortsetzung.

29	*Squatina japonica*	BLEEKER, 1858	20/20	WALSH & EBERT 2007	61
30	*Squatina legnota*	LAST & WHITE, 2008	18/18		57, 71
31	*Squatina mexicana*	CASTRO-AGUIRRE et al., 2007	20/20		31
32	*Squatina nebulosa*	REGAN, 1906	20/20	WALSH & EBERT 2007	61
33	*Squatina occulta*	VOOREN & DA SILVA, 1991	18–20/18–22	VAZ & DE CARVALHO 2013	41
34	*Squatina oculata*	BONAPARTE, 1840	15-19/15-19	EBERT et al. 2013	34, 37, 47
35	*Squatina pseudocellata*	LAST & WHITE, 2008	16/14-16		57
36	*Squatina squatina*	LINNAEUS, 1758	18-22/18-22	EBERT et al. 2013	27, 34, 37
37	*Squatina tergocellata*	MCCULLOCH, 1914	18/20	EBERT et al. 2013	57
38	*Squatina tergocellatoides*	CHEN, 1963	20/20	THEISS & EBERT 2013	71
39	*Squatina varii*	VAZ & DE CARVALHO, 2018	16-19/16-20		41
Echinorhiniformes: Echinorhinidae					
40	*Echinorhinus brucus*	BONNATERRE, 1788	20-26/21-26	LAST & STEVENS 2009	27, 37, 34, 47, 41, 31, 21, 81, 57, 71, 61, 51
41	*Echinorhinus cookei*	PIETSCHMANN, 1928	21-23/20-22	LAST & STEVENS 2009	87, 77, 67, 61, 71, 81, 57
Squaliformes: Centrophoridae					
42	*Centrophorus atromarginatus*	GARMAN, 1913	42/30	EBERT et al. 2013	51, 57, 61, 71
43	*Centrophorus granulosus*	BLOCH & SCHNEIDER, 1801	30–37/27–32	EBERT et al. 2013; WHITE et al. 2013	37, 27, 34, 47, 31, 21, 61, 71, 57, 51
44	*Centrophorus harrissoni*	MCCULLOCH, 1915	37-39/30-31	LAST & STEVENS 2009	57, 81
45	*Centrophorus isodon*	CHU et al., 1981	33-37/27-30	EBERT et al. 2013	51, 61, 71
46	*Centrophorus lesliei*	WHITE et al., 2017a	33–42/29–31		34, 51
47	*Centrophorus longipinnis*	WHITE et al., 2017a	38–43/30–31		57, 61, 71
48	*Centrophorus moluccensis*	BLEEKER, 1860	36-45/31-35	LAST & STEVENS 2009	51, 57, 81, 71, 61
49	*Centrophorus seychellorum*	BARANES, 2003	33/30		51
50	*Centrophorus squamosus*	BONNATERRE, 1788	30-38/27-32	LAST & STEVENS 2009	27, 34, 47, 51, 57, 61, 7181
51	*Centrophorus tessellatus*	GARMAN, 1906	42/31	EBERT et al. 2013	31, 61, 77
52	*Centrophorus uyato*	RAFINESQUE, 1810	?	WEIGMANN 2016	21, 27, 37, 51
53	*Centrophorus westraliensis*	WHITE et al., 2008	38/29		57
54	*Centrophorus zeehaani*	WHITE et al., 2008	37-45/30-33		57
55	*Deania calcea*	LOWE, 1839	25-35/27-33	LAST & STEVENS 2009	27, 34, 47, 87, 81, 57, 71, 61,
56	*Deania hystricosa*	GARMAN, 1906	33/30	EBERT et al. 2013	81, 61, 34, 47
57	*Deania profundorum*	SMITH & RADCLIFFE, 1912	?	EBERT et al. 2013	71, 31, 34, 27, 47, 51
58	*Deania quadrispinosa*	MCCULLOCH, 1915	28-33/29-31	LAST & STEVENS 2009	47, 51, 57, 81, 71, 61
Squaliformes: Dalatiidae					
59	*Dalatias licha*	BONNATERRE, 1788	16-21/17-20	LAST & STEVENS 2009	37, 27, 34, 47, 57, 81, 71, 61, 77
60	*Euprotomicroides zantedeschia*	HULLEY & PENRITH, 1966	28-30/34	HERMAN et al. 1989; EBERT et al. 2013	41, 47
61	*Euprotomicrus bispinatus*	QUOY & GAIMARD, 1824	21/19-23	LAST & STEVENS 2009	47, 34, 31, 41, 77, 87, 81, 71, 61, 57, 51

Tab. 1: Continued.
Tab. 1: Fortsetzung.

62	*Heteroscymnoides marleyi*	Fowler, 1934	12-14/22-24	Herman et al. 1989; Ebert et al. 2013	47, 87
63	*Isistius brasiliensis*	Quoy & Gaimard, 1824	31-37/25-31	Last & Stevens 2009	47, 34, 31, 41, 77, 87, 81, 71, 61, 57, 51
64	*Isistius plutodus*	Garrick & Springer, 1964	21-29/17-19	Last & Stevens 2009	71, 61, 81, 31, 41, 34, 27
65	*Mollisquama parini*	Dolganov, 1984	12-1-12/15-1-15	Ebert et al. 2013	87
66	*Squaliolus aliae*	Teng, 1959	23/21	Last & Stevens 2009	81, 71, 57, 61
67	*Squaliolus laticaudus*	Smith & Radcliffe, 1912	20-22/18	Herman et al. 1989; Ebert et al. 2013	71, 61, 51, 31, 21, 41, 34, 27,
Squaliformes: Etmopteridae: clade unkown					
68	*Etmopterus tasmaniensis*	Myagkov & Pavlov, 1986	?	maybe no valid species, see Weigmann 2016	57
Squaliformes: Etmopteridae: *gracilispinis*-clade					
69	*Etmopterus gracilispinis*	Krefft, 1968	24-27/25-32	Ebert et al. 2013	21, 31, 41, 47, 51
70	*Etmopterus perryi*	Springer & Burgess, 1985	25-30/32-34		31
71	*Etmopterus polli*	Bigelow et al., 1953	27-34/28-30	Ebert et al. 2013	31, 34, 47
72	*Etmopterus robinsi*	Schofield & Burgess, 1997	?		31
73	*Etmopterus schultzi*	Bigelow et al., 1953	32-38/32-32		31
74	*Etmopterus virens*	Bigelow et al., 1953	29-34/24-32		31
Squaliformes: Etmopteridae: *lucifer*-clade					
75	*Etmopterus brachyurus*	Smith & Radcliffe, 1912	?	Last & Stevens 2009	57, 61, 71
76	*Etmopterus bullisi*	Bigelow & Schroeder, 1957	38/58	Ebert et al. 2013	31
77	*Etmopterus burgessi*	Schaaf-Da Silva & Ebert, 2006	24–26/32–36		61
78	*Etmopterus decacuspidatus*	Chan, 1966	25/32		61
79	*Etmopterus dislineatus*	Last et al., 2002	?		71
80	*Etmopterus evansi*	Last et al., 2002	?		57, 71
81	*Etmopterus lailae*	Ebert et. al., 2017	22–24/26–26		77
82	*Etmopterus lucifer*	Jordan & Snyder, 1902	21-26/29-39	Last & Stevens 2009	57, 61, 71, 81
83	*Etmopterus marshae*	Ebert & Van Hees, 2018	30–36/30–38		71
84	*Etmopterus molleri*	Whitley, 1939	13/18 (?)	Last & Stevens 2009; Ebert et al. 2013	61, 81
85	*Etmopterus pycnolepis*	Kotlyar, 1990	28/36-40		87
86	*Etmopterus samadiae*	White et al., 2017b	27–28/28–31		71
87	*Etmopterus schmidti*	Dolganov, 1986	25-28/38-41		61
88	*Etmopterus sculptus*	Ebert et al., 2011	23–25/36–43		47, 51
89	*Etmopterus sheikoi*	Dolganov, 1986	55/52		61
90	*Etmopterus villosus*	Gilbert, 1905	27/29		77
91	*Etmopterus alphus*	Ebert et al., 2016	26–30/31–34		51

Tab. 1: Continued.
Tab. 1: Fortsetzung.

		Squaliformes: Etmopteridae: *pusillus*-clade			
92	*Etmopterus bigelowi*	SHIRAI & TACHIKAWA, 1993	19-24/25-39	LAST & STEVENS 2009	47, 51, 34, 41, 31, 77, 81, 57, 71, 61
93	*Etmopterus carteri*	SPRINGER & BURGESS, 1985	28-32/27-31		31
94	*Etmopterus caudistigmus*	LAST et al., 2002	31-35/37-39		71
95	*Etmopterus fusus*	LAST et al., 2002	?		57
96	*Etmopterus joungi*	KNUCKEY et al., 2011	25-30/33-36		61
97	*Etmopterus pseudosqualiolus*	LAST et al., 2002	29-34/32-34		71
98	*Etmopterus pusillus*	LOWE, 1839	23-30/35-44	EBERT et al. 2013	47, 34, 27, 31, 41, 81, 71, 61, 57, 51,
99	*Etmopterus sentosus*	BASS et al., 1976	24/37	EBERT et al. 2013	51
100	*Etmopterus splendidus*	YANO, 1988	26-34/31-40		61
		Squaliformes: Etmopteridae: *spinax*-clade			
101	*Etmopterus benchleyi*	VASQUEZ et al., 2015	26–30/30–36		77
102	*Etmopterus compagnoi*	FRICKE & KOCH, 1990	?		47
103	*Etmopterus dianthus*	LAST et al., 2002	?		71
104	*Etmopterus granulosus*	GÜNTHER, 1880	29/25-27	GARRICK 1957 (as *E. baxteri*); EBERT et al. 2013 (for *E. granulosus* and *E. baxteri*)	87, 41, 47, 51, 57, 81
105	*Etmopterus hillianus*	POEY, 1861	24-26/36-38	EBERT et al. 2013	31
106	*Etmopterus litvinovi*	PARIN & KOTLYAR, 1990	30-40/(20-24)-(0-1)-(20-25)	KOTLYAR 1990	87
107	*Etmopterus princeps*	COLLETT, 1904	29-32/40-50	BIGELOW et al. 1953; EBERT et al. 2013	21, 27, 34
108	*Etmopterus spinax*	LINNAEUS, 1758	22-32/26-40	HERMAN et al. 1989; EBERT et al. 2013	27, 34, 37
109	*Etmopterus unicolor*	ENGELHARDT, 1912	28/34-38	EBERT et al. 2013	61
110	*Etmopterus viator*	STRAUBE, 2011	26/37		47, 58, 81
		Squaliformes: Etmopteridae			
111	*Aculeola nigra*	DE BUEN, 1959	60/60	HERMAN et al. 1989; EBERT et al. 2013	87
112	*Centroscyllium excelsum*	SHIRAI & NAKAYA, 1990	51-66/48-65		61
113	*Centroscyllium fabricii*	REINHARDT, 1825	64-102/66-104	HERMAN et al. 1989; EBERT et al. 2013	47, 34, 27, 21, 31, 41
114	*Centroscyllium granulatum*	GÜNTHER, 1887	45-75/43-76	EBERT et al. 2013	87
115	*Centroscyllium kamoharai*	ABE, 1966	45-75/43-76	EBERT et al. 2013	81, 71, 57, 61
116	*Centroscyllium nigrum*	GARMAN, 1899	45-75/43-76	EBERT et al. 2013	77, 87
117	*Centroscyllium ornatum*	ALCOCK, 1889	45-75/43-76	EBERT et al. 2013	51, 57
118	*Centroscyllium ritteri*	JORDAN & FOWLER, 1903	45-75/43-76	EBERT et al. 2013	61
119	*Trigonognathus kabeyai*	MOCHIZUKI & OHE, 1990	15-20/15-20	EBERT et al. 2013	61, 77
		Squaliformes: Oxynotidae			
120	*Oxynotus bruniensis*	OGILBY, 1893	14-18/11-13	EBERT et al. 2013	57, 81
121	*Oxynotus caribbaeus*	CERVIGÓN, 1961	?/9-13	EBERT et al. 2013	31
122	*Oxynotus centrina*	LINNAEUS, 1758	9-11/9	YANO & MATSUURA 2002; EBERT et al. 2013	47, 34, 37, 27

Tab. 1: Continued.
Tab. 1: Fortsetzung.

123	*Oxynotus japonicus*	YANO & MUROFUSHI, 1985	16-19/11-13	YANO et al. 2002	61
124	*Oxynotus paradoxus*	FRADE, 1929	13/9-11	YANO & MATSUURA 2002; EBERT et al. 2013	27, 34
Squaliformes: Somniosidae					
125	*Centroscymnus coelolepis*	BARBOSA DU BOCAGE & DE BRITO CAPELLO, 1864	43-68/29-42	LAST & STEVENS 2009	51, 57, 81, 71, 61, 21, 31, 41, 27, 37, 34, 47
126	*Centroscymnus owstonii*	GARMAN, 1906	36-39/32-40	LAST & STEVENS 2009	57, 81, 61, 87, 31, 41, 34, 47
127	*Centroselachus crepidater*	BARBOSA DU BOCAGE & DE BRITO CAPELLO, 1864	36-51/30-36	LAST & STEVENS 2009	51, 57, 81, 71, 61, 87, 27, 34, 47
128	*Scymnodalatias albicauda*	TANIUCHI & GARRICK, 1986	57-62/35	LAST & STEVENS 2009	81, 57, 51, 47, 58
129	*Scymnodalatias garricki*	KUKUEV & KONOVALENKO, 1988	52/31	CIGALA-FULGOSI 1996	27
130	*Scymnodalatias oligodon*	KUKUEV & KONOVALENKO, 1988	33/42		87
131	*Scymnodalatias sherwoodi*	ARCHEY, 1921	57/34	EBERT et al. 2013	57, 81
132	*Scymnodon ichiharai*	YANO & TANAKA, 1984	38–58/27–31	WHITE et al. 2015	61
133	*Scymnodon macracanthus*	REGAN, 1906	?	WHITE et al. 2015, probably conspecific with *S. plunketi*	81, 87
134	*Scymnodon plunketi*	WAITE, 1910	48/32-35	LAST & STEVENS 2009; COMPAGNO 1984	81, 57, 51
135	*Scymnodon ringens*	BARBOSA DU BOCAGE & DE BRITO CAPELLO, 1864	28-50/28-30	HERMAN et al. 1989; EBERT et al. 2013	27, 81
136	*Somniosus antarcticus*	WHITLEY, 1939	37-48/49-59	YANO et al. 2004; EBERT et al. 2013	57, 81, 87, 41, 47, 58,
137	*Somniosus longus*	TANAKA, 1912	56-57/31-32	YANO et al. 2004; EBERT et al. 2013	61, 81, 87
138	*Somniosus microcephalus*	BLOCH & SCHNEIDER, 1801	35-39/45-57	YANO et al. 2004; EBERT et al. 2013	21, 27, 31
139	*Somniosus pacificus*	BIGELOW & SCHROEDER, 1944	30-48/46-63	YANO et al. 2004; EBERT et al. 2013	67, 18, 77, 61,
140	*Somniosus rostratus*	RISSO, 1827	60/32-36; 53/31-36	HERMAN et al. 1989; YANO et al. 2004; EBERT et al. 2013	31, 34, 37, 27
141	*Zameus squamulosus*	GÜNTHER, 1877	47-60/32-38	LAST & STEVENS 2009	51, 57, 61, 71, 81, 77, 31, 41, 27, 34
Squaliformes: Squalidae					
142	*Cirrhigaleus asper*	MERRETT, 1973	24-28/22-24	EBERT et al. 2013	77, 31, 41, 51.
143	*Cirrhigaleus australis*	WHITE et al., 2007a	27/24		57, 81
144	*Cirrhigaleus barbifer*	TANAKA, 1912	26/26; 27-30/23-24	KEMPSTER et al. 2013	81, 61
Squaliformes: Squalidae: *acanthias*-clade					
145	*Squalus acanthias*	LINNAEUS, 1758	22-30/22-24 18-30/16-28	HERMAN et al. 1989; LAST & STEVENS 2009; VIANA et al. 2016	51, 58, 57, 81, 61, 67, 77, 87, 41, 31, 21, 27, 37, 34, 47
146	*Squalus lalannei*	BARANES, 2003	24-26/22-24		51
147	*Squalus suckleyi*	GIRARD, 1855	26-29/20-27	EBERT et al. 2013	61, 67, 77

Tab. 1: Continued.
Tab. 1: Fortsetzung.

Squaliformes: Squalidae: *megalops*-clade					
148	*Squalus acutipinnis*	Regan, 1908	23-28/20-25	Viana & De Carvalho 2016	47, 51
149	*Squalus albicaudus*	Viana et al., 2016	24-27/22-23		41
150	*Squalus albifrons*	Last et al., 2007e	27/22-23		71, 81
151	*Squalus altipinnis*	Last et al., 2007c	27/22		57
152	*Squalus brevirostris*	Tanaka, 1917	24-27/20-21	Ebert et al. 2013; Viana & De Carvalho 2016	61
153	*Squalus bucephalus*	Last et al., 2007c	26/23		71
154	*Squalus crassispinus*	Last et al., 2007a	27/23		57
155	*Squalus cubensis*	Howell Rivero, 1936	28/22	Ebert et al. 2013	31, 41
156	*Squalus formosus*	White & Iglésias, 2011	27/20		61
157	*Squalus mahia*	Viana et al., 2017	24-26/20-22		47, 51
158	*Squalus margaretsmithae*	Viana et al., 2017	23-27/21-24		47
159	*Squalus megalops*	Macleay, 1881	25-27/21-24	Ebert et al. 2013; Viana & De Carvalho 2016	57, 71, 81,
160	*Squalus notocaudatus*	Last et al., 2007c	27/23		71
161	*Squalus probatovi*	Myagkov & Kondyurin, 1986	27/23	Viana & De Carvalho 2018a	47, 51, 34
162	*Squalus raoulensis*	Duffy & Last, 2007	26/23-24		81
Squaliformes: Squalidae: *mitsukurii*-clade					
163	*Squalus bahiensis*	Viana et al., 2016	27/22-23		41
164	*Squalus bassi*	Viana et al., 2017	20-28/20-23		47, 51
165	*Squalus blainville*	Risso, 1827	30/28(?)	Ebert et al. 2013	27, 34, 37, 47
166	*Squalus chloroculus*	Last et al., 2007d	29/24		57, 81
167	*Squalus clarkae*	Pfleger et al., 2018	27–29/23–24		31
168	*Squalus edmundsi*	White et al., 2007b	25/22		57
169	*Squalus grahami*	White et al., 2007b	27/23		71
170	*Squalus griffini*	Phillipps, 1931	26-27/21-24	Duffy & Last 2007	81
171	*Squalus hawaiiensis*	Daly-Engel et al., 2018	26–28/23		77
172	*Squalus japonicus*	Ishikawa, 1908			
173	*Squalus lobularis*	Viana et al., 2016	26/21-23		41
174	*Squalus melanurus*	Fourmanoir, 1979	27/23	Viana & De Carvalho 2018b	71, 81
175	*Squalus mitsukurii*	Jordan & Snyder, 1903	25-29/22-25	Ebert et al. 2013	61, 71, 77, 87, 41, 31, 34, 47, 51
176	*Squalus montalbani*	Whitley, 1931	?	Ebert et al. 2013	57, 71, 81

Tab. 1: Continued.
Tab. 1: Fortsetzung.

177	*Squalus nasutus*	LAST et al., 2007b	26/22		57, 71
178	*Squalus quasimodo*	VIANA et al., 2016	28/22		41
Squaliformes: Squalidae: no clade					
179	*Squalus hemipinnis*	WHITE et al., 2007c	26/23		57

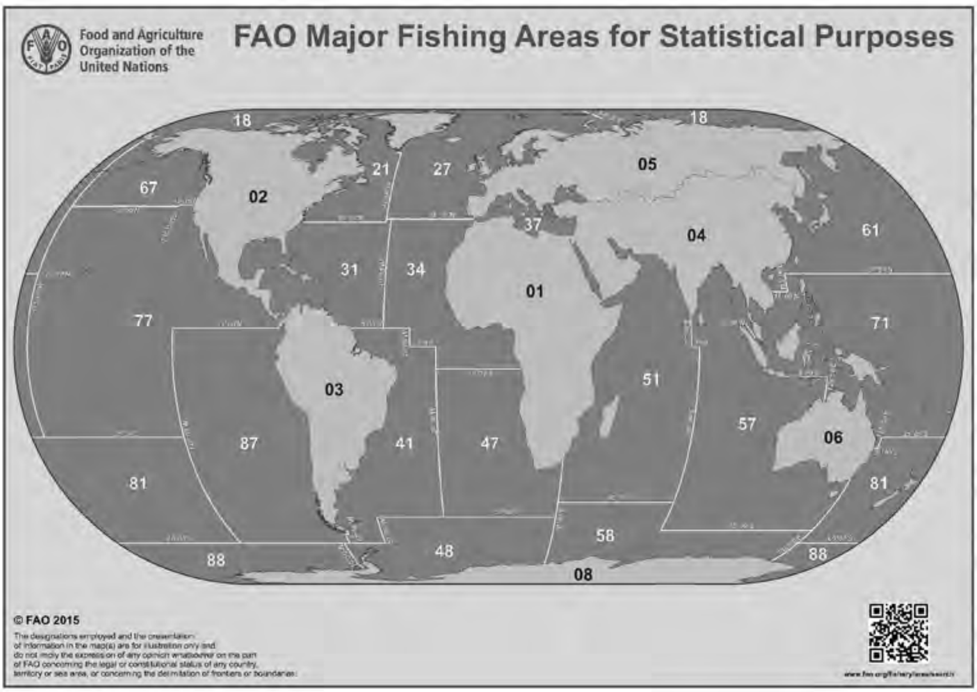


Fig. 1: Map of the FAO Major Fishing Areas (http://www.fao.org/fishery/area/search/en).
Abb. 1: Karte der Hauptfischereigebiete der FAO (http://www.fao.org/fishery/area/search/en).

3. Morphological identification key to teeth of squalomorph sharks

The following key has been developed for identification at the genus 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. Specific groups of teeth, such as symphyseal teeth or commissural teeth have not been taken into consideration. This key is most useful when teeth from the lateral area of the jaws are used.

Key to squalomorph genera based on dental characters: the number in brackets after genera names indicates the number of valid species (POLLERSPÖCK & STRAUBE 2019), for monospecific genera the corresponding species is indicated.

Tab. 2: FAO Major Fishing Areas (http://www.fao.org/fishery/area/search/en).
Tab. 2: Hauptfischereigebiete der FAO (http://www.fao.org/fishery/area/search/en).

Code	Major fishing areas	km²	%
	MARINE AREAS	360.900.000,00	100,00
	Atlantic Ocean and adjacent seas		
18	Arctic Sea	9.300.000,00	2,60
21	Atlantic, Northwest	6.300.000,00	1,70
27	Atlantic, Northeast	14.400.000,00	4,00
31	Atlantic, Western Central	14.500.000,00	4,00
34	Atlantic, Eastern Central	14.100.000,00	3,90
37	Mediterranean and Black Sea	3.000.000,00	0,80
41	Atlantic, Southwest	17.500.000,00	4,80
47	Atlantic, Southeast	18.300.000,00	5,10
	Indian Ocean		
51	Indian Ocean, Western	29.300.000,00	8,10
57	Indian Ocean, Eastern	31.100.000,00	8,60
	Pacific Ocean		
61	Pacific, Northwest	21.500.000,00	6,00
67	Pacific, Northeast	7.600.000,00	2,10
71	Pacific, Western Central	33.300.000,00	9,20
77	Pacific, Eastern Central	48.100.000,00	13,30
81	Pacific, Southwest	27.700.000,00	7,70
87	Pacific, Southeast	30.800.000,00	8,50
	Southern Ocean		
848	Atlantic, Antarctic	11.800.000,00	3,30
858	Indian Ocean, Antarctic	12.700.000,00	3,50
888	Pacific, Antarctic	9.600.000,00	2,70

3.1. Glossary (tooth morphological characters, after Casier 1961; Ledoux 1972; Cappetta 2012)

3.1.1. Glossary: orientation

Apical: direction towards the root tip (fig. 2).
Basal: direction towards the crown tip (fig. 2).
Distal: direction to roof of the mouth (fig. 2).
Labial: direction to mouth opening, outer face.
Lingual: direction to throat, inner face (fig. 2).
Mesial: direction towards the anterior midline of the jaw (fig. 2).
Occlusal: direction towards the biting surface.
Symphyseal tooth: usually one symmetrical tooth, crown mostly erected, position exactly midway between the two jaw halves (e.g. sometimes in the lower jaws of hexanchids or squalids).
Parasymphyseal tooth: first tooth of the right/left jaw side, reduced in size, distorted cusp, asymmetrical root.
Anterior teeth: teeth in the anterior region of the jaw, often characterized by a strongly erected crown; anterior squalomorph shark teeth are often less wide but higher compared to posterior teeth.
Posterior teeth: teeth in the posterior region of the jaw, often characterized by a distally inclined crown; posterior squalomorph shark teeth are

Tab. 3: Taxonomy of the superorder Squalomorphii.
Tab. 3: Taxonomie der Überordnung Squalomorphii.

Superorder	Order	Family	Genus	TL max in cm	max. width of the jaws in cm
Squalomorphii	Hexanchiformes	Chlamydoselachidae	*Chlamydoselachus*	200	20
		Hexanchidae	*Heptranchias*	140	14
			Hexanchus	550	55
			Notorynchus	300	30
	Pristiophoriformes	Pristiophoridae	*Pliotrema*	140	7
			Pristiophorus	160	8
	Squatiniformes	Squatinidae	*Squatina*	250	30
	Squaliformes	Echinorhinidae	*Echinorhinus*	450	45
		Centrophoridae	*Centrophorus*	170	17
			Deania	130	13
		Dalatiidae	*Dalatias*	190	19
			Euprotomicroides	50	5
			Euprotomicrus	30	3
			Heteroscymnoides	40	4
			Isistius	50	5
			Mollisquama	50	5
			Squaliolus	30	3
		Etmopteridae	*Aculeola*	70	7
			Centroscyllium	110	11
			Etmopterus	90	9
			Trigonognathus	60	6
		Oxynotidae	*Oxynotus*	150	15
		Somniosidae	*Centroscymnus*	130	13
			Scymnodalatias	110	11
			Scymnodon	170	17
			Somniosus	730	73
			Zameus	150	15
			Centroselachus	110	11
		Squalidae	*Cirrhigaleus*	130	13
			Squalus	200	20

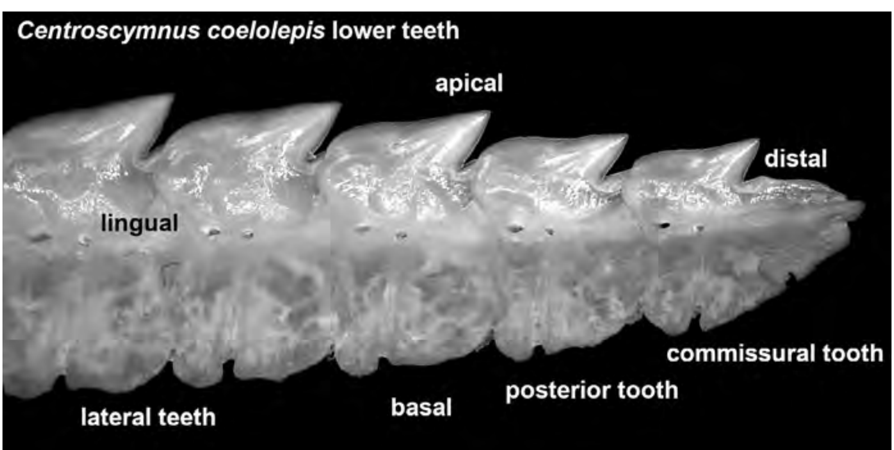


Fig. 2: Terms of orientation; lower teeth of *Centroscymnus coelolepis*.
Abb. 2: Begriffe der Orientierung; Unterkieferzähne von *Centroscymnus coelolepis*.

often wider and lower compared to anterior ones (fig. 2).

Commissural tooth: teeth near the corner of the mouth, in squalomorphs, especially in the lower jaw, one single commissural tooth is present and differs very clearly from the posterior one in its morphology (fig. 2).

3.1.2. Glossary: characters of tooth crown

Apron (Apr, fig. 3): also referred to as tablier, a variable long and thick labial expansion of the cusp (consist of an enameloid covered part of the root, e.g. species of the genera *Squalus* spp., *Squatina* spp.). Absent in various species of the genera *Hexanchus* spp., *Heptranchias* spp., *Echinorhinus* spp.

Distal/mesial cusplets: small, left and/or right arranged cusplets (e.g. at the upper jaw teeth of *Etmopterus* spp. or the upper/lower teeth of *Centroscyllium* spp.).

Distal/mesial cutting edge: enameloid margin of the tooth; the cutting edge can e.g. be absent, partially present or ranging from the top to the crown base.

Comb- or sawblade-like tooth: multicuspid tooth with the distinctive character that the first mesial cusp is always the largest and size of consecutive cusps decrease gradually towards distal.

Talon or mesial/distal heel (Dih, Mhe, fig. 3): squalomorph teeth without cusplets often show mesially and/or distally prolonged more or less marked enameloid heels at the bases of the cusp.

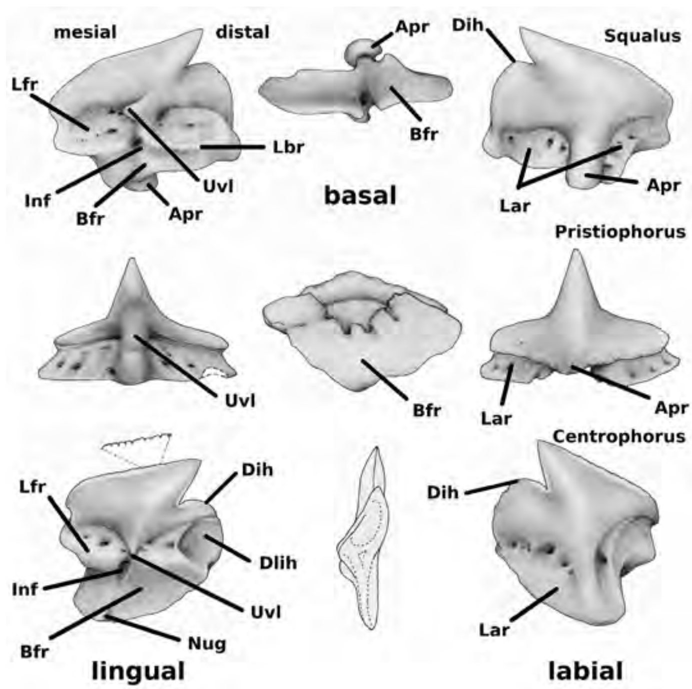


Fig. 3: Squalomorph tooth forms; abbreviations: Apr (apron); Nug (nutritive or basal groove), Bfr (basal face of the root), Lar (labial face of the root), Lfr (lingual face of the root), Dih (distal heel or talon), Uvl (uvula), Dlih (distolingual hollow or overlapping surface), Inf (infundibulum or central lingual foramen), Lbr (lingual bulge of the root). © drawings: Helmut Bracher, Altdorf.

Abb. 3: Squalomorphe Zahnformen; Abkürzungen: Apr (Apron); Nug (Basalfurche), Bfr (basale Wurzelfläche), Lar (labiale Wurzelfläche), Lfr (linguale Wurzelfläche), Dih (distaler Höcker, Talon), Uvl (Uvula), Dlih (distolinguale Überlappungsfläche), Inf (Infundibulum oder zentrales linguales Foramen), Lbr (lingualer Wurzelgrat). © Zeichnungen: Helmut Bracher, Altdorf.

Uvula (Uvl, fig. 3): like an apron, mostly short and conical, only at the lingual side of the tooth and sometimes very distinctive (e.g. *Squalus* spp., *Deania* spp., *Centrophorus* spp.). Absent in various genera (e.g. *Hexanchus* spp., *Heptranchias* spp., *Echinorhinus* spp.).

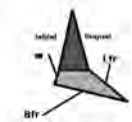
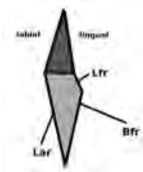
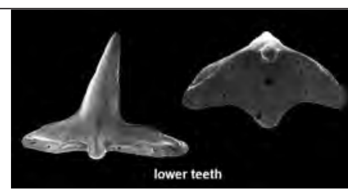
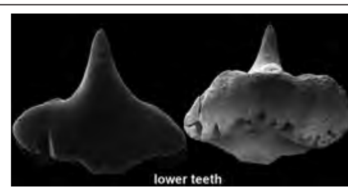
3.1.3. Glossary: characters of the tooth root

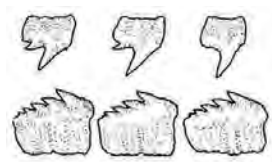
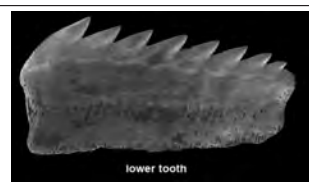
Basal face of the root (Bfr, fig. 3): the part of the root with which the tooth is connected to the jaw, in several studies (e.g. Kitamura 2013; Welton 2016), this part of the root is falsely referred to as the lingual root face, in squalomorph teeth, the basal root face is often separated by a horizontal ridge (= lingual bulge of the root) from the lingual face of the root.
Nutritive or basal groove (Nug, fig. 3) or Sulcus: lingual pronounced groove, which usually begins at the base of the root and ends in a central foramen.
Foramen: Openings for e.g. blood and nerve vessels, the foramen are differentiated according to their location (labial/lingual/mesial/distal/axial or central) and size.
Labial face of the root (Lar): see figure 3.
Lingual face of the root (Lfr): see figure 3.
Root vascularization: how the tooth is supplied with the necessary nutrients. There are four basic evolutionary systems (after Casier 1961):
a) anaulacorhizid stage: several, mostly smaller and irregularly scattered foramina are present on both sides of the root (e.g., in hybodontoids, notidanoids and presquatinoid tooth types); according to Casier (1961) squaliform sharks teeth belong to the anaulacorhizid stage.
b) Hemiaulacorhizid stage: medial vascular canal opens into a centralized foramen at the basal face of the root. This face is more or less perpendicular to the axis of the crown (typical of squatinoid, orectoloboid or chlamydoselachid tooth types).
c) Holaulacorhizid stage: central foramen ends in a nutritive or basal groove that divides the basal surface of the root into two areas (typically at scyliorhinoid or rhinobatoid tooth types, e.g. order Lamniformes, Carcharhiniformes, Rajiformes, Torpediniformes and some myliobatiforms).
d) Polyaulacorhizid stage: transverse enlargement of the root, which is often separated by more or less wide and deep parallel laminae with several small foramina, is developed. This stage especially occurs in myliobatoid tooth types.
Button hole or Boutonnière: this hole of the root is created by the union of a central lingual and labial foramen. According to Casier (1961) this character is present especially in *Dalatias licha* and *Isistius* spp.
Infundibulum: central labial and lingual foramen merged to a central labial foramen, e.g. *Somniosus* spp., *Squalus* spp., *Centrophorus* spp.
Mesial labial hollow/distal lingual hollow or overlapping surface: typical character that occurs essentially only in squaliform lower teeth and differs greatly within the different genera. With the exception of the last tooth in the dentition (commissural tooth), all lower jaw teeth have two overlapping surfaces.
Root lobes: root split in two long and distinct branches; usually not present in lower squalomorph shark teeth, typical for e.g. galeomorph shark teeth.

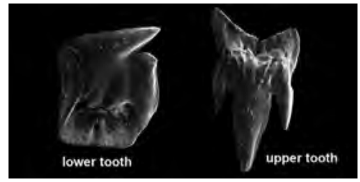
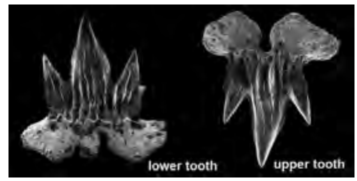
3.1.4. Glossary: heterodonty/homodonty

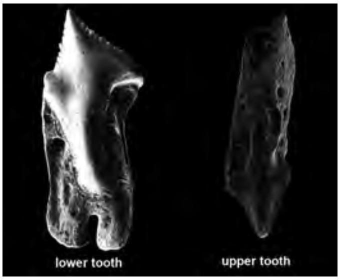
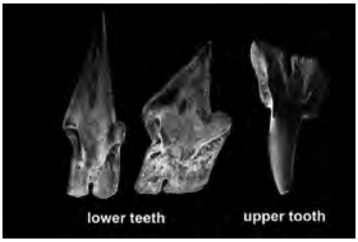
Dignathic heterodonty: present, when teeth of upper and lower jaws have different morphologies.
Disjunct monognathic heterodonty: different type of teeth present in one jaw, e.g. symphyseal, parasymphyseal, anterior, lateral or posterior teeth.
Gradient monognathic heterodonty: tooth morphology changes continuously from row to row within one jaw.
Gynandric or sexual heterodonty (sexual dimorphism): present if teeth of both sexes differ in morphology.
Homodonty: teeth in the upper and lower jaws show a very similar morphology.

3.2. Morphological identification key

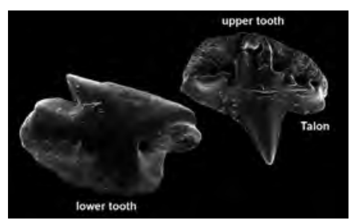
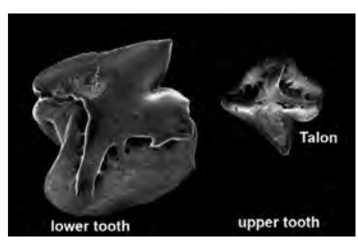
1	a	Basal face of the root (Bfr) at (approximately) right angle to the crown, hemiaulacorhizid vascularisations stage: → 2	
1	b	Basal face of the root (Bfr) almost in a line with the crown, anaulacorhizid vascularisations stage: → 4	
2	a	Upper and lower teeth multicuspid: → ***Chlamydoselachus* (2)**	
2	b	Upper and lower teeth monocuspid: → 3	
3	a	Labial apron conical, overhanging the basis of the root, crown high erected, slender: → ***Squatina* (24)**	
3	b	Labial apron clearly rectangular, (not) overhanging the basis of the root, crown low, wide at the base of the crown: → ***Pliotrema* (*Pliotrema warreni* Regan, 1906a)**	
3	c	Labial apron weak developed, (not) overhanging the basis of the root, crown low, wide at the base of the crown: → ***Pristiophorus* (7)**	
4	a	Lateral upper and lower teeth multicuspid and comb- or sawblade-like: → 5	

4	**b**	Lateral upper and lower teeth mono- or multicuspid, but **<u>not</u>** comb- or sawblade-like: → **7**	
5	**a**	Cusps of the lateral lower teeth gradually decreasing in size, distal cusp always smaller than the previous one: → **6**	
5	**b**	Cusps of the lateral lower teeth not gradually decreasing in size, distal cusp always smaller than the previous one, distal cusps with sometimes the same size or larger than the previous one: → ***Heptranchias - H. perlo*** **(Bonnaterre, 1788)**	
6	**a**	Number of cusplets on lateral lower teeth 3-5, ratio of lateral lower teeth approximate height to width 1/1: → ***Notorynchus - N. cepedianus*** **(Péron, 1807)**	
6	**b**	Number of cusplets on lateral lower teeth 6-11, lateral lower teeth significantly wider than high: → ***Hexanchus*** **(3)**	
7	**a**	Lateral lower teeth always wider than high: → ***Echinorhinus*** **(2)** Remarks: distinct ontogenetic heterodonty (juvenile: without mesial/distal cusplets, adult with mesial/distal cusplets) and monognathic heterodonty (number of the cusplets) present	
7	**b**	Lateral lower teeth always higher than wide: → **8**	

8	**a**	Upper teeth multicuspid, lower teeth monocuspid: → ***Etmopterus* (41)**	
8	**b**	Upper teeth multicuspid, lower teeth multicuspid: → ***Centroscyllium* (7)**	
8	**c**	Upper teeth monocuspid, lower teeth monocuspid: → **9**	
9	**a**	Anterior and lateral lower teeth always erected vertically / approximately vertically, no mesial or distal heel (talon) present, lower teeth wide, crown shape triangular: → ***Isistius* (2)**	
9	**b**	Anterior and lateral lower teeth always erected vertically / approximately vertically, no mesial or distal heel (talon) present, upper and lower teeth slender, anterior teeth lingual and labial with weak enameloid folds, crown dagger-shaped, crown sigmoidal in profile, big gaps between the teeth, basal view of the root outline oval, no root lobes, homodont dentition: → ***Trigonognathus - T. kabeyai* Mochizuki & Ohe 1990**	
9	**c**	Lateral lower teeth always erected vertically / approximately vertically, no mesial or distal heel (talon) present, strong lingually ornamentation, particularly at the basis of the crown, root bilobed → ***Aculeola - A. nigra* de Buen 1959**	

9	**d**	Anterior and lateral lower teeth always erected vertically / approximately vertically, mesial or distal heel (talon) present: → **10**	
9	**e**	Anterior and lateral lower teeth clearly inclined distally, mesial or distal heel (talon) present: → **11**	
10	**a**	Mesial and distal cutting edge of the main cusp serrated, long monolobed apron, prominent labial central foramen absent, base of the apron arched and clearly bordered to the root: → ***Oxynotus*** **(5)**	
10	**b**	Mesial and distal cutting edge of the main cusp serrated, long bilobed apron, prominent labial central foramen present, enclosed by the apron, base of the apron clearly bordered to the root: → ***Dalatias*** **-** ***D. licha*** **(Bonnaterre 1788)**	
10	**c**	Mesial and distal cutting edge of the main cusp not serrated, apron is reaching approximately to the middle of the root, wide near the crown-root border, reducing towards the base, base of the apron arched and clearly bordered to the root: → ***Scymnodon*** **(4)**	

10	**d**	Mesial and distal cutting edge of the main cusp not serrated, apron is reaching approximately to the middle of the root, wide near the crown-root border, broadening towards the base, not clearly bordered to the root: → ***Zameus – Z. squamulosus* (Günther 1877)**	
10	**e**	Mesial and distal cutting edge of the main cusp not serrated, apron long, reaching over the middle of the root, broadening towards the base, not clearly bordered to the root, looks frayed: → ***Scymnodalatias* (4)**	
10	**f**	Mesial and distal cutting edge of the main cusp not serrated, apron long, reaching over the middle of the root, very wide, reaching across the whole crown-root border, slightly curled lower edge, bordered by several foramina: → ***Euprotomicroides – E. zantedeschia* Hulley & Penrith, 1966**	
11	**a**	Anterior and lateral lower teeth clearly inclined distally, mesial or distal heel (talon) present, apron monolobed: **→ 12**	
11	**b**	Anterior and lateral lower teeth clearly inclined distally, mesial or distal heel (talon) present, apron bilobed: **→ 16**	

12	a	Dignathic homodont dentition in the upper and lower jaw, very strong distinct conical apron, basal face of the root at right angles to the labial/lingual face of the root: → ***Squalus* (35)*** → ***Cirrhigaleus* (3)*** *** from a tooth-morphological perspective, *Squalus* and *Cirrhigaleus* are indistinguishable at the present state of knowledge**	
12	b	Heterodont dentition in the upper and lower jaw: → 13	
13	a	Lateral upper teeth wide, distal heel (talon) present: → 14	
13	b	Lateral upper teeth narrow, distal heel (talon) absent: → 15	
14	a	Lateral lower teeth always wider than high: → ***Deania* (4)**	
14	b	Lateral lower teeth approximately at least as wide as high: → ***Centrophorus* (12)** *Remarks: Another clear distinguishing character between the two genera is present in the lower jaw teeth on the lingual side present. In *Deania* there is always a central foramen above and below the lingual bulge of the root, in *Centrophorus* this bulge is broken by a central foramen (infundibulum).	

15	a	Apron of the lateral lower teeth long, reaching almost to the basis of the root, crown strongly inclined distally (<45°): → ***Centroscymnus*** **(2)**	
15	b	Apron of the lateral lower teeth short, wide, crown weakly inclined distally (>45°<80°): → ***Centroselachus*** **-** ***C. crepidater*** **(Barbosa Du Bocage & de Brito Capello 1864)**	
15	c	Apron of the lateral lower teeth short, narrow, pointed, crown strongly inclined distally (<45°): → ***Somniosus*** **(5)** *Remarks: According to HERMAN et al. (1989) the genus can be divided into two morphological groups: the *microcephalus* group, which labial apron is extremely narrow and pointed (picture 1) and in the *rostratus* group, which has a short but wider apron (picture 2).	
16	a	Apron bilobed, both parts of the apron narrow, prominent labial central foramen in the upper third of the root present, enclosed by the apron: → ***Euprotomicrus*** **-** ***E. bispinatus*** **(Quoy & Gaimard 1824)**	
16	b	Apron bilobed, both parts of the apron wide, prominent labial central foramen in the middle of the root present, enclosed by the apron: → ***Squaliolus*** **(2)**	

16	**c**	Apron bilobed, both parts of the apron wide, prominent labial central foramen in the lower third of the root present, enclosed by the apron: → ***Heteroscymnoides - H. marleyi*** **Fowler 1934**	

©: SEM-images: J. Herman, Belgium; drawings from Compagno (1984a, b).
* The identification key does not include the genus *Mollisquama* (monotypic: *Mollisquama parini* Dolganov, 1984), as only line drawings or phase-contrast synchrotron microtomographic scan of the teeth are available (Dolganov 1984; Cigala-Fulgosi 1996; Denton et al. 2018). These figures illustrate lower teeth, which show a mesial talon, a slender and pointed cusp and an overlapping area, which reaches to the base of the root. The teeth appear morphologically close to *Euprotomicroides*.

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