

## Morphological Comparison of *Squalus blainvillei* and *S. megalops* in the Eastern Atlantic, with Notes on the Genus

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**Abstract** Morphological comparisons are made from the study of 64 specimens belonging to the following species: *Squalus acanthias*, *S. blainvillei*, *S. megalops* and *S. acutirostris*. The results suggest conspecificity between *S. acutipinnis* and *S. megalops*. The differences between *S. blainvillei* and *S. megalops* in the E-Atlantic are stressed. The Indo-Pacific species called *S. blainvillei* by Chen et al. (1979) is regarded in this paper as probably an undescribed species. Some consideration on the status of several nominal species and the species grouping within *Squalus* are also made.

Most elasmobranch taxonomists agree that the taxonomy and relationships of the worldwide genus *Squalus* are subjected to some degree of confusion. Several nominal species have been locally described without an extensive comparison of material, resulting in a complex synonymy.

The first attempt to revise the genus was made by Bigelow and Schroeder (1948, 1957) who established three species groups, headed respectively by *S. acanthias*, *S. fernandinus*, and *S. megalops*-*S. cubensis*. This grouping has been accepted by many authors with some modifications (Garrick, 1960; Bass et al., 1976; Chen et al., 1979). For example, *S. fernandinus*, in its original description, was recorded as having an ocellated body and was treated as a junior synonym of *S. acanthias* by Garrick (1960).

The features defining these groups and the main nominal species in each one, after the quoted authors, are as follows:

*Squalus acanthias* group: Spine of the first dorsal fin over or behind the inner pectoral fin corner; dermal denticles tricuspidate; generally with white spots along the upper half of the trunk. *S. acanthias* Linnaeus, 1758, *S. suckleyi* (Girard, 1854) and *S. fernandinus* Molina, 1782 are commonly included in this group, though the latter two have been regarded as synonyms of the first one (Garrick, 1960; Compagno, 1984).

*S. blainvillei* group (Bigelow and Schroeder's *fernandinus* group): Spine of the first dorsal fin before the rounded inner pectoral corner. Dermal denticles tricuspidate. *S. mitsukurii* Jordan et Snyder (in Jordan and Fowler, 1903), *S. japonicus*

Ishikawa, 1908 and *S. blainvillei* (Risso, 1826) are included in this group after Chen et al. (1979). Other nominal species are quoted by Bigelow and Schroeder (1957).

*S. megalops*-*S. cubensis* group: Dorsal fin position and absence of white spots as in the *S. blainvillei* group, but these species possess pointed inner corner and concave posterior margin of the pectoral fins, dagger-shaped dermal denticles and thick-bodied shape. Four nominal species are usually deemed as belonging to this group: *S. megalops* MacLeay, 1881, described from southern Australia, *S. acutipinnis* Regan, 1908, found in SE-Atlantic, *S. cubensis* Rivero, 1936, and *S. brevirostris* Tanaka, 1917, species from the Caribbean Sea and western Pacific, respectively.

A fourth group would be constituted by two species, after Bass et al. (1976): *S. barbifer* (Tanaka, 1912) and *S. asper* Merret, 1973. However, the inclusion of both species in the genus *Squalus* is arguable, since *S. barbifer* has been most commonly included in the genus *Cirrhigaleus* Tanaka, 1912, as accepted by Bass (1979) and Compagno (1984).

Two other species, *S. melanurus* and *S. rancureli*, have been recently described by Fourmanoir and Rivaton (1979). These long-snouted species seem to be morphologically related to *S. japonicus*, but comparative studies will be necessary to establish their relationships with other *Squalus* species. Another moderately long-snouted species is *S. acutirostris* Zhu, Meng et Li, 1984, described from the South China Sea and recorded in this paper from the southern Australia waters.

Some authors do not agree with the grouping of species made by Bigelow and Schroeder (1948). Ledoux (1970) stated that *S. blainvillei* was a polytypic species, with *S. megalops* and *S. cubensis* as extreme subspecies. However, part of his observations was based on the Mediterranean *S. megalops* (see Muñoz-Chápuli et al., 1984). Merret (1973) pointed out a close similarity between *S. blainvillei* and *S. megalops*, when compared phenetically with *S. acanthias* and *S. asper*. Cadenat and Blache (1981) suggested synonymy of all species of the *megalops-cubensis* group with *S. megalops*.

The aim of this paper is to review the grouping of species within *Squalus* and to clarify the status of the species inhabiting the E-Atlantic and Mediterranean. Two species are commonly recorded in this area, *S. acanthias* and *S. blainvillei* (sometimes recorded as *S. fernandinus*). However, we have found a third species belonging to the *megalops-cubensis* group. Since *S. acanthias* is a well-known spurdog fish, the study was focused on the other two species.

The results agree with Bass et al. (1976) and Compagno (1984) recognizing conspecificity of *S. megalops* and *S. acutipinnis* (at least sensu Krefft, 1968). For this reason, specimens collected from the E-Atlantic will herein be called *S. megalops*, defining their locality when it is necessary. The Indo-Pacific species called *S. blainvillei* by Chen et al. (1979) will be referred in this paper as *Squalus* sp. because of the reasons stated in the discussion.

### Material studied

*Squalus acanthias*: UMDZ (University of Málaga, Department of Zoology) 83030901, mature male, and other six uncatalogued specimens, two males and four females, 386–788 mm TL. All caught off Málaga (southern Spain), 300–400 m depth.

*Squalus blainvillei*: UMDZ 83012501, mature male, 560 mm TL; UMDZ 83071305, male, 730 mm TL; UMDZ 83072001, male, 713 mm TL; UMDZ 83072701, male, 695 mm TL; UMDZ 83101703, male, 706 mm TL; UMDZ 83022404, male, 700 mm TL; UMDZ 84102604, male, 720 mm TL; UMDZ 84111506, female, 728 mm TL; UMDZ 84111507, male, 720 mm TL; UMDZ 84112202, female, 890 mm TL; UMDZ 85020504, male, 484 mm TL; Other four uncatalogued specimens, two males and two females, 402–740 mm TL. All caught off the Atlantic and

Mediterranean coasts of Morocco and southern Spain.

E-Atlantic *Squalus megalops*: UMDZ 83011201, female, 585 mm TL; UMDZ 83080501, male, 560 mm TL; UMDZ 83082401, male, 558 mm TL; UMDZ 83091401, male, 545 mm TL; UMDZ 83110806, male, 328 mm TL; UMDZ 83111605, male, 570 mm TL; UMDZ 83112403, male, 485 mm TL; UMDZ 83112802, male, 492 mm TL; UMDZ 84012503, male, 613 mm TL; UMDZ 84012504, male, 534 mm TL; UMDZ 84020804, male, 517 mm TL; UMDZ 84022205, male, 492 mm TL; UMDZ 84022206, male, 492 mm TL; UMDZ 84040905, male, 547 mm TL; UMDZ 84062602, male, 574 mm TL; UMDZ 84062603, female, 680 mm TL; UMDZ 84070704, male, 458 mm TL; UMDZ 84072708, male, 585 mm TL; UMDZ 84072709, male, 560 mm TL; UMDZ 84072711, male, 530 mm TL; UMDZ 84022207, male, 495 mm TL; UMDZ 84072712, male, 561 mm TL; UMDZ 84090608, male, 473 mm TL; UMDZ 84090609, female, 462 mm TL; UMDZ 84110205, female, 712 mm TL; UMDZ 84110206, female, 359 mm TL; UMDZ 84110207, female, 370 mm TL; Other seven uncatalogued specimens, two males and five females, 318–742 mm TL. All caught in the northeastern Atlantic, from off the Mauritanian coast to southern Portugal and the Alboran Sea (western Mediterranean).

Indo-Pacific *Squalus megalops*: An uncatalogued specimen, mature male, 444 mm TL; collected off New South Wales, donated by the Australian Museum.

*Squalus cubensis*: Two uncatalogued specimens, mature male and female, 546 and 690 mm TL, respectively. Three embryos obtained from the above female specimen. Caught off San Juan (Puerto Rico), 380–440 m depth, and donated by the Florida State Museum, University of Florida.

*Squalus* sp.: An uncatalogued female, 615 mm TL, from New South Wales, donated by the Australian Museum.

*Squalus acutirostris*: A mature male, 607 mm TL, caught off New South Wales, donated by the Australian Museum.

### Methods

Measurements of the specimens were done according to the criteria described by Bigelow and Schroeder (1948). All were expressed as percent of the total length (TL).

The chondrocrania were cleaned in hot water. Chondrocranial measurements were expressed as percent of the total length of chondrocranium (TLC).

Vertebral numbers were established by dissection, boiling or from radiographs, according to

Table 1. Measurements of the studied *Squalus* specimens in % of TL.

Locality	<i>S. blainvillei</i>			<i>S. megalops</i>			<i>S. cubensis</i>			<i>Squalus</i> sp.	<i>S. acutirostris</i>
	E-Atlantic and Mediterranean						Australia	Puerto Rico		Australia	Australia
	Sex	10M, 5F			23M, 11F		M	M	F	F	M
Size range (mm TL)	N	402-890	SD	N	318-742	SD	444	546	690	615	607
Snout tip to:											
Nostrils	15	3.41	0.65	34	3.49	0.57	3.15	3.10	3.23	3.14	4.45
Eye	15	5.55	0.78	34	6.01	0.51	5.99	5.71	5.51	5.67	7.25
Mouth	8	8.40	0.44	25	8.65	0.53	9.73	9.80	9.32	8.98	10.61
1st gill opening	15	16.68	0.78	34	16.62	0.88	17.79	18.86	16.81	17.79	17.99
5th gill opening	15	20.50	0.95	35	19.97	1.03	20.20	22.53	20.72	21.79	23.06
1st dorsal fin	14	28.53	0.97	34	28.99	0.89	29.32	29.12	28.55	27.15	31.47
Anus (anterior edge)	14	50.57	1.37	34	49.18	2.06	48.87	50.37	49.13	49.76	50.25
Upper caudal origin	15	78.93	0.89	34	78.92	1.08	79.95	81.87	77.97	77.40	80.07
Distance between bases:											
1st and 2nd dorsal	14	25.82	2.11	34	24.49	1.99	27.25	27.11	28.26	24.39	26.04
2nd dorsal and caudal	15	11.03	0.47	34	11.16	0.60	10.20	11.36	10.14	10.10	10.76
Pectoral and pelvic	15	22.89	1.55	33	23.10	2.64	21.44	22.16	21.16	22.93	20.10
Pelvic and caudal	12	27.26	1.13	30	27.73	1.44	17.70	28.75	25.80	25.69	26.69
Nostrils:											
Between inner corners	15	4.53	0.48	34	3.83	0.26	4.64	4.30	4.13	4.93	4.86
Between outer corners	15	6.79	0.59	34	6.58	0.57	7.39	7.51	7.35	7.93	7.97
Length	15	1.48	0.28	34	1.60	0.20	1.37	1.83	1.67	1.66	1.58
Mouth:											
Width	15	7.49	0.89	34	7.69	0.45	7.39	7.51	7.35	7.93	7.97
Length of preoral clefts	15	2.85	0.92	33	3.30	1.10	4.98	4.95	4.36	—	—
Eye:											
Diameter	15	4.03	0.39	33	4.27	0.53	4.84	5.22	4.58	4.59	4.99
Spiracles:											
Distance between inner tips	15	8.11	0.90	33	8.10	0.60	9.30	8.08	8.70	8.83	8.38

<b>Gill openings:</b>											
Length of 1st	15	1.95	0.23	34	2.00	0.30	2.03	1.96	1.96	2.16	1.58
Length of 3rd	15	2.23	0.26	34	2.09	0.24	2.23	2.14	2.36	2.31	1.73
Length of 5th	15	2.49	0.42	34	2.46	0.39	2.45	2.62	2.39	2.50	1.94
Distance 1st and 5th	15	4.18	0.63	34	4.48	0.92	3.72	3.17	4.09	3.50	3.91
<b>1st dorsal fin:</b>											
Base length	14	8.44	1.54	34	8.06	0.57	7.07	7.73	8.91	8.23	6.67
Height	15	8.09	0.61	34	8.48	0.81	7.14	7.33	8.49	9.80	7.23
Free posterior margin	15	6.10	0.53	34	6.72	0.54	6.19	6.08	6.39	6.78	—
Length of exposed spine	14	4.32	0.71	30	4.63	0.49	3.22	3.85	4.97	5.25	2.59
<b>2nd dorsal fin:</b>											
Base length	14	6.42	1.27	34	6.98	1.40	6.24	5.00	5.41	8.18	7.53
Height	15	4.46	0.56	34	5.20	1.10	3.83	4.40	5.26	5.01	4.17
Free posterior margin	15	4.79	0.46	34	5.47	0.38	5.32	5.11	5.51	5.06	4.60
Length of exposed spine	13	4.92	0.94	32	5.37	0.92	—	5.42	5.93	5.25	2.59
<b>Pectoral fins:</b>											
Base length	15	6.77	0.70	32	6.51	0.76	5.32	4.69	4.93	6.02	5.50
Length anterior margin	15	13.99	1.02	34	15.30	0.83	13.18	13.42	15.13	16.01	14.22
Length posterior margin	15	11.10	0.80	34	12.20	0.97	11.31	11.17	13.26	12.80	10.08
Length inner margin	15	7.18	0.51	34	9.34	0.69	10.27	9.32	9.30	7.54	7.61
<b>Pelvic fins:</b>											
Length anterior margin	15	5.86	0.72	34	6.36	0.65	5.34	6.01	5.42	6.10	6.18
Overall length	15	9.69	0.68	34	11.21	1.15	11.17	11.17	10.25	10.47	10.87
<b>Caudal fin:</b>											
Length upper margin	15	21.10	0.54	34	21.36	0.76	20.36	20.33	22.03	24.88	20.43
Length lower margin	14	11.08	0.70	34	11.39	1.14	10.47	10.99	10.87	12.85	11.19
<b>Trunk at pectoral origin:</b>											
Width	8	11.72	0.94	19	11.29	0.59	13.42	12.42	12.75	13.77	8.00

the criteria stated by Springer and Garrick (1964).

Skin samples for the observation of dermal denticles were obtained from the laterodorsal area, anterior to the first dorsal spine. Dermal denticles were observed and photographed by scanning electronic microscopy (SEM).

Clasper skeleton was studied by dissection, boiling or maceration of the claspers in a KOH bath. Clasper terminology followed Leigh-Sharpe (1920).

## Results

**Body measurements.** Table 1 shows body measurement values of the study material. Measurements for 40 characters were compared between *S. blainvillei* and E-Atlantic *S. megalops* through a t-Student test of difference between means (Table 2). Out of these, 11 showed significant differences ( $p < 0.05$ ). *S. megalops* had a longer snout, shorter trunk, more closely placed nasal openings and dorsal fins, longer basal free margin in both dorsal fins and larger paired fins than *S. blainvillei*. The most striking difference was the length of the inner pectoral margin. Specimens possessing inner margins of pectoral fins more than 8.3% TL belong to *S. megalops* at the 95% confidence level (Muñoz-Chápuli et al., 1984).

Our measurements agree in general with those given by Bass et al. (1976) for South African *S. blainvillei* and *S. megalops*, though a detailed comparison is difficult because of the way in which these authors show the morphometric results. Comparison between our data on *S. blainvillei* and the measurements given by Garrick (1970) for this species is shown in Table 3.

According to Krefft (1968), the *S. acutipinnis* specimens proceeding from the E-Atlantic can be distinguished from the Indo-Pacific *S. megalops* in having a shorter and broader snout and slightly longer pectorals. Bass et al. (1976) remarked that Krefft's statements were partially based on data given by Garrick (1960) for *S. blainvillei*; thus, these differences were not tenable. Table 1 shows some differences between the only Indo-Pacific measured specimen of *S. megalops* and the E-Atlantic samples. The differences are mainly related to the size of the pectoral and both dorsal fins and spines (lower and shorter in the Indo-Pacific specimen). The measurements given by Garrick (1960) for *S. megalops* from New Zealand clearly agree with those of our Indo-Pacific specimen. These data will be dealt with in the discussion.

Measurements of only two specimens of *S. cubensis* did not allow any statistical comparison,

Table 2. Morphometrical comparison between *Squalus blainvillei* and *S. megalops*. \*  $p < 0.05$ ; \*\*  $p < 0.01$ .

Species:	<i>S. blainvillei</i>		<i>S. megalops</i>		Degrees of freedom	t-Student
	Mean	SD	Mean	SD		
Snout tip to:						
Eye	5.55	0.78	6.01	0.51	47	2.38*
Anus	50.57	1.37	49.18	2.06	46	2.26*
Distance between bases:						
1st and 2nd dorsal	25.82	2.11	24.49	1.99	46	2.03*
Nostrils:						
Distance between inner corners	4.53	0.48	3.83	0.26	47	6.39**
1st dorsal fin:						
Free posterior margin	6.1	0.53	6.72	0.54	47	3.58**
2nd dorsal fin:						
Height	4.46	0.56	5.2	1.1	47	2.38*
Free posterior margin	4.79	0.46	5.47	0.38	47	5.18**
Pectoral fins:						
Length of anterior margin	13.99	1.02	15.3	0.83	47	5.63**
Length of posterior margin	11.1	0.8	12.2	0.97	47	3.76**
Length of inner margin	7.18	0.51	9.34	0.69	47	10.64**
Pelvic fins:						
Overall length	9.69	0.68	11.21	1.15	47	4.67**

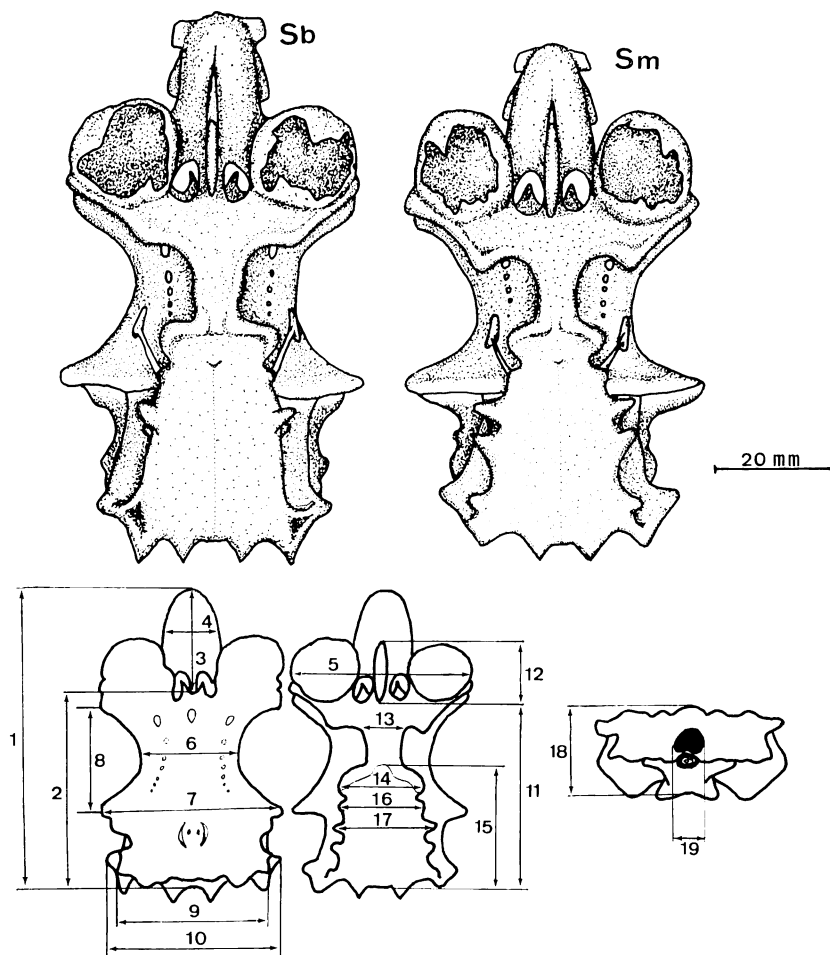


Fig. 1. Chondrocrania of *Squalus*. Above: *S. blainvillei* (Sb), UMDZ 83072701, male, 695 mm TL, and *S. megalops* (Sm), UMDZ 84012503, male, 613 mm TL. Below: Measurement scheme for chondrocrania. The numbers are the same as in Table 4.

although some differences can be seen in Table 1. The studied specimens showed a longer and wider snout and head, narrower mouth, more separated dorsal fins and shorter pectoral fin base than the E-Atlantic *S. megalops*.

The specimen of *Squalus* sp. from Australia fits very well with the specimens described by Chen et al. (1979) as *S. blainvillei*, especially in the size of the caudal and the height of both first dorsal fin and spine, larger than in any other studied species of the genus.

The specimen of *S. acutirostris* can be differentiated from the remaining species by its longer snout tip-eye distance, comprised about twice in the length of the anterior pectoral margin, and its

tricuspidate dermal denticles. These are in accordance with the original diagnosis by Zhu et al. (1984).

**Chondrocranial measurements.** The chondrocranial measurements made on *S. blainvillei* and the E-Atlantic *S. megalops* are shown in Table 4. Nine of the 19 sample means compared between these species are significantly different in a t-Student test ( $p < 0.05$ ). The chondrocranium of *S. megalops* has a wider precerebral fenestra, lesser interorbital distance, narrower olfactory capsules, lesser subethmoidean width, larger foramen magnum and, especially, a narrower anterior basal plate than those of *S. blainvillei*, resulting in a lighter chondrocranium.

Table 3. Comparison between measurements of *Squalus blainvillei* (E-Atlantic and W-Pacific) and *Squalus* sp. \*Measured from spine base.

	<i>Squalus blainvillei</i>						<i>Squalus</i> sp.		
	This paper			Garrick (1960)			Chen et al. (1979)		
	Locality	E-Atlantic-Mediterranean		W-Pacific (New Zealand)			W-Pacific (Japan)		
Sex		10M, 5F		3F			1M, 4F		
Size range (mm TL)		402-890		545-1008			631-814		
Snout tip to:									
Nostrils	15	3.41	0.65	—	—	—	5	3.20	0.22
Eye	15	5.55	0.78	3	6.30	0.46	5	5.74	0.41
Mouth	8	8.40	0.44	—	—	—	5	8.64	0.13
1st gill opening	15	16.68	0.78	3	17.16	0.25	5	17.36	0.58
5th gill opening	15	20.50	0.95	3	20.83	0.45	5	20.86	0.72
1st dorsal fin	14	28.53	0.97	3	32.57*	0.81	5	30.70*	0.92
Anus (anterior edge)	14	50.57	1.37	3	51.00	2.64	—	—	—
Upper caudal origin	15	78.93	0.89	3	79.57	1.83	5	79.10	0.86
Distance between bases:									
1st and 2nd dorsal	14	25.82	1.11	3	28.43*	0.66	5	29.00	0.85
2nd dorsal and caudal	15	11.03	0.47	3	9.77	0.65	5	10.36	0.37
Pectoral and pelvic	15	22.89	1.55	—	—	—	—	—	—
Pelvic and caudal	12	27.26	1.13	3	22.87	0.83	—	—	—
Nostrils:									
Between inner corners	15	4.53	0.48	3	4.77	0.32	5	4.68	0.22
Between outer corners	15	6.79	0.59	—	—	—	—	—	—
Length	15	1.48	0.28	—	—	—	—	—	—
Mouth:									
Width	15	7.49	0.89	3	5.83	0.11	5	7.88	0.50
Length of preoral clefts	15	2.85	0.92	—	—	—	—	—	—
Eye:									
Diameter	15	4.03	0.39	3	4.37	0.21	5	4.24	0.24
Spiracles:									
Distance between inner tips	15	8.11	0.90	—	—	—	—	—	—

Gill openings:									
Length of 1st	15	1.95	0.23	3	1.90	0.42	5	1.76	0.27
Length of 3rd	15	2.23	0.26	—	—	—	5	2.06	0.11
Length of 5th	15	2.49	0.42	3	2.33	0.21	5	2.38	0.08
Distance 1st and 5th	15	4.18	0.63	—	—	—	—	—	—
1st dorsal fin:									
Base length	14	8.44	1.54	3	6.07*	0.68	5	5.82*	0.19
Height	15	8.09	0.61	3	8.03	0.15	5	9.70	0.46
Free posterior margin	15	6.10	0.53	—	—	—	—	—	—
Length of exposed spine	14	4.32	0.71	—	—	—	4	6.27	0.76
2nd dorsal fin:									
Base length	14	6.42	1.27	3	4.80*	0.78	5	4.1*	0.64
Height	15	4.46	0.56	3	4.93	0.32	5	5.76	0.36
Free posterior margin	15	4.79	0.46	—	—	—	—	—	—
Length of exposed spine	13	4.92	0.94	—	—	—	5	6.52	0.53
Pectoral fins:									
Base length	15	6.77	0.70	—	—	—	5	5.36	0.46
Length anterior margin	15	13.99	1.02	3	14.43	0.91	5	15.58	0.91
Length posterior margin	15	11.10	0.80	—	—	—	5	12.28	0.43
Length inner margin	15	7.18	0.51	—	—	—	5	8.12	0.29
Pelvic fins:									
Length anterior margin	15	5.86	0.72	—	—	—	5	6.86	0.32
Overall length	15	9.69	0.68	—	—	—	5	10.50	0.48
Caudal fin:									
Length upper margin	15	21.10	0.54	3	21.27	0.99	5	21.87	1.25
Length lower margin	14	11.08	0.70	3	11.07	0.42	5	11.56	0.68
Trunk at pectoral origin:									
Width	8	11.72	0.94	3	14.27	1.01	5	13.54	0.29



The presence of two cartilaginous processes on each side of the basal plate in *S. megalops* (only one in *S. blainvillei*, see Fig. 1) allows discrimination between these two species.

**Pectoral shape.** Most authors agree that the main feature for distinguishing between *S. blainvillei* and the species of the *S. megalops*-*S. cubensis* group is the shape of the pectoral fin corner, i.e. rounded in the former and pointed in the latter. The more or less concave posterior margins of these fins have also been used for this purpose. However, some variation has been observed in the studied specimens, and occasionally *S. blainvillei* had a pectoral shape like *S. megalops*. Ledoux (1970) figured this range of variation, although his observations were based partially on *S. megalops* specimens.

The specimens of *S. cubensis* showed a well-marked concavity in the posterior pectoral margin which agrees with the figures by Bigelow and Schroeder (1948, 1957), Ledoux (1970) and Compagno (1984).

**Nostril shape and snout-nostril-preoral cleft distances.** The nostril shape only separates *S. acanthias* from all the remaining *Squalus* species, because it lacks a bilobed nasal flap. All the

studied specimens of the remaining species had a more or less developed bilobed flap in the nostrils. This flap is larger in *S. megalops* and *S. cubensis* than in the other species.

The relationships of the distances from tip of snout to nostrils and from these to preoral clefts, which were proposed by Bass et al. (1976) as the best features for discriminating between *S. blainvillei* and *S. megalops*, proved to be of little use in the studied material. The level of confidence of this feature was about 70% in the E-Atlantic and Mediterranean samples.

**Dermal denticles.** Dermal denticles of selected adult specimens are shown in Fig. 2. *S. acanthias*, *S. blainvillei* and *S. acutirostris* have, at least in adults, wide scutes with three longitudinal keels. *S. megalops* and *S. cubensis* have dagger-shaped denticles with the anterior part thickened and lateral keels little developed or absent. *Squalus* sp. shows dermal denticles of intermediate shape, with lateral keels, but also bearing a thick anterior part of the central keel, giving a dagger-shaped appearance to the denticles, especially to the smaller ones.

These descriptions agree with those published by Garrick (1960), Bass et al. (1976) and others.

Table 4. Chondrocranial measurements of *Squalus blainvillei* and E-Atlantic *S. megalops*, and comparison through a t-Student test. The character numbers refer to those in Fig. 1.  
\*  $p < 0.05$ ; \*\*  $p < 0.01$ .

	<i>S. blainvillei</i>			<i>S. megalops</i>			t-Student
	N	Media	SD	N	Media	SD	
1 Total length of chondrocranium (TLC)	57.9–115.7 mm			32.0–83.8 mm			
2 Posterior tip-precerebral fenestra	9	63.85	1.36	22	65.08	1.14	2.52*
3 Length precerebral fenestra	9	36.18	1.77	22	35.70	1.02	—
4 Width precerebral fenestra	9	14.95	1.45	22	16.99	1.84	2.70*
5 Width across nasal capsules	9	54.39	1.73	21	50.93	2.44	4.19**
6 Interorbital width	9	31.18	1.17	22	28.57	1.26	5.18**
7 Postorbital width	9	56.49	1.36	22	55.38	2.00	—
8 Distance between orbital processes	9	42.60	1.72	19	32.85	2.58	—
9 Width between pterotic processes	9	37.52	1.53	22	37.30	1.24	—
10 Width between hyomandibular facets	9	45.61	1.16	22	45.62	1.16	—
11 Posterior tip-rostral keel	9	64.79	1.35	22	63.60	3.12	—
12 Length rostral keel	9	20.05	2.94	22	22.82	2.69	2.39*
13 Subethmoidean width	9	17.22	1.12	22	15.57	1.31	3.21**
14 Width basal angle	9	21.20	1.77	22	17.82	1.36	5.55**
15 Length basal plate	9	39.53	1.62	22	40.56	1.09	—
16 Width anterior basal plate	8	21.90	2.11	21	18.97	1.12	4.64**
18 Width between processes of basal plate	9	30.39	1.01	22	31.08	0.85	—
19 Maximum sagittal height	9	29.12	0.78	22	28.84	0.85	—
20 Width of foramen magnum	9	7.23	0.54	22	8.03	0.42	4.28**

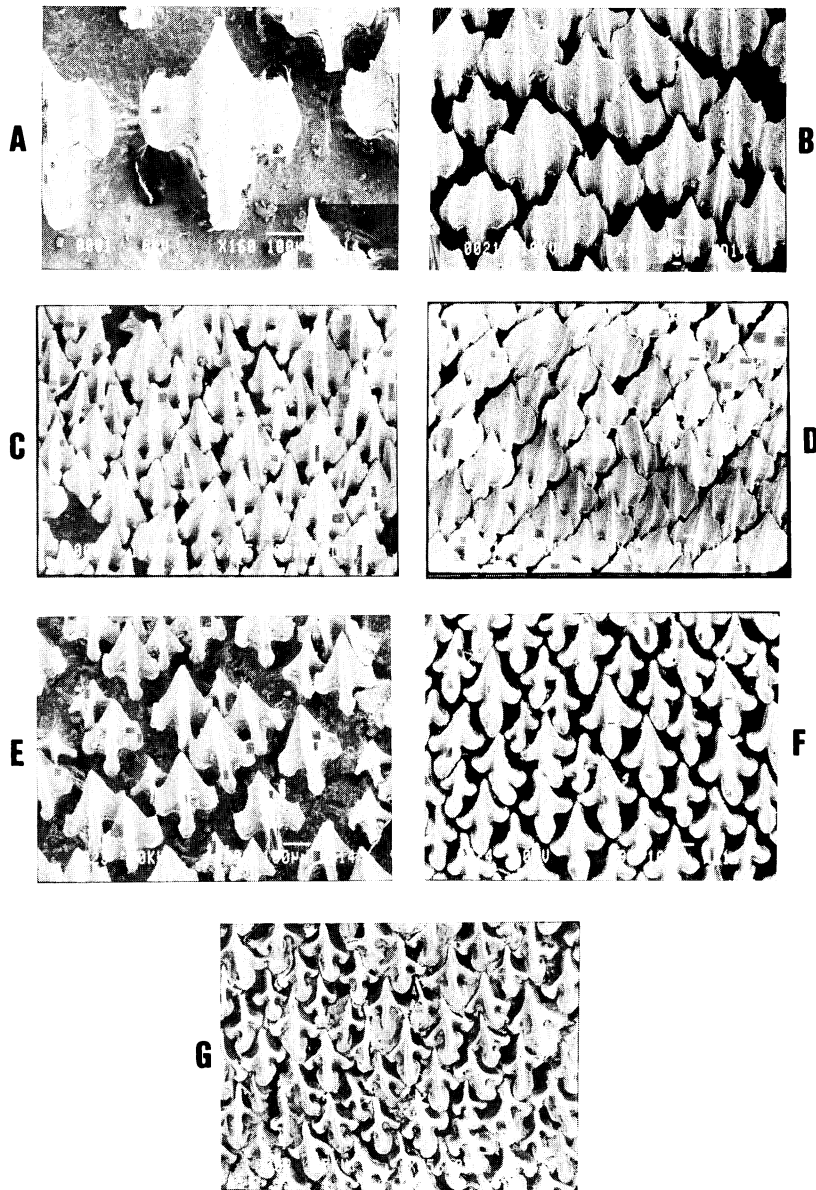


Fig. 2. Dermal denticles of selected *Squalus* specimens. A, *S. acanthias*, uncatalogued male, 788 mm TL; B, *S. blainvillei*, uncatalogued female, 850 mm TL; C, *Squalus* sp., uncatalogued female, 615 mm TL; D, *S. acutirostris*, uncatalogued male, 607 mm TL; E, E-Atlantic *S. megalops*, UMDZ 84012503, male, 613 mm TL; F, Indo-Pacific *S. megalops*, uncatalogued male, 444 mm TL; G, *S. cubensis*, uncatalogued female, 650 mm TL. Scale bars indicate 100  $\mu$ m.

The dermal denticles of *Squalus blainvillei* (sensu Chen et al., 1979) are similar to those observed in our specimen of *Squalus* sp. in having lateral keels less developed, thicker anterior part of the central keel and lesser width than the *S. blainvillei* denticles.

To evaluate the dermal denticles changes with body growth in some of these species, see Garrick (1960).

**Clasper skeleton.** The terminal clasper cartilages, called 'spur' and 'claw' by Leigh-Sharpe (1920), were the best way of discriminating be-

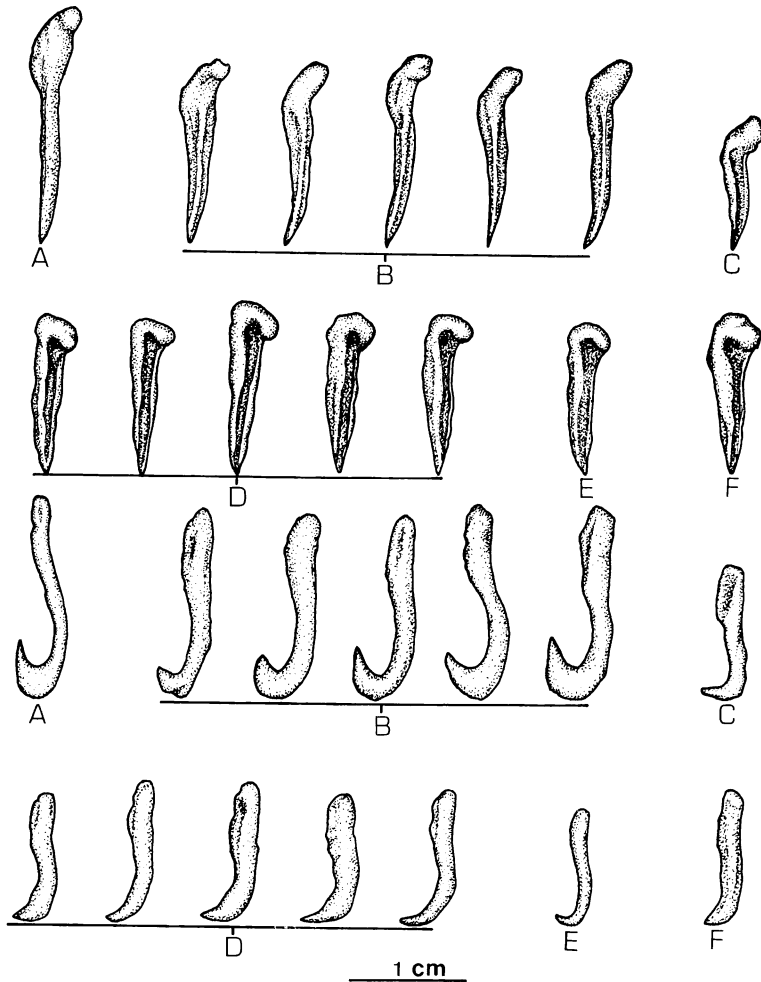


Fig. 3. Clasper spurs (above) and clasper claws (below) from selected *Squalus* specimens. A, *S. acanthias*, UMDZ 83030901, 788 mm TL; B, *S. blainvillei*, UMDZ 83101703, UMDZ 83072001, UMDZ 83022404, UMDZ 83071305, and UMDZ 83072701, 695–730 mm TL; C, *S. acutirostris*, uncatalogued, 607 mm TL; D, E-Atlantic *S. megalops*, UMDZ 84012504, UMDZ 83091401, UMDZ 83080501, UMDZ 83082401, and UMDZ 84040905, 534–600 mm TL; E, Indo-Pacific *S. megalops*, uncatalogued 444 mm TL; F, *S. cubensis*, uncatalogued 546 mm TL.

tween mature male specimens. Fig. 3 shows the clasper spurs and claws of 14 *Squalus* specimens. The intraspecific variation was lesser than the interspecific one. Indo-Pacific and E-atlantic *S. megalops* showed very similar skeletons, although their populations are very far apart geographically. *S. blainvillei* and *S. acanthias* shared hook-like claws and slender spurs. The less bent claw and the more massive spur differentiate *S. cubensis* from *S. megalops*.

*S. acutirostris* had spurs and claws intermediate between *S. blainvillei* and *S. megalops*.

**Number of vertebrae.** Monospondylous and precaudal vertebral numbers of the studied specimens are shown in Table 5, together with the counts taken from the literature, E-Atlantic and Indo-Pacific *S. megalops* had similar numbers of vertebral centra. *S. cubensis* had more centra, especially in precaudal counts. These species differed from *S. blainvillei* in 4–8 monospondylous centra.

*Squalus* sp. seems to have more precaudal centra than *S. blainvillei*. Chen et al. (1979) gave a range between 90–96 centra, with a mean of 94. The

Table 5. Monospondylous and precaudal vertebral numbers in some species of *Squalus*. \*Sensu Chen et al. (1979). (1), present study; (2), Bass et al. (1976); (3), Springer and Garrick (1964); (4), Chen et al. (1979). Lines represent observed range. †, mean vertebral number.

	Monospondylous										Precaudal																								
	38	39	40	41	42	43	44	45	46	47	48	49	50	...	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	97		
<i>S. blainvillei</i> (1)						1	4	1																3	2	1									
<i>S. blainvillei</i> (2)						not given																													
<i>S. blainvillei</i> (3)						not given																													
<i>S. blainvillei</i> * (= <i>Squalus</i> sp.) (4)																																			
<i>Squalus</i> sp. (1)									1																										
<i>S. mitsukurii</i> (4)																																			
E-Atl. <i>S. megalops</i> (1)	3	6	2	1											1	5	3	2	1																
S-Africa <i>S. megalops</i> (2)																																			
Indo-Pac. <i>S. megalops</i> (1)				1																															
Indo-Pac. <i>S. megalops</i> (3)																																			
<i>S. cubensis</i> (1)					3	1																													
<i>S. cubensis</i> (3)																																			
<i>S. acutirostris</i> (1)				1																															

only *Squalus* sp. specimen studied by us had 90 centra. On the other hand, we counted 88–90 precaudal centra in the eastern Atlantic *S. blainvillei*. This range agrees with the four NW-Pacific *S. blainvillei* specimens studied by Springer and Garrick (1964), which have 86–89 precaudal centra.

*S. acutirostris* showed a striking vertebral count, with a low number of monospondylous centra (39), typical of the *S. megalops*-*S. cubensis* group, and a relatively high number of precaudal centra (86) which is somewhat fewer than in *S. blainvillei*.

The confusion between *S. blainvillei* and *S. megalops* could explain the low values of precaudal centra (78–80) found by Springer and Garrick (1964) in the Mediterranean *S. blainvillei* specimens. These, proceeding from Italy, must probably be ascribed to *S. megalops*.

### Discussion

These results provide a better outlook on the species of the genus *Squalus*. Thus, we think that the differences in pectoral size and height of both dorsal fins and spines between the E-Atlantic and Indo-Pacific populations of *S. megalops* are balanced by the similarities in the clasper skeleton, number of vertebral centra, pectoral fin shape, inner pectoral margin length, ventral fin length and dermal denticle shape. These support the proposal of synonymy between *S. acutipinnis* and *S. megalops* (Bass et al., 1976; Compagno 1984), at least until new comparative studies are made to provide a basis to resurrect *S. acutipinnis*.

*S. blainvillei* poses some taxonomical problems since no type material is available, and the original description by Risso (1826) fits with several species of the genus. After our field studies, only two forms which can be called *S. blainvillei* inhabit the Mediterranean, the type locality of the Risso's nominal species. The most abundant form in the western Mediterranean agrees very well with the description by Krefft (1968) of *S. acutipinnis* and that by Bass et al. (1976) of *S. megalops*. This form also fits with the original description of *S. megalops* and the differences from Indo-Pacific material of this species do not seem enough to justify its allocation in a separate species, as stated above. Thus, two of the three Mediterranean species, *S. acanthias* and *S. megalops*, do not pose any special taxonomical problems except

for what was mentioned above about the *S. megalops*-*S. acutipinnis* relationships.

The third Mediterranean form agrees very well with the description given by Bigelow and Schroeder (1948, 1957) of the *S. blainvillei* species group. It also agrees with the descriptions by Garrick (1960) and Bass et al. (1976) of New Zealand and South African *S. blainvillei*, respectively. Although we are at present unable to decide which form really was the one described as *S. blainvillei* by Risso (1826), it appears to be the most suitable for the nomenclatural stability to consider this form, with shorter inner pectoral dermal denticles and hook-like clasper claw, as *S. blainvillei*.

However, Chen et al. (1979) identify some specimens (herein named as *Squalus* sp.) caught in the W-Pacific with high first dorsal fin and spine as *S. blainvillei*. This proposal was based on the original figure by Risso (1826) and a drawing made by Poll (1951) on a specimen taken off Gabon, at the central E-Atlantic. However, the original figure can hardly be useful as reference since it does not correspond with any known shark species, showing quite strange dorsal fins without free posterior margins, and pelvic fins longer than the pectoral fins. Regarding the Poll's drawing, it lacks detailed measurements and descriptions that allow both the comparison with the Mediterranean and Pacific materials and the decision as to whether this specimen, called *S. fernandinus* by Poll, is actually *S. blainvillei* or *S. megalops*. Furthermore, the central Atlantic is rather far away from the type locality.

Since Compagno (1984) followed Chen et al. (1979) in considering *S. blainvillei* as a species characterized by their high first dorsal fin and spine, we are in an odd situation. By using the Compagno's identification keys, the Mediterranean material is identified as *S. mitsukurii*, a nominal species described in the Pacific Ocean, because of its lower dorsal fins. However, the NW-Pacific specimens, bearing high dorsal fins, are identified as *S. blainvillei*, a nominal species described in the Mediterranean Sea.

No other references have been made to specimens with high dorsal fins from the E-Atlantic or Mediterranean sea, excepting the statement made by Tortonese (1956) about two morphotypes of *S. fernandinus* (= *S. blainvillei*) in the Italian coasts, with differences in the height of the dorsal

fins. However this observation is supported, at least partially, by the Mediterranean *S. megalops* as proved by the dagger-shaped dermal denticles and other details of the accompanying drawings.

It could be possible that the specimens called *S. blainvillei* by Chen et al. (1979) were actually local populations of this species, characterized by their higher dorsal fins and spines. However, we think that this possibility is not tenable firstly because of the observed differences in the numbers of vertebrae (88–90 vs. 90–96) between these two forms which were not recorded by Springer and Garrick (1964) in *S. blainvillei* from the NW-Pacific. But the main reason to exclude the hypothesis of separate populations of the same species is the comparison between the specimen of *Squalus* sp. proceeding from Australia, and the descriptions of *S. blainvillei* from New Zealand waters by Garrick (1960). As it has been commented above, the *Squalus* sp. specimen belongs to the same species as the specimens called *S. blainvillei* by Chen et al. (1979). But the specimens described by Garrick (1960) clearly agree with the Mediterranean sample of *S. blainvillei* studied by us in the number of the vertebrae, pectoral fin shape, dermal denticles and, mainly, in the height of the dorsal fins and pectoral size, as shown in Table 3.

The occurrence of both forms in the same geographic region is a strong argument against the view that the high-dorsal-fin specimens belong to *S. blainvillei*. By reasons of nomenclatural stability we propose to retain the name *S. blainvillei* for the specimens bearing low dorsal fins, short inner pectoral margins, tricuspidate dermal denticles and hook-like clasper claw, currently included in the *S. blainvillei* group. We also propose the review of the Indo-Pacific material in order to establish its taxonomic status, since *Squalus* sp. could be an undescribed species.

The question of the validity and diagnosis of *S. mitsukurii* remains unsolved. Its original description by Jordan and Snyder (in Jordan and Fowler, 1903) was based on a specimen of *S. blainvillei* group, but the accompanying illustration fitted better with the *S. acanthias* group (Bigelow and Schroeder, 1948, 1957; Chen et al., Compagno, 1984). For this reason, the nominal species *S. mitsukurii* has been used for more than a single species. Tanaka (1917) first referred a white-spotted species to *S. mitsukurii*, but sub-

sequently he synonymized *S. brevirostris* Tanaka, 1917, a non-spotted species, with *S. mitsukurii*, Kibesaki (1954) assigned this name to some long-snouted specimens which could well have been *S. acutirostris*.

The specimens called *S. mitsukurii* by Chen et al. (1979) are similar to the Mediterranean *S. blainvillei* in having short inner pectoral margins (7.2–8.8% TL) and low first dorsal fin height (7.5–8.2% TL). However, the dermal denticles are different, with very thin lateral keels. On the other hand, at least one of these specimens approaches to the diagnosis of *S. acutirostris* in having the snout tip-eye distance twice in the anterior pectoral margin (1.8 times in *S. acutirostris*). Thus, there are three possibilities in classifying *S. mitsukurii*, namely as a valid species, junior synonym of *S. blainvillei* or senior synonym of *S. acutirostris*. The study of the type material will allow one to decide among them.

Myagkov and Kondyurin (1986) published a wide review of the genus *Squalus* in the Atlantic ocean, recognizing the validity of *S. acutipinnis*, *S. fernandinus* and *S. lebruni*, describing a new species, *S. probatovi*, and considering two different forms of *S. blainvillei*, sensu Risso (1826) and sensu Garrick (1960). Their findings have added more confusion since they use very variable features as key characters, such as the presence of a middle tooth on the jaws, the shape of the nasal flap, and the dorsoventral/ventrodorsal distances which are subjected to allometric changes with growth. Their descriptions are very short and the current diagnostic features are not mentioned in some instances. For all these reasons, it is very difficult to compare their results with those stated in this paper.

The grouping of the *Squalus* species proposed by Bigelow and Schroeder (1948, 1957) and described above, does not fit with the results formerly reported. *S. acanthias* is, probably, the only species of its own group. The *S. blainvillei* group is a ragbag of forms, including all the *Squalus* species except *S. acanthias*, *S. megalops* and *S. cubensis*. The third group, also in its original sense, would only hold to *S. megalops* and *S. cubensis*. The heterogeneity of the second group and the existence of only one species in the first, suggest a redefining of the species grouping within *Squalus*.

Further study of other character complexes on

a worldwide basis will allow better analysis of the relationships within *Squalus*, including the clarification of some nominal species and more accurate phylogenetic knowledge of the genus.

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大西洋東部海域のツノザメ *Squalus blainvillei* と *S. megalops* について

Ramón Muñoz-Chápuli • Fernando Ramos

アブラツノザメ *Squalus acanthias* Linnaeus, 1758, *S. blainvillei* (Risso, 1826) (模式産地: 地中海), *S. megalops* MacLeay, 1881 および *S. acutirostris* Zhu, Meng et Li, 1984 を形態学的に比較した。その結果, *S. acutipinnis* Regan, 1908 は *S. megalops* と同一種であることが示唆され, 大西洋東部海域では *S. blainvillei* と *S. megalops* の間に差異が認められた。インド・大平洋海域において Chen et al. (1979) が *S. blainvillei* とし, ヒレタカツノザメという和名で呼ばれているものは未記載種と思われる。