Zoosyst. Evol. 96 (2) 2020, 345–395 | DOI 10.3897/zse.96.52420

Phylogenetic relationship of catshark species of the genus *Scyliorhinus* (Chondrichthyes, Carcharhiniformes, Scyliorhinidae) based on comparative morphology

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http://zoobank.org/54EC7875-F785-4263-8254-8EF8E8D66B98

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Academic editor: Peter Bartsch ♦ **Received** 25 March 2020 ♦ **Accepted** 18 May 2020 ♦ **Published** 19 June 2020

Abstract

The genus *Scyliorhinus* is part of the family Scyliorhinidae, the most diverse family of sharks and of the subfamily Scyliorhininae along with *Cephaloscyllium* and *Poroderma*. This study reviews the phylogenetic relationships of species of *Scyliorhinus* in the subfamily Scyliorhininae. Specimens of all *Scyliorhinus* species were examined as well as specimens of four of the 18 species of *Cephaloscyllium*, two species of *Poroderma*, representatives of almost all other catshark (scyliorhinid) genera and one proscylliid (*Proscyllium habereri*). A detailed morphological study, including external and internal morphology, morphometry and meristic data, was performed. From this study, a total of 84 morphological characters were compiled into a data matrix. Parsimony analysis was employed to generate hypotheses of phylogenetic relationships using the TNT 1.1. *Proscyllium habereri* was used to root the cladogram. The phylogenetic analysis, based on implied weighting ($k = 3$; 300 replications and 100 trees saved per replication), resulted in three equally most parsimonious cladograms with 233 steps, with a CI of 0.37 and an RI of 0.69. The monophyly of the subfamily Scyliorhininae is supported as well as of the genus *Scyliorhinus*, which is proposed to be the sister group of *Cephaloscyllium*. The phylogenetic relationships amongst *Scyliorhinus* species are presented for the first time.

Key Words

Scyliorhinus, catsharks, Scyliorhininae, *Cephaloscyllium*, *Poroderma*, phylogeny, morphology

Introduction

Contrasting hypotheses on the classification of catsharks are widespread in literature and divide opinions of many authors (e.g. White 1936, 1937; Compagno 1973, 1988a; Maisey 1984; Nakaya 1975; Iglésias et al. 2005; Human et al. 2006; Naylor et al. 2005, 2012a; Nelson et al. 2016; Weigmann 2016; Weigmann et al. 2018). On the basis of morphological data, Compagno (1988a) proposed that the family Scyliorhinidae is composed of 17 genera, following the traditional arrangement for the group (Nakaya 1975; Springer 1979). Posteriorly, Iglésias et al. (2005), analysing molecular data, hypothesised that the family Scyliorhinidae is paraphyletic and proposed the re-allocation of 11 catshark genera to the family Pentanchidae, elevated in rank from subfamily (Compagno 1988a). According to Iglésias et al. (2005), both families could be morphologically distinguished by the presence/absence of the supraorbital crest on the neurocranium.

Although the paraphyly of Scyliorhinidae has been corroborated by later works (Human et al. 2006; Naylor et al. 2012a, 2012b), recent molecular analysis, including a larger sample of taxa, recovered three different paraphyletic lineages of catsharks instead of two and species of *Parmaturus* were placed in distinct clades (Naylor et al. 2012a, 2012b). No cladistic analysis considering morphological data has been performed to elucidate the phylogenetic relationships of catshark species and enlarge our knowledge about the evolution and distribution of morphological characters, such as the supraorbital crest. Thus, we decided to adopt here Scyliorhinidae *sensu lato* (Compagno 1988a; Weigmann et al. 2018) until a more extensive evaluation of morphological characters is done, thus providing a better definition for Scyliorhinidae *sensu stricto* and Pentanchidae (Nelson et al. 2016).

Compagno (1988a) united the genera *Scyliorhinus*, *Cephaloscyllium* and *Poroderma* in the subfamily Scyliorhininae, following Gill (1862) and on the basis of muscle and neurocranial characters. Herman et al. (1990) proposed the same arrangement, based on dental characters. Later, studies using molecular data corroborated the monophyly of the subfamily (Iglésias et al. 2005; Human et al. 2006; Naylor et al. 2012a, 2012b), although divergences in phylogenetic relationships amongst its taxa have been observed between morphological and molecular data (cf. Compagno 1988a; Naylor et al. 2012a, 2012b).

Doubts concerning the monophyly of the genus *Scyliorhinus* are found in many works and focus mainly on the relationships amongst *S. canicula* and its congeners (Springer 1966, 1979; Compagno 1988a). *Scyliorhinus canicula* presents unique characteristics in the nasoral region, such as the presence of nasoral grooves and anterior nasal flaps very close to each other. Similar features are also found in the catshark genera *Atelomycterus* and *Haploblepharus* (Compagno 1988a). These differences would be, according to Springer (1979), sufficiently great and unique to guarantee the allocation of the other species of *Scyliorhinus* to a distinct genus, as was proposed by Jordan & Evermann (1896) and Danois (1913). Compagno (1988a) even suggested the adoption of the name *Betascyllium* Leigh-Sharpe, 1926, if this new arrangement should prove to be necessary. Bell (1993) pointed out the importance of cautiously analysing the characters of the nasoral region and examining a representative number of taxa to better comprehend the evolution of these characters amongst scyliorhinids.

Scyliorhinus presents a unique configuration of the labial furrows comprised of the absence of an upper furrow concomitant with the presence of a narrow lower furrow (Compagno 1988a). The presence of a projecting flap ventral to and covering the lower labial furrow, cited by some authors as a reliable character to identify species belonging to *Scyliorhinus* (Bigelow and Schroeder 1948; Springer 1966, 1979), was not considered as synapomorphy for the genus by Compagno (1988a). Yet, according to some authors (Springer 1979; Compagno 1988a), the labial furrows observed in *Poroderma* and in some species of *Cephaloscyllium* are poorly developed or absent and could be easily confused with the configuration present in *Scyliorhinus* species (Compagno 1988a).

Detailed descriptions of all *Scyliorhinus* species, mainly based on external morphology, neurocranium and claspers, were provided in the generic revision of Soares and de Carvalho (2019). The morphological characters raised and analysed in that study, as well as additional morphological characters and broader comparisons with other scyliorhinid and proscyllid genera, are included in the present paper, which aims to provide a phylogenetic hypothesis amongst scyliorhinine species. As mentioned, the most recent phylogenetic hypotheses to infer relationships amongst catsharks are based on molecular evidence (Iglésias et al. 2005; Human et al. 2006; Naylor et al. 2012a, 2012b); we set out to provide a phylogenetical appraisal, based on a renewed examination of morphological characters. The main objective of the present study is to clarify the phylogenetic significance of the interspecific morphological variation in *Scyliorhinus* and shed light on the relationships amongst its species and other scyliorhinines.

Material and methods

Selection of taxa

Thirty-five taxa were included as terminals in the phylogenetic analysis. Species representing the three genera assigned to the Scyliorhininae by Compagno (1988a) were included. Specimens of all 16 valid species of *Scyliorhinus* were examined (Soares and de Carvalho 2019) and, amongst these, 41 specimens were dissected for anatomical investigation corresponding to 14 species of this genus. Specimens of *S. comoroensis* and *S. garmani* were not dissected due to the lack of available material for study. Data on meristics, external morphology and internal anatomy of *S. cabofriensis*, *S. haeckelii* and *S. ugoi* were extracted from Soares et al. (2015, 2016). Specimens of the other genera of the subfamily Scyliorhininae were examined and dissected, including four of the 18 species of *Cephaloscyllium* and the two species of *Poroderma*. For comparative taxa, we examined *Proscyllium habereri* (family Proscylliidae) and other representatives of Scyliorhinidae *sensu lato* (Table 1). Specimens of *Bythaelurus* were not available for dissection and not included in the analysis. The other genus not included here, *Pentanchus*, is only known from two specimens; one is the holotype of *P. profundicolus* (USNM 70260; in poor preservational condition) and the other is a specimen cited by Nakaya and Séret (2000) (MNHN 1999-0270) that could not be found. In any case, *Pentanchus* may not be valid (Compagno 1988a). All material examined and collection data are listed in Appendix 1.

Specimen preparation and characters examined

This study was based on the examination of 84 morphological characters (79 qualitative and five quantitative) that included external morphology, branchiomeric and hypobranchial cranial muscles, clasper morphology, dermal denticles and skeleton. External morphological characters were observed directly or with the aid of a stereomicroscope. Anatomical preparation was performed through manual dissections. For the examination of clasper anato-

Table 1. List of species examined (except *Scyliorhinus*), data available for each species and institutions where the material is deposited. Abbreviations for institutions follow Sabaj (2016).

Species examined	Data available	Origin of material
Scyliorhininae		
Cephaloscyllium isabella	External morphology, dermal denticles, musculature, skeleton	AMNH, USNM
C. sufflans	External morphology, dermal denticles, musculature, skeleton, clasper	SAIB
C. umbratile	External morphology, dermal denticles, musculature, skeleton	USP
C. variegatum	External morphology, dermal denticles, musculature, skeleton	AMS
Poroderma africanum	External morphology, dermal denticles, musculature, skeleton, clasper	SAIAB
P. pantherinum	External morphology, dermal denticles, musculature, skeleton, clasper	SAIAB
Comparative taxa		
Apristurus longicephalus	External morphology, dermal denticles, musculature, skeleton, clasper	HUMZ
Asymbolus rubiginosus	External morphology, dermal denticles, musculature, skeleton, clasper	AMS
Atelomycterus fasciatus	External morphology, dermal denticles, musculature, skeleton, clasper	CSIRO, MZUSP
Aulohalaelurus labiosus	External morphology, neurocranium, clasper	ZMH
Cephalurus cephalus	External morphology, dermal denticles, musculature, skeleton, clasper	USNM
Figaro boardmani	External morphology, dermal denticles, musculature, skeleton, clasper	CSIRO, MZUSP
Galeus antillensis	External morphology, dermal denticles, musculature, skeleton, clasper	UF
Halaelurus natalensis	External morphology, dermal denticles, musculature, skeleton, clasper	SAIAB
Haploblepharus edwardsii	External morphology, dermal denticles, musculature, skeleton, clasper	AMNH, BMNH
Holohalaelurus regani	External morphology, dermal denticles, musculature, skeleton, clasper	SAIAB
Parmaturus xaniurus	External morphology, dermal denticles, musculature, skeleton, clasper	CAS
Proscyllium habereri	External morphology, musculature, skeleton, clasper	CAS
Schroederichthys saurisqualus	External morphology, dermal denticles, musculature, skeleton, clasper	UERJ, ZMH

my, the left clasper was chosen to study the external morphology and the right clasper for the internal anatomy. Neurocrania and musculature of adult specimens were examined through dissection. Skin samples were taken for examination of dermal denticles from the right side of the body above the pectoral fin, below the origin of the first dorsal fin and below the insertion of the second dorsal fin. Dermal denticles were photographed using scanning electron microscopes (DSM 940 and ZEISS SIGMA VP), housed in the Departamento de Zoologia of the Universidade de São Paulo. Data of intestinal valves, tooth and vertebral counts were obtained directly from the examined specimens or taken from Compagno (1988a) and other works (Compagno and Stevens 1993a, 1993b; Last et al. 1999; Human 2006a, 2006b, 2007; Gledhill et al. 2008; Last and White 2008; Last et al. 2008; Sato et al. 2008; Nakaya et al. 2013).

Radiographs were taken in the Faculdade de Medicina Veterinária e Zootecnia da Universidade de São Paulo (FMVZ-USP) and in the radiology facilities of the following institutions: BMNH, HUMZ, MCZ, NRM, NSMT, USNM and ZMUC (according to Sabaj, 2016). Counts of monospondylous and diplospondylous vertebrae were based on Compagno (1988a). The vertebral centra present in the transition zone between monospondylous and diplospondylous vertebrae is generally smaller than the last monospondylous centrum and larger than the diplospondylous one and is included in the counts of monospondylous vertebrae.

Terminology for neurocranium and jaws follows Compagno (1988a) and Motta and Wilga (1995), respectively. Terminology for gill arches follows de Beer (1937) and Shirai (1992a). Clasper terminology for external anatomy and skeletal components are based on Jungersen (1899) and Compagno (1988a). Terminology for neurocranial, hyoid and hypobranchial musculature follows Huber et al. (2011). Nomenclature for dermal denticles follows Herman et al. (1990) and Cappetta (2012).

Character descriptions, related to meristic data, are presented first, followed by characters of external morphology, myology, skeleton and clasper. Skeletal characters are grouped into character complexes, such as neurocranium, jaws, hyoid and gill arches and pectoral girdle. The number preceding each character in the description corresponds to its number presented in the character matrix. A brief summary of each character and its states is followed by its recovered consistency and retention indices (CI and RI, respectively) which reflect their ACCTRAN optimisations (chosen because it maximises initial homology hypotheses). Multistate qualitative characters (6, 22, 43 and 49) and quantitative characters (1–5) were analysed as ordered.

Characters were illustrated with photographs and schematic drawings made from digital photographs. Photographs were taken with a digital camera (Canon Power Shot SX610 HS). Characters and their states are indicated by arrows and numbers in the figures. Figures were digitised and edited with the aid of Adobe Photoshop CS6. Whenever a character is described in the text for a genus without a species citation, that citation refers only to the species examined in the present study and does not imply that the character is present in all congeners.

Phylogenetic procedures

Hypotheses of phylogenetic relationships were proposed using the cladistic method formalised by Hennig (1950, 1965, 1966) and operationally detailed in other works (Farris 1969; Nelson and Platnick 1981; Goloboff 1993, 1995, 1999; Goloboff et al. 2006, 2008). Qualitative and quantitative characters were considered in the analysis;

values for meristic data were normalised and concatenated with the other characters (Goloboff et al. 2006). Character polarity was determined by outgroup comparison (Nixon and Carpenter 1993); the outgroups are composed of *Proscyllium habereri* (Proscylliidae) and taxa from the subfamilies Atelomycterinae, Pentanchinae and Schroederichthyinae. *Proscyllium habereri* was chosen to root the cladogram, as it was recovered as closely related to scyliorhinids in previous studies (Compagno 1988a; Human et al. 2006; Naylor et al. 2012). The data matrix (Appendix 2) was assembled and analysed with the aid of TNT 1.1 (Goloboff et al. 2003, 2008). Parsimony analysis was performed with implied weighting (k = 3) and the 'Traditional Search' option, using the TBR (tree bisection reconnection) algorithm, with 500 replications and 100 trees retained per replica. A strict consensus cladogram was used to summarise the equally most-parsimonious hypotheses obtained from the different topologies yielded by the analysis. Tree edition was performed with the aid of Figtree version 1.4.3 and Adobe Photoshop CS6.

CI and RI values and synapomorphies of the various nodes were obtained from the set of equally most-parsimonious trees. Relative Bremer support was calculated for each clade using TBR and retaining suboptimal trees by seven steps. Missing entries were used to represent two different instances where characters could not be determined: (1) lack of appropriate study material; and (2) inapplicable character state. For *Scyliorhinus comoroensis* and *S. garmani*, it was not possible to extract information on internal anatomical characters (e.g. musculature, neurocranium). Adult males of the terminal taxa *Cephaloscyllium isabella*, *C. umbratile*, *C. variegatum* and *Scyliorhinus garmani* were not available for dissection and, thus, claspers were not examined for these species. Autapomorphies were not included in the phylogenetic analysis, but are detailed in the section 'Non-informative characters'.

The section 'Description and character analysis' presents the description of each character, its variation within the subfamily Scyliorhininae and other taxa of Scyliorhinidae. Character optimisation and character transformations are presented in Appendices 4 and 5, respectively.

Results

Character descriptions and analysis

Meristics

1 Counts of monospondylous vertebrae: minimum = 28; maximum = 54. (CI = 26; RI = 43–46).

Springer and Garrick (1964) pointed out the relevance of vertebral counts to elucidate phylogenetic relationships in Carcharhinidae and other shark families, stating that the values would increase in less inclusive taxonomic levels. These authors considered only precaudal and caudal vertebral counts. Springer (1966, 1979) highlighted the importance of counts of monospondylous vertebrae in distinguishing species of *Scyliorhinus* distributed in the Western Atlantic. According to our results, *Scyliorhinus torrei* presents the lowest values for counts (30–35) in *Scyliorhinus*, followed by *S. torazame* (32–37). Most species of this genus present a similar range, from 38 to 44 vertebrae, whereas higher values were observed for *S. capensis* (44–46), *S. garmani* (48), *S. meadi* (46–48) and *S. stellaris* (43–47). In *Cephaloscyllium* spp., values range from 44 to 54 and in *Poroderma*, from 32 to 46. The lowest value for all taxa was found in *Holohalaelurus regani* (28).

2 Counts of diplospondylous vertebrae: minimum = 67; maximum = 131. (CI = 34; RI = 31).

Compagno (1988a) reported an increase in counts of total vertebrae from Scyliorhinidae to Carcharhinidae, indicating a possible transformation series for this character in Carcharhiniformes. In the present study, we opted to analyse counts of diplospondylous vertebrae, aiming to exclude the influence of monospondylous vertebrae in counts. In *Scyliorhinus* spp., counts of diplospondylous vertebrae range from 73 to 97. Similar values were observed in species of *Cephaloscyllium* and *Poroderma*, except for *C. umbratile* (110–131). In the outgroups, counts range from 67 to 131, with the lowest values found in *Cephalurus cephalus* (67–71).

3 Upper tooth row counts: minimum = 33; maximum = 110. (CI = 41; RI = 56).
4 Lower tooth row counts: minimum = 29; maximum = 102. (CI = 36; RI = 49).

Tooth row counts are presented for many species in descriptions or taxonomic reviews, but never used as a phylogenetic character. Regarding the differences between upper and lower jaws, we considered upper and lower tooth row counts as distinct characters. In *Scyliorhinus* spp., tooth row counts range 33 to 85, considering both jaws; *S. torrei* (33–42) presented the lowest values and *S. capensis* and *S. torazame* (45–81) the greatest ones. Amongst scyliorhinines, *Cephaloscyllium umbratile* (77–110) presented the highest values. In the outgroups, counts range from 35 to 102 with the lowest values found in *Apristurus longicephalus* (35–45).

5 Counts of intestinal valves: minimum = 5; maximum = 17. (CI = 37; RI = 42).

White (1937) divided intestinal valves into three types, considering the numbers of valves observed: i) 2–4; ii) 5–10; iii) 11–30. The family Scyliorhinidae would be classified in the 'intermediary' type, presenting 5–10 valves, although White (1937) reported 16 valves for *Atelomycterus*. Compagno (1988a) suggested that low variation ranges in counts of intestinal valves in carcharhiniforms would comprise a useful character for systematic studies. Thus, counts of intestinal valves of examined taxa are considered here and analysed as quantitative characters. Amongst *Scyliorhinus* species, counts ranged from 6 to 11, with higher values for *S. capensis* (10–11) and lower for *S. torazame* and *S. torrei* (6–7); similar values were found in species of *Cephaloscyllium*. In *Poroderma* spp., higher values (11–13) were found. Other scyliorhinids present a similar range for counts of intestinal valves, with the exception of *Apristurus* spp. (14–20) and *Atelomycterus* spp. (14–16).

Nasoral region

6 Extension of anterior nasal flap: (0) entirely covering excurrent nasal aperture and posterior nasal flap, but not covering the upper lip; (1) partially covering excurrent nasal aperture and not covering posterior nasal flap nor upper lip; (2) entirely covering excurrent aperture, posterior nasal flap and upper lip. (ordered; CI = 29; RI = 64).

The anterior nasal flap is a triangular or subrectangular structure and is situated medial to the incurrent aperture and lateral to the excurrent one. This flap can cover partially or entirely the excurrent aperture and posterior nasal flap, which is situated on the posterior border of the excurrent aperture (Compagno 1988a, 1999). Scyliorhinines present a nasal flap that entirely covers the excurrent aperture and posterior nasal flap and is separated from the mouth by a short distance (state 0; Fig. 1); the same condition is found in *Aulohalaelurus*, *Asymbolus*, *Holohalaelurus*, *Parmaturus* and *Proscyllium*. In *S. canicula* and *S. duhamelii*, the anterior nasal flap is longer and covers the upper lip and laterally the lower jaw, as in *Atelomycterus* and *Haploblepharus* (state 2; Fig. 1A). In *Schroederichthys*, *Halaelurus*, *Figaro*, *Galeus*, *Apristurus* and *Cephalurus*, the anterior nasal flap partially covers the excurrent aperture and ends at a considerable distance from the mouth (state 1; Fig. 1B).

7 Distance between anterior nasal flaps: (0) distant by one-half or more of the width of the flap; (1) distant by less than one-half. (CI = 33; RI = 33).

In relation to the distance between anterior nasal flaps, these are separated by one-half or more of the width of the flaps in *Cephaloscyllium*, *Poroderma* and *Scyliorhinus* (state 0; Figs 1–3), except in *S. canicula* and *S. duhamelii*. In these species, anterior flaps are separated by a short distance, shorter than one-half of their width, as in *Atelomycterus* (state 1; Figs 1–3). In the other taxa examined, anterior flaps are separated by a similar to slightly larger distance than the width of the flaps.

8 Configuration of anterior nasal flap: (0) flap consisting of a single structure; (1) flap separated into lateral and medial two portions. (CI = 33; RI = 33).

Most scyliorhinids present a single anterior nasal flap. In *Poroderma*, the anterior nasal flap is divided into two portions (Fig. 2C) as in *Cephalurus* and *Schroederichthys* (Fig. 1A).

9 Mesonarial crest: (0) inconspicuous; (1) prominent. (CI = 50; RI = 92).

The presence of a mesonarial crest was observed and described by Compagno (1988b) for *Scyliorhinus comoroensis*. The same structure was also found in the other *Scyliorhinus* species, *Cephaloscyllium* and *Schroederichthys* (state 1; Figs 1 and 2). In *S. stellaris*, this crest is well developed and extends beyond the posterior border of the anterior nasal flap; this condition is considered here as an autapomorphy for this species (Soares and de Carvalho 2019). In *Poroderma*, a nasal barbel is found in the same position as the mesonarial crest (Fig. 2). Compagno (1988a) proposed a hypothesis of homology between the barbel of *Poroderma* and the mesonarial crest of *Scyliorhinus* which was followed by Human et al. (2006). This hypothesis is rejected here; the nasal barbel in *Poroderma* is composed by muscle fibres which overlap the external nasal cartilage, whereas, in *Scyliorhinus*, the mesonarial crest corresponds to extensions of the external nasal cartilage. Therefore, we considered that *Poroderma* presents an inconspicuous mesonarial crest as in the other examined taxa (state 0; Fig. 2C).

10 Muscular nasal barbel on anterior nasal flap: (0) absent; (1) present. (CI = 100; RI = 100).

The presence of a muscular nasal barbel is observed in *Poroderma* (state 1; Fig. 2C) and its extension varies between the two species of the genus, *P. africanum* and *P. pantherinum*. In the latter, the nasal barbel is much longer and reaches the upper lip, while, in the former, it is shorter and distant from the mouth. This barbel originates on the ventromedial surface of each anterior nasal flap and is totally separated from the posterior tip of the nasal flap (Compagno 1988a). Considering other carcharhiniforms, only the genus *Furgaleus* presents a similar nasal barbel. In *Leptocharias*, the lateral portion of the nasal flap is well developed and long, but does not form a muscular barbel. The nasal barbel present in some orectolobiforms (*Chiloscyllium*, *Ginglymostoma*, *Hemiscyllium*, *Orectolobus* and *Stegostoma*) originates on the rostral surface, medial and partially anterior to the anterior nasal flap (Compagno 1988a) and has a cartilaginous base (Goto 2001), differing from the condition observed in *Poroderma* and *Furgaleus*.

11 Posterior nasal flap: (0) present; (1) absent. (CI = 33; RI = 0).

A posterior nasal flap, associated with the excurrent nasal aperture, is present in all scyliorhinines, most scyliorhinids and *Proscyllium* (state 0; Fig. 2). This flap is absent

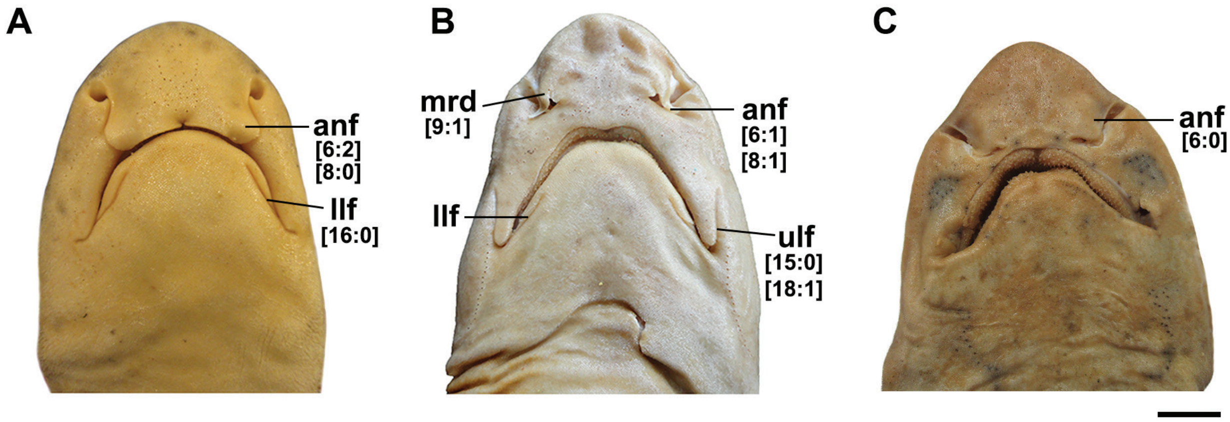

Figure 1. Ventral view of the head. A, *Scyliorhinus canicula*, MNHN 1999–1732, female, 418.5 mm TL; B, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL; C, *Holohalaelurus regani*, SAIAB 25717, male, 610 mm TL. **anf**, anterior nasal flap; **llf**, lower labial furrow; **mrd**, mesonarial crest; **ulf**, upper labial furrow. Scale bar: 20 mm.

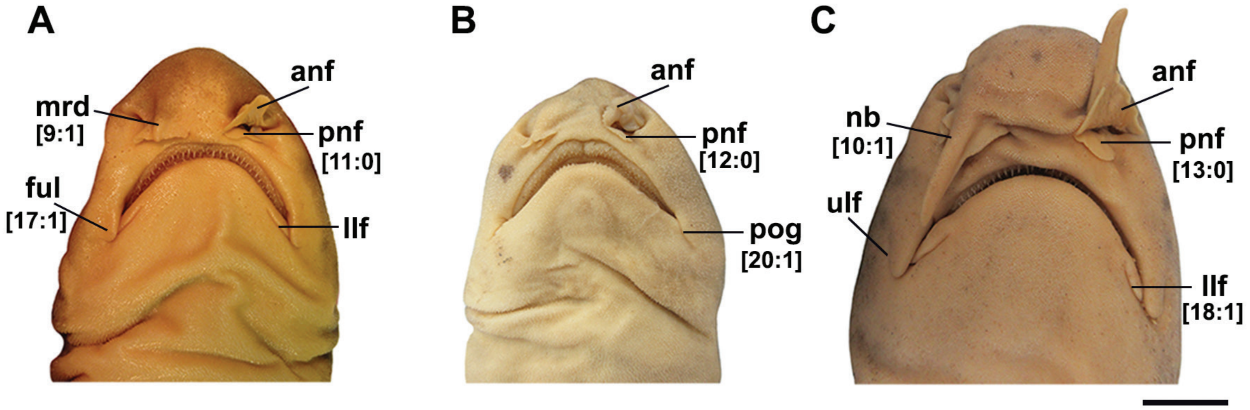

Figure 2. Nasoral region with lifted anterior nasal flap and exposed posterior nasal flap. A, *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, *Cephaloscyllium isabella*, USNM 320594, female, 390 mm TL; *Poroderma pantherinum*, SAIAB 34577, male, 640 mm TL. **anf**, anterior nasal flap; **ful**, flap on the upper lip margin; **llf**, lower labial furrow; **mrd**, mesonarial crest; **nb**, nasal barbel; **pnf**, posterior nasal flap; **pog**, postoral groove; **ulf**, upper labial furrow. Scale bar: 20 mm.

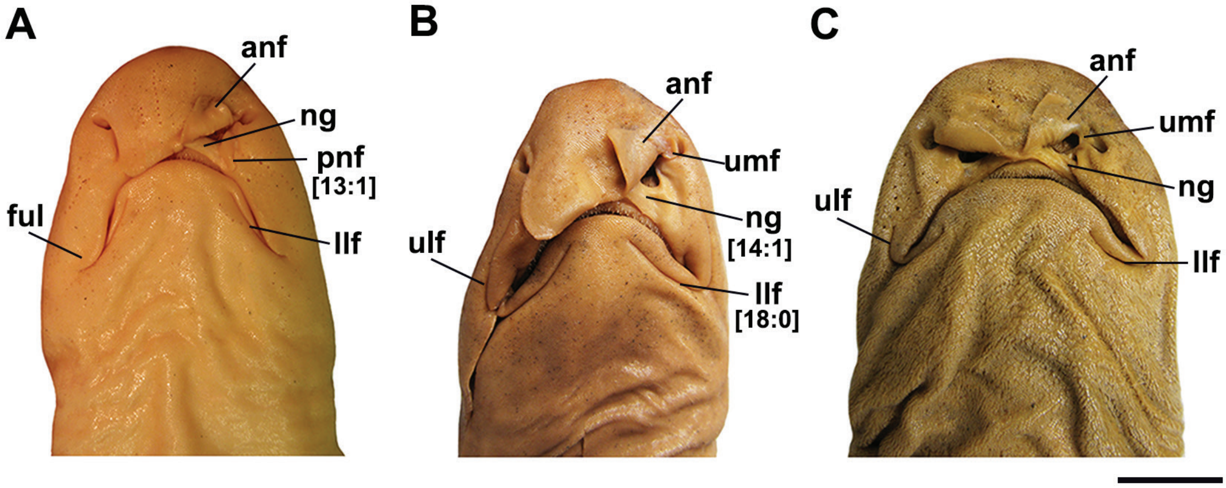

Figure 3. Nasoral region with lifted anterior nasal flap and exposed posterior nasal flap. A, *Scyliorhinus canicula*, USNM 221470, female, 438 mm TL; B, *Atelomycterus fasciatus*, CSIRO H1298-7, male, 370 mm TL; C, *Haploblepharus edwardsii*, AMNH 40988, male, 480 mm TL. **anf**, anterior nasal flap; **ful**, flap on the upper lip margin; **llf**, lower labial furrow; **ng**, nasoral groove; **pnf**, posterior nasal flap; **pog**, postoral groove; **ulf**, upper labial furrow; **umf**, upper mesonarial flap. Scale bar: 20 mm.

in *Apristurus*, *Atelomycterus*, *Aulohalaelurus* and *Haploblepharus* (state 1; Fig. 3B, C).

12 Degree of development of posterior nasal flap: (0) corresponding to one-half of the area of the anterior nasal flap; (1) reduced and only bordering the posterior tip of the excurrent aperture. (CI = 100; RI = 100).

Scyliorhinines present a well-developed posterior nasal flap, corresponding to one-half of the area of anterior nasal flap, as do the genera *Asymbolus* and *Halaelurus* (state 0; Fig. 2). The posterior flap is rudimentary in other taxa, corresponding to one fourth or less of the area of the anterior nasal flap (state 1).

13 Position of the posterior nasal flap: (0) situated on the posterior border of the excurrent aperture; (1) laterally situated to the excurrent aperture. (CI = 100; RI = 100).

In relation to the position of the posterior nasal flap, *Scyliorhinus canicula* and *S. duhamelii* present a unique condition, i.e. the posterior nasal flap is anteroposteriorly elongated and laterally situated at the excurrent aperture (state 1; Fig. 3A). In other species of *Scyliorhinus* and carcharhiniforms, this flap is situated along the posterior margin of the excurrent aperture (state 0; Fig. 2). In orectolobiforms, a posterior nasal flap is also laterally situated at the excurrent aperture (Goto 2001). The similarity to the position of the posterior flap in *S. canicula*, *S. duhamelii* and in orectolobiforms may be related to the presence of a nasoral groove (Bell 1993).

14 Nasoral grooves: (0) absent; (1) present. (CI = 33; RI = 33).

A nasoral groove, which links the excurrent aperture and the mouth, is observed only in *Scyliorhinus canicula* and *S. duhamelii*, amongst scyliorhinines (state 1; Fig. 3A). Nasoral grooves are also observed in the scyliorhinids, *Atelomycterus* and *Haploblepharus* (Fig. 3B, C). White (1937) pointed out that the occurrence of nasoral grooves, as well as the distance of nasal flaps from the mouth, may be directly related to the environment in her Catuloidea (= Scyliorhinidae). However, species that present the same habitats and same geographic range as *S. canicula* and *S. duhamelii* (e.g. *S. stellaris*) lack these structures. Shirai (1996) and de Carvalho (1996) listed and coded the occurrence of nasoral grooves in their analyses, but did not comment on the differences found in the nasoral region of scyliorhinids and orectolobiforms. In carcharhiniforms, such flaps are shallow and wide, distinguishing them from the deep nasoral grooves of orectolobiforms that are flanked by a complex arrangement of flaps and projections. According to Bell (1993), the sporadic occurrence of nasoral grooves and associated features suggest that such structures have evolved independently at least three times in scyliorhinids and once in triakids.

15 Upper labial furrow: (0) present; (1) absent. (CI = 33; RI = 83).

An upper labial furrow is absent in *Scyliorhinus*, *Cephaloscyllium*, *Holohalaelurus* and *Poroderma africanum* (state 1; Figs 1–3). This furrow is present in *Poroderma pantherinum*, *Proscyllium habereri* and other scyliorhinids (state 0; Figs 1–3).

16 Lower labial furrow: (0) present; (1) absent. (CI = 50; RI = 75).

A lower labial furrow is present in *Scyliorhinus*, *Poroderma*, *Proscyllium* and other scyliorhinids (state 0; Figs 1–3) and absent in *Cephaloscyllium* and *Holohalaelurus* (state 1; Figs 1–3). In *Cephaloscyllium sufflans* and *C. variegatum*, we observed small notches close to the commissure of the mouth, which do not, however, correspond to labial furrows.

17 Projected flap on the upper lip margin: (0) absent; (1) present. (CI = 50; RI = 94).

In *Scyliorhinus* species and *Poroderma africanum*, there is a projected flap on the upper lip margin that laterally covers the lower labial furrow and its external margin does not extend anteriorly (state 1; Figs 1A, 2A, 3A); this is a unique condition in the family Scyliorhinidae. The presence of this flap was considered a diagnostic character of *Scyliorhinus* by Springer (1979), Compagno (1988a) and Soares and de Carvalho (2019) and may be related to the position of the upper labial cartilage, which is internal to the *preorbitalis* muscle anteriorly and ventral and external to the m. *adductor mandibulae* posteriorly.

18 Configuration of labial furrows: (0) continuous and fused laterally; (1) discontinuous and upper furrow ventral to the lower one. (CI = 33; RI = 0).

In taxa, where both labial furrows are found, there is a difference concerning their configuration. In *Poroderma pantherinum*, these furrows are narrow and discontinuous and the posterior tip of the upper furrow is ventrally situated at the lower one (state 1; Fig. 2C). The same condition is also found in *Parmaturus* and *Schroederichthys*. In *Proscyllium* and all other scyliorhinids, labial furrows are continuous and laterally fused (state 0; Fig. 3B, C). The configuration of labial furrows may be related to the presence or absence of a fusion between labial cartilages; taxa, in which the furrows are continuous, also presented fused labial cartilages, whereas the furrows are discontinuous in taxa with separated labial cartilages.

19 Number of upper labial cartilages: (0) two; (1) one. (CI = 50; RI = 92).

Compagno (1988a) pointed out that the reduction or loss of labial furrows and flaps may be related to loss or reduction of labial cartilages. Shirai (1992a) divided labial cartilages into four states, according to their number: (1) three cartilages present (two upper and one lower); (2) two cartilages (one upper and one lower); (3) only one upper cartilage present (lower absent); (4) both cartilages absent. In this study, only the number of upper labial cartilages was considered, ranging between one and two. In *Scyliorhinus*, as well as in *Cephaloscyllium* and *Schroederichthys*, only one upper cartilage was observed (state 1; Fig. 4A). In *Proscyllium* and the other catsharks, two upper cartilages were found (state 0; Fig. 4B), with the exception of *Holohalaelurus*, which presents no upper labial cartilage, but only a lower one (an autapomorphy for this genus).

20 Postoral groove: (0) absent; (1) present. (CI = 100; RI = 100).

In species of *Cephaloscyllium*, a postoral groove is found, consisting of a slit extending from the oral commissure by an extension of up to one-fifth of the width of the mouth (state 1; Fig. 2B); the extension of this groove is variable amongst species of this genus. In other taxa examined, this groove is absent (state 0; Figs 1–3). In *Holohalaelurus*, in which labial furrows are absent as in *Cephaloscyllium*, no notch or postoral groove is observed (Fig. 1C).

Fins

21 Pelvic apron: (0) absent; (1) present. (CI = 33; RI = 87).

The fusion of the pelvic inner margins, known as the pelvic apron and defined by Compagno (1988a), is observed in males of species of *Scyliorhinus*, covering their claspers (state 0; Fig. 5). In *Cephaloscyllium* and *Poroderma*, the pelvic inner margins are fused only at their origin; however, this condition is not considered a true pelvic apron because it has also been observed in females where no claspers are found. This fusion is absent in most other scyliorhinids, except in *Asymbolus* and *Holohalaelurus*.

22 Extension of pelvic apron: (0) fusion extending up to one-half the length of pelvic inner margins; (1) fusion extending up to two thirds of the length of pelvic inner margins; (2) pelvic inner margins almost entirely fused. (ordered; CI = 100; RI = 100).

Amongst the taxa presenting the pelvic apron, there is some variation in its extension. In *Asymbolus* and *Holohalaelurus*, the pelvic apron may be present only in the proximal portion of the pelvic inner margins, corresponding to less than one-half of the length of the inner margins. Species of *Scyliorhinus* present a more developed pelvic apron, ranging from up to two thirds of the length of the pelvic inner margins (most of species; Fig. 5A) to almost their entire length (*S. canicula*, *S. capensis*, *S. duhamelii*, *S. torazame* and *S. torrei*). In these species, claspers of juveniles are totally concealed ventrally by the pelvic apron and visible only when it is lifted (state 2; Fig. 5B). The more developed pelvic apron, extending up to two thirds of the length of pelvic inner margins, was considered by Soares and de Carvalho (2019) as a synapomorphy for *Scyliorhinus* species.

23 Origin of the first dorsal fin: (0) closer to the vertical line that passes through the insertion of pelvic fins; (1) closer to the vertical line that passes through the origin of pelvic fins. (CI = 33; RI = 0).

The posteriormost origin of the first dorsal fin is the main character used to diagnose the family Scyliorhinidae (Springer 1979; Compagno 1988a; Compagno et al. 2005; Ebert et al. 2013). Most of its genera present the origin of the first dorsal fin well posterior to the vertical line that passes through the origin of the pelvic fins and closer to their insertion, ranging from opposite the insertion to half-length of pelvic inner margins. In general, dorsal fins are more posteriorly situated in males than in females. The exception is observed in *Cephalurus* and *Parmaturus*, in which the origin of the first dorsal fin is slightly anterior or opposite to the origin of pelvic fins. In *Proscyllium* and other carcharhiniforms, the first dorsal fin is completely anterior to pelvic fins and its origin may be opposite to the posterior tip or to the half-length of the pectoral inner margins. According to White (1937) and Nakaya (1975), the relative position of the dorsal fins is more anterior in more derived carcharhiniforms and is a character of great phylogenetic relevance. By this criterion, the Scyliorhinidae would be considered the most basal clade within carcharhiniforms. However, Compagno (1988a) pointed out that this character should be cautiously interpreted and better investigated. Regarding the fossil record and the widespread occurrence amongst diverse groups, the anterior position of the first dorsal fin would be primitive in carcharhiniforms, whereas posterior dorsal fins might be a secondary condition, correlated with a more derived benthic habit (Compagno 1988a).

24 Origin of second dorsal fin: (0) posterior to the vertical line that passes through half-length of anal fin base; (1) anterior to the vertical line that passes through half-length of anal fin base. (CI = 25; RI = 50).

Two conditions were observed concerning the origin of the second dorsal fin: posterior (most scyliorhinids; state 0, Fig. 6) or anterior to the vertical line that passes through half-length of anal fin base (*Cephaloscyllium*, *Cephalurus*, *Parmaturus* and *Proscyllium*; state 1, Fig. 6).

Dermal denticles

25 Cusplets of dermal denticles on dorsolateral body surface: (0) present; (1) absent. (CI = 33; RI = 0).

The crown of the dermal denticles on the dorsolateral surface of the body varies from ‘teardrop’ to ‘trident’ shape due to the presence or absence of cusplets lateral to the

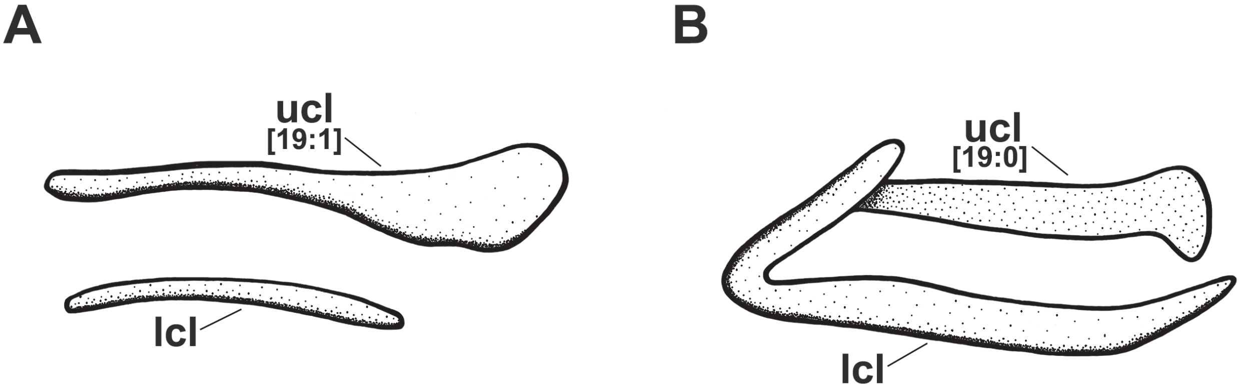

Figure 4. Labial cartilages. A, detail of labial cartilages in *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, detail of labial cartilages in *Asymbolus rubiginosus*, AMS I.30393-004, male, 527 mm TL. **ucl**, upper labial cartilage; **lcl**, lower labial cartilage.

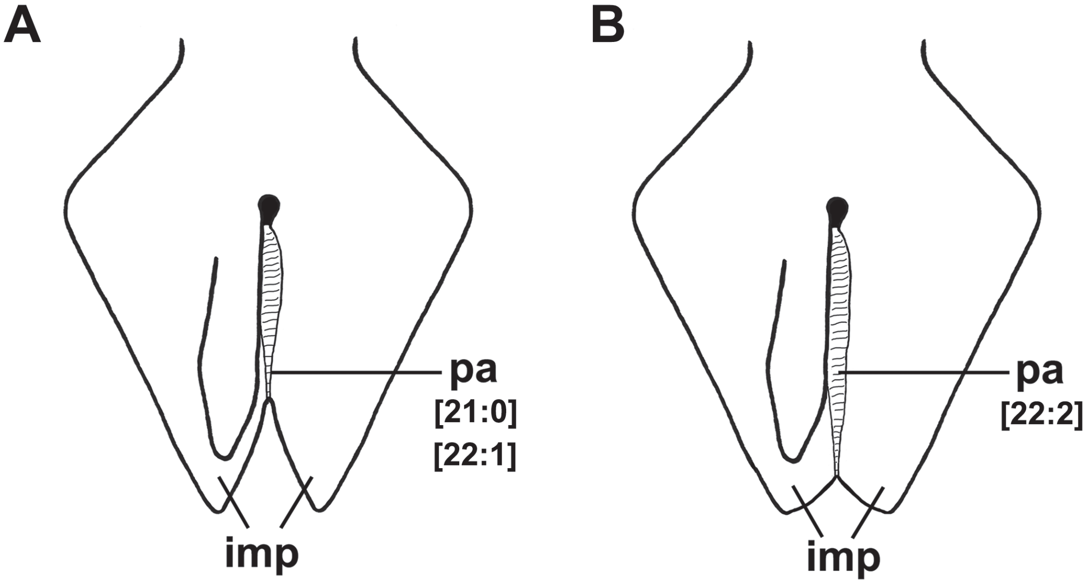

Figure 5. Pelvic apron. A, detail of pelvic apron in *Scyliorhinus comoroensis*, MNHN 1984–0701, male, 457.2 mm TL; B, detail of pelvic apron in *S. capensis*, SAIAB 27577, male, 863 mm TL. **imp**, inner margins of pelvic fins; **pa**, pelvic apron. Modified from Soares and de Carvalho (2019).

principal cusp of the crown. Cusplets are present in most scyliorhinids (state 0; Fig. 7), but absent in *Cephalurus*, *Parmaturus* and *Schroederichthys* (state 1; Fig. 7). According to Reif (1985), a greater number of cusplets and ridges would contribute to drag reduction during swimming, improving hydrodynamics.

26 Extension of ectodermal pits in dorsal surface of the crown denticles: (0) extending through more than half the length of the crown; (1) restricted to anterior portion of the crown (CI = 25; RI = 50).

Ectodermal pits were observed and illustrated by Reif (1982) in dermal denticles of carcharhiniforms and named by Muñoz-Chápuli (1985). In scyliorhinines, *Atelomycterus*, *Cephalurus*, *Haploblepharus* and *Schroederichthys*, only the proximal portion of the crown denticles is covered by these pits (state 0; Fig. 7). In other scyliorhinids, ectodermal pits extend through more than half or almost the entire length of the crown, mainly in denticles on anteriormost regions of the body (*Apristurus*, *Asymbolus*, *Figaro*, *Galeus*, *Halaelurus*, *Holohalaelurus* and *Parmaturus*) (state 1; Fig. 7).

27 Median ridges on dermal denticles: (0) two ridges; (1) one ridge. (CI = 33; RI = 50).

White (1937) categorised the dermal denticles of elasmobranchs according to the features observed in the crown. According to her, scyliorhinids have dermal denticles with flat crowns presenting incomplete median ridges not extending to the distal tip of the crown (e.g. *Scyliorhinus retifer* and *Schroederichthys bivius*) or complete median ridges, extending to the distal tip of the crown (e.g.

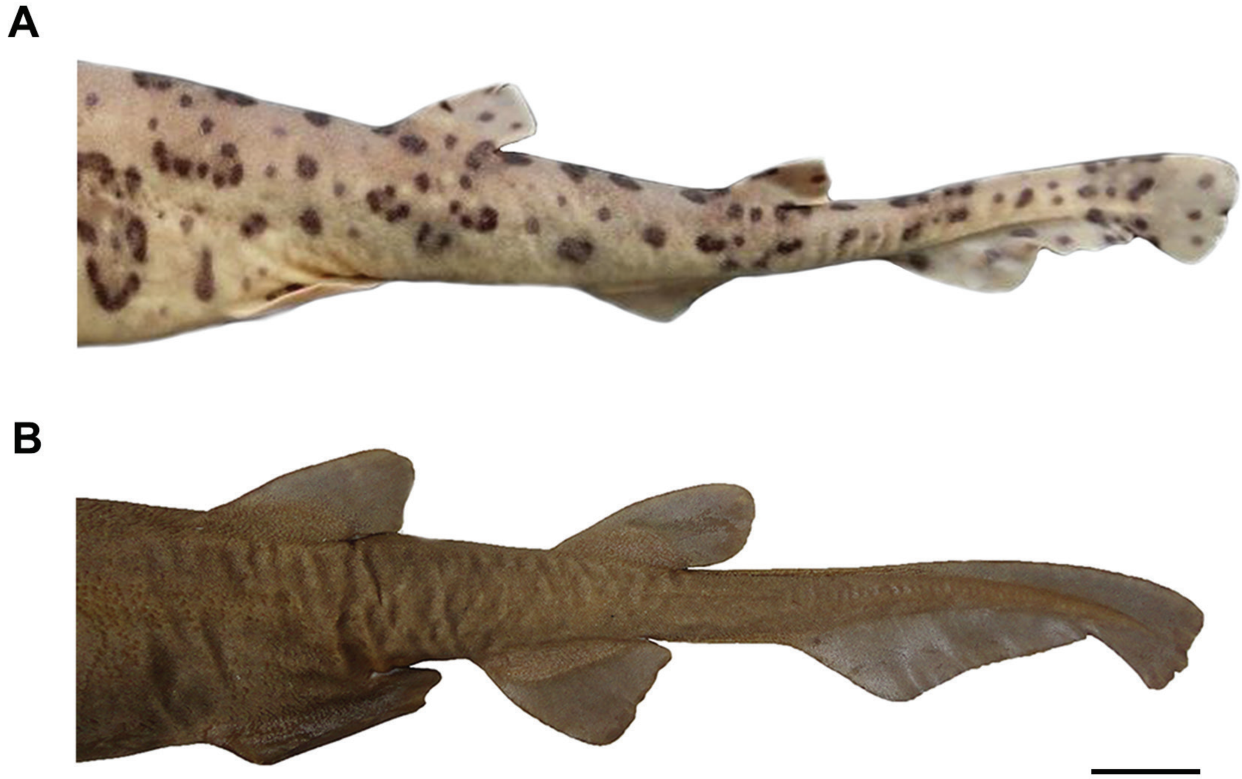

Figure 6. Caudal region. A, detail of dorsal fins in *Scyliorhinus haeckelii*, UERJ 2202, male, 444 mm TL; B, detail of dorsal fins in *Parmaturus xaniurus*, CAS 232152, female, 450 mm TL. Scale bar: 25 mm.

Atelomycterus spp., *Halaelurus burgeri* and *Parmaturus* spp.). We observed that the extension and degree of development of median ridges present variation according to taxa and body region examined. However, the number of ridges varies in a consistent manner, making it possible to separate the dermal denticles into two categories: one or two median ridges present on the dorsal surface of the crown, extending from its base to the distal tip or close to it. In scyliorhinines, *Apristurus*, *Cephalurus*, *Galeus* and *Holohalaelurus*, only one median ridge, more prominent than lateral ridges, is observed (state 1; Fig. 7). In other scyliorhinids, two prominent median ridges, forming a gutter in between them, are present (state 0; Fig. 7).

28 Caudal crest of enlarged dermal denticles: (0) absent; (1) present. (CI = 100; RI = 50).

The presence of a caudal crest of dermal denticles distinct from the denticles on dorsolateral surfaces and situated on the upper lobe of caudal fin, is found in *Figaro*, *Galeus*, *Parmaturus* and some species of *Apristurus* (state 1; Fig. 8), varying widely amongst species of these genera. This crest is absent in other taxa examined. In *Figaro*, a crest of enlarged dermal denticles on the lower lobe of the caudal fin was also observed. The occurrence of a caudal crest of dermal denticles is widely used in taxonomic studies of the family Scyliorhinidae (Linnaeus 1758; Regan 1908; Garman 1913; Bigelow and Schroeder 1948; Springer 1966, 1979), but has never been analysed in a cladistic study until now.

Musculature

29 Muscle *depressor palpebrae nictitantis*: (0) present; (1) absent. (CI = 100; RI = 100).

The postorbital musculature is composed of three muscles: m. *depressor palpebrae nictitantis*, m. *levator palpebrae nictitantis* and m. *retractor palpebrae nictitantis*. These muscles are responsible for elevation and depression of the nictitating lower eyelid, which is a diagnostic character for carcharhiniforms. These muscles were found in most of the taxa examined, except in scyliorhinines, in which only the muscles *levator palpebrae nictitantis* and *retractor palpebrae nictitantis* are present (state 1; Fig. 9A). The absence of the *depressor palpebrae nictitantis* in the subfamily Scyliorhininae was already reported by Compagno (1988a) and is one of the characters used by that author to diagnose it. Specimens of *Aulohalaelurus labiosus*, *Scyliorhinus comoroensis* and *S. garmani* were not available for dissection (these taxa are scored with a question mark in the matrix).

30 Insertion of the muscle *coracomandibularis*: (0) on the articular region of the antimeres of Meckel's cartilage; (1) near the mid-length of the lower jaws, on their anteromedial borders. (CI = 50; RI = 0).

In most taxa examined, the m. *coracomandibularis* inserts on the articular region of the antimeres of Meckel's cartilage (state 0; Fig. 10A). In *Haploblepha-*

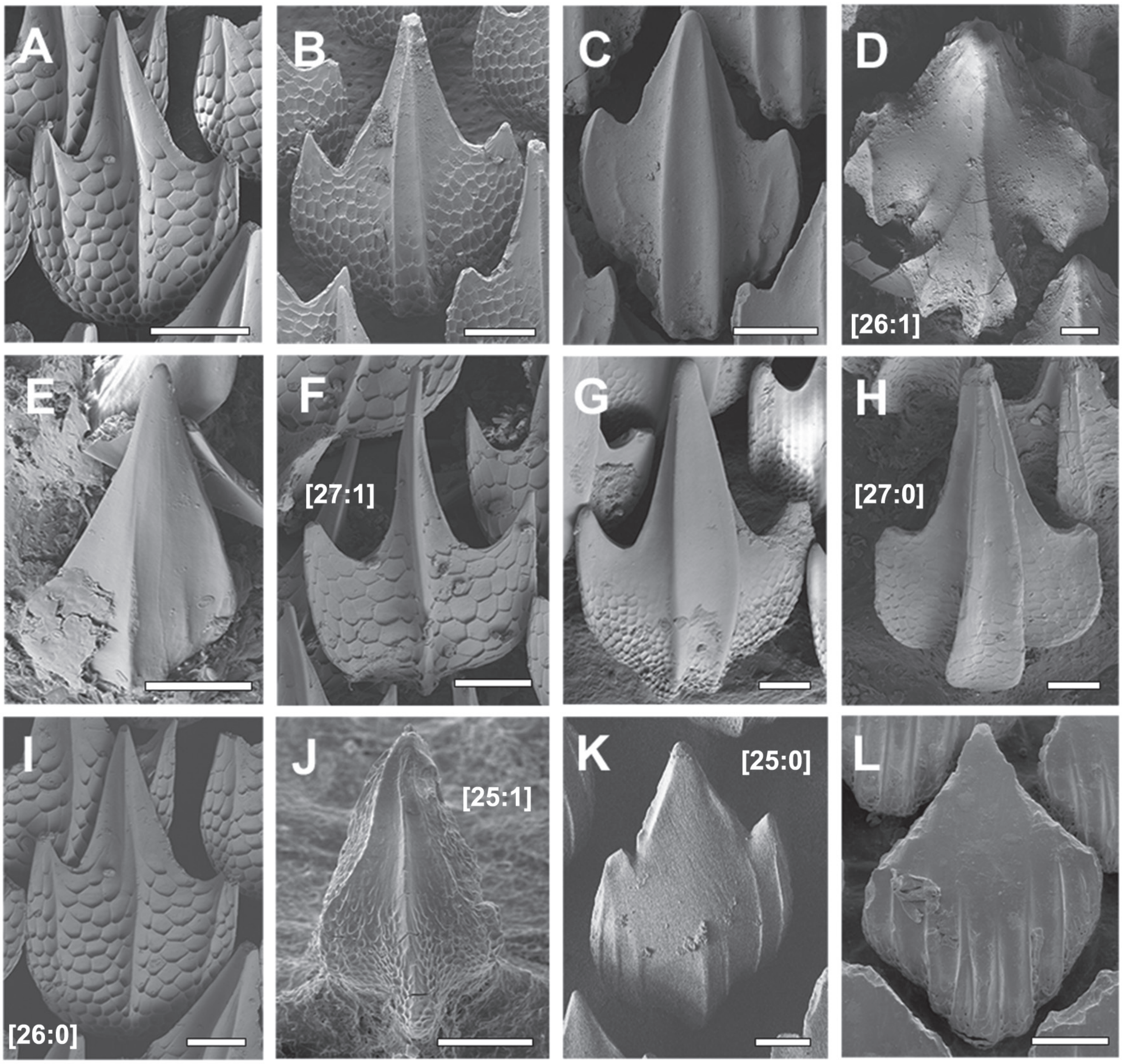

Figure 7. Dermal denticles above the origin of the first dorsal fin. A, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL; B, *Asymbolus rubiginosus*, AMS I.30393-004, male, 527 mm TL; C, *Atelomycterus fasciatus*, CSIRO H1298-7, male, 370 mm TL; D, *Cephaloscyllium sufflans*, SAIAB 6242, male, 800 mm TL; E, *Cephalurus cephalus*, USNM 221527, female, 285 mm TL; F, *Galeus antillensis*, UF 77853, female, 370 mm TL; G, *Halaelurus natalensis*, SAIAB 26951, male, 400 mm TL; H, *Haploblepharus edwardsii*, AMNH 40988, male, 480 mm TL; I, *Holohalaelurus regani*, SAIAB 25717, male, 610 mm TL; J, *Parmaturus xaniurus*, CAS 232152, female, 450 mm TL; K, *Poroderma africanum*, SAIAB 25343, male, 920 mm TL; L, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL. Scale bar: 250 µm.

rus edwardsii and *Poroderma africanum*, this muscle is divided into two portions anteriorly, each of them inserting on the anteromedial borders of the antimeres of Meckel's cartilage and not occupying the symphysial region of the jaws (state 1; Fig. 10B). In these taxa, a basimandibular cartilage is observed at the symphysial region of jaws, connecting the antimeres of Meckel's cartilage.

31 Insertion of the muscle *coracohyoideus*: (0) on the ventral surface of the basihyal cartilage; (1) on connective tissue adjacent to the basihyal cartilage. (CI = 50; RI = 0).

In most taxa examined, the muscle *coracohyoideus* inserts on the ventral surface of the basihyal (state 0; Fig. 11). In *Apristurus* and *Holohalaelurus* this muscle inserts on lateral (*Apristurus longicephalus*) or anterior (*Holohalaelurus regani*) connective tissue projections of the basihyal (state 1; Fig. 11D).

32 Configuration of muscles bundles of the m. *coracohyoideus*: (0) juxtaposed muscle bundles; (1) separated muscle bundles. (CI = 33; RI = 60).

The presence of m. *coracohyoideus* composed of two distinct muscle bundles originating in the fascia of the

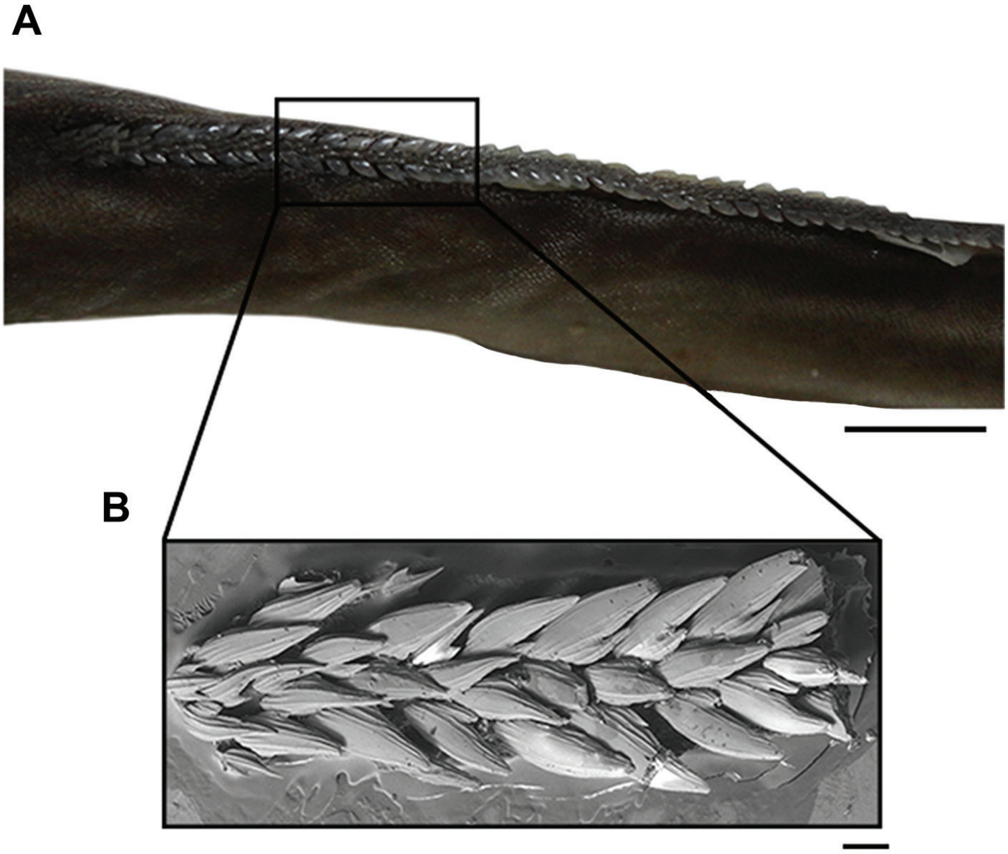

Figure 8. Detail of the caudal crest in *Galeus antillensis*, UF 77853, female, 370 mm TL. A, general view, B, closed view. Scale bar:10 mm (A); 200 µm (B).

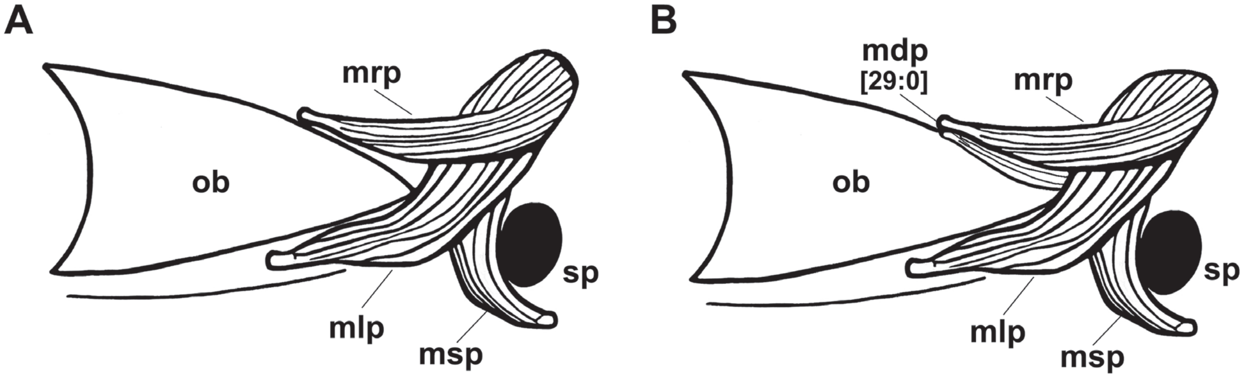

Figure 9. Detail of the postorbital musculature. A, *Schroederichthys maculatus*, UF 65846, male, 313 mm TL; B, *Poroderma africanum*, AMNH 43134, male, 505 mm TL. **mdp**, muscle *depressor palpebrae nictitantis*; **mlp**, m. *levator palpebrae nictitantis*; **mrp**, m. *retractor palpebrae nictitantis*; **msp**, m. *espiracularis*, **ob**, orbit; **sp**, spiracle.

m. *coracoarcualis* was observed in *Proscyllium* and all scyliorhinids. These bundles can be juxtaposed (most taxa examined) or separated by a distance of at least one-half the width of each bundle (*Cephaloscyllium*, *Cephalurus* and *Halaelurus*; state 1, Fig. 11A).

33 Origin of the muscles *coracobranchialis* II, III and IV: (0) on the coracoid bar; (1) on the pericardial membrane. (CI = 50; RI = 75).

In *Proscyllium* and some scyliorhinids, the origin of the muscles *coracobranchialis* II, III and IV is on the coracoid bar (*Apristurus*, *Asymbolus*, *Atelomycterus*, *Cephaloscyllium*, *Figaro*, *Galeus*, *Parmaturus*, *Poroderma* and *Scyliorhinus*; state 0, Fig. 12A). In other scyliorhinids, these muscles originate from the pericardial membrane, a layer of connective tissue anterior to the coracoid bar and ventral to the heart (*Cephalurus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus* and *Schroederichthys*; state 1, Fig. 12B).

The insertion of the m. *coracobranchialis* presents the following pattern in the taxa examined: *coracobranchialis* II, on the medial border of the ceratobranchial II cartilage and anterolateral border hypobranchial II; *coracobranchialis* III, on the medial border of the ceratobranchial III cartilage and anterolateral border of hypobranchial III; *coracobranchialis* IV, on the medial border of the ceratobranchial IV cartilage and anterolateral border of hypobranchial IV. Muscle *coracobranchialis* V presents the same pattern in the taxa examined, originating from the anterolateral borders of the coracoid bar and inserting on the medial border of ceratobranchial V and lateral border of the basibranchial copula.

Neurocranium

34 Rostral cartilages: (0) fused; (1) united only by connective tissue. (CI = 100; RI = 100).

In scyliorhinines, *Atelomycterus* and *Aulohalaelurus*, the rostrum is formed by three rostral cartilages anteriorly united only by connective tissue (state 1; Fig. 13A–D), whereas in other taxa examined, these cartilages are fused anteriorly, sometimes forming or not a rostral node (state 0; Fig. 13E–G). Compagno (1988a) proposed that the absence of fusion between rostral cartilages could be an independently derived and the secondary condition for scyliorhinids and proscylliids based on their proximity to taxa in which the fused condition is present.

35 Relation between lateral rostral cartilages and anterior fontanelle: (0) rostral cartilages distant from anterior fontanelle; (1) rostral cartilages confluent with lateral borders of anterior fontanelle. (CI = 100; RI = 100).

The distance between lateral rostral cartilages may vary, positioned medially or laterally to the lateral borders of the anterior fontanelle. In some cases, the lateral rostral cartilages are confluent with the lateral borders of the anterior fontanelle, connected to it through ridges that extend from the base of the rostral cartilages to the border of the fontanelle; this condition was observed in *Apristurus*, *Figaro*, *Galeus* and *Parmaturus* (state 1; Fig. 13F, G). In other taxa examined, the lateral rostral cartilages are distant from the anterior fontanelle and do not present ridges in between both structures (state 0; Fig. 13).

36 Relationship between median rostral cartilage and anterior fontanelle: (0) median rostral cartilage and anterior fontanelle separated by internasal space; (1) median rostral cartilage confluent with anterior fontanelle. (CI = 50; RI = 50).

The distance between the median rostral cartilage and anterior fontanelle varies amongst taxa examined. In scyliorhinines and other taxa examined, the median rostral cartilage and the anterior fontanelle are separated by the internasal space, distant by at least two thirds of the length of the median rostral cartilage (state 0; Fig. 13A). In *Cephalurus*, *Haploblepharus* and *Holohalaelurus*, the anterior border of the anterior fontanelle is adjacent to the base of the medial rostral cartilage, without an internasal space separating them (state 1; Fig. 14). Compagno (1988a) listed the measurement 'distance from the ventral border of the anterior fontanelle to the base of the median rostral cartilage' as a way of measuring the space between these structures.

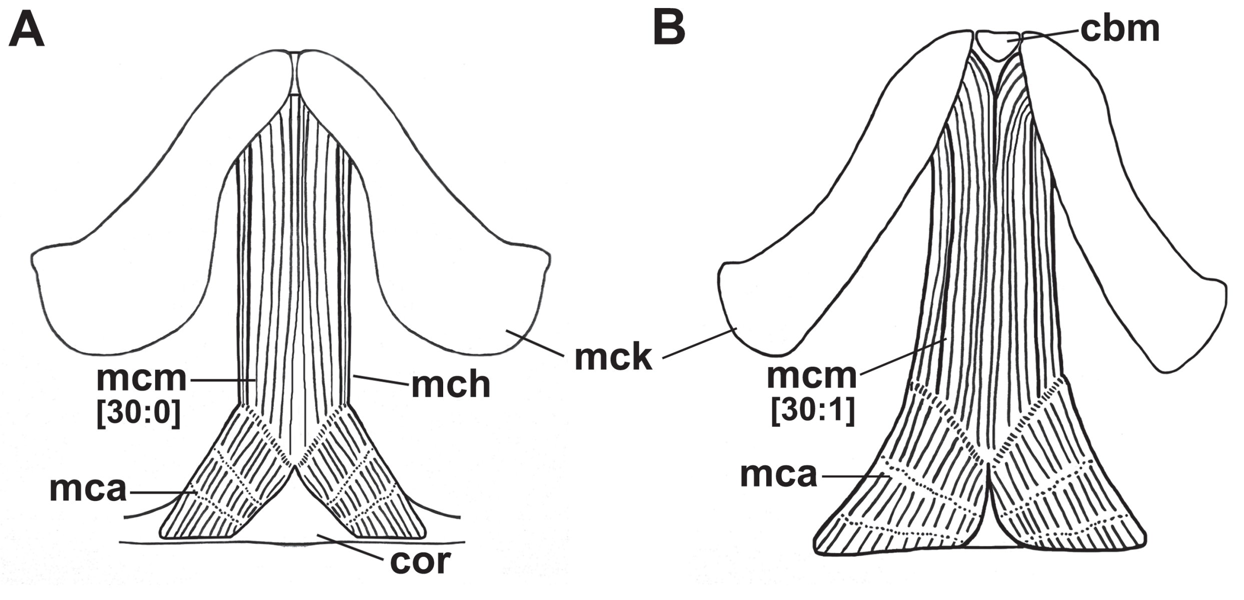

Figure 10. Detail of the insertion region of the muscle *coracomandibularis*. A, *Cephaloscyllium umbratile*, USP uncatalogued, male, 409 mm TL; B, *Haploblepharus edwardsii*, AMNH 40988, male, 480 mm TL. **cbm**, basimandibular cartilage; **cor**, coracoid bar; **mca**, muscle *coracoarcualis*; **mch**, m. *coracohyoideus*; **mck**, Meckel's cartilage; **mcm**, m. *coracomandibularis*.

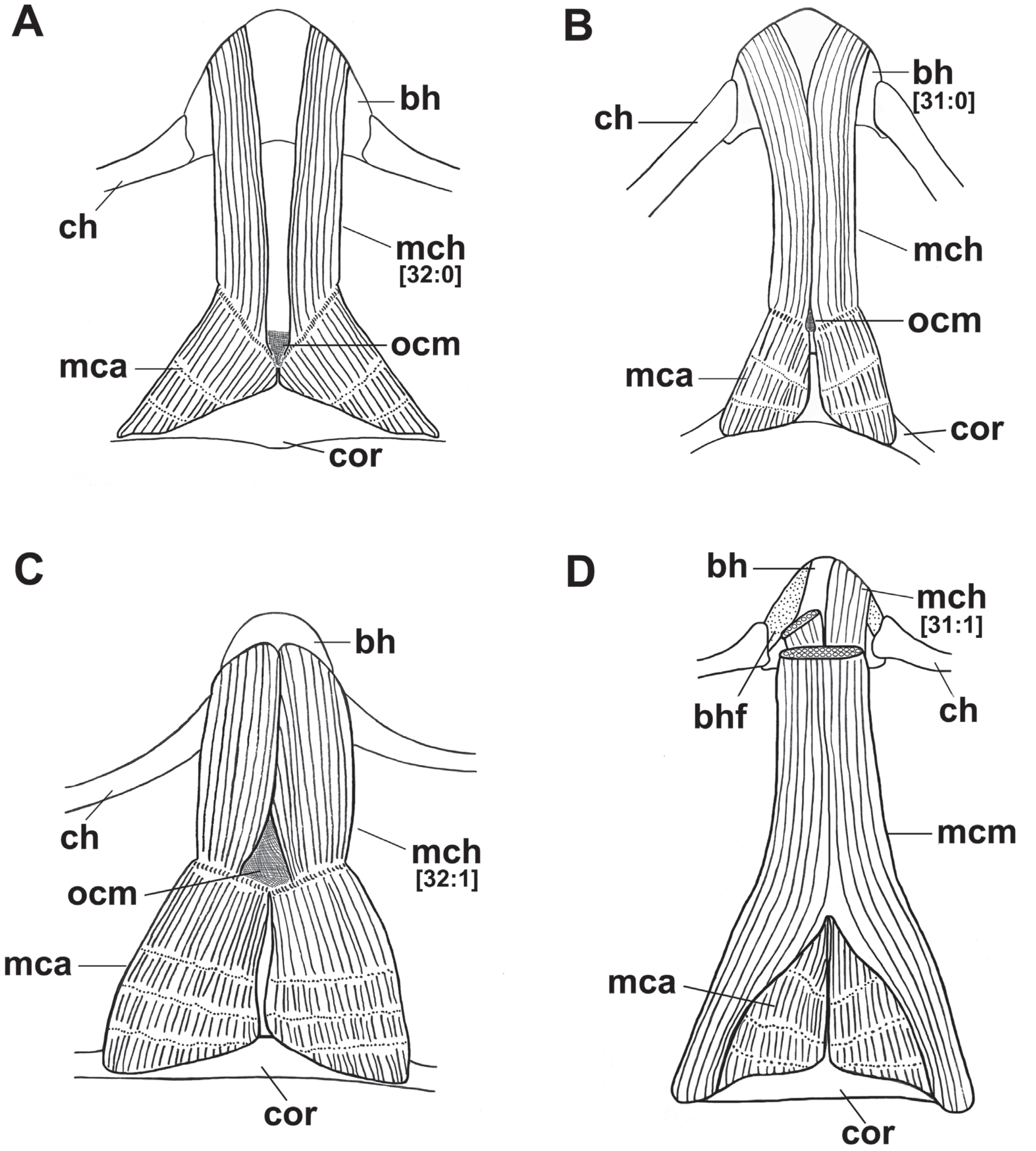

Figure 11. Hypobranchial musculature. A, *Cephaloscyllium umbratile*, uncatalogued, male, 409 mm TL; B, *Galeus antillensis*, UF 77853, female, 370 mm TL; C, *Holohalaelurus regani*, SAIAB 25717, male, 610 mm TL; D, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL; **bh**, basihyal; **bhf**, adjacent flap of the basihyal; **ch**, ceratohyal; **cor**, coracoid bar; **mca**, muscle *coracoarcualis*; **mch**, m. *coracohyoideus*; **mcm**, m. *coracomandibularis*; **ocm**, origin of the m. *coracomandibularis*.

37 Orientation of nasal capsules: (0) nasal capsules perpendicular to the anteroposterior axis of the neurocranium; (1) nasal capsules oblique. (CI = 50; RI = 0).

In *Apristurus* and *Galeus*, the nasal capsules are obliquely orientated to the anteroposterior axis of the neurocranium (state 1; Fig. 15), whereas in the other scyliorhinids, the nasal capsules are orientated perpendicularly and laterally expanded (state 0; Fig. 15).

38 Relative position between nasal apertures: (0) incurrent aperture anterior to excurrent one; (1) nasal apertures at the same level. (CI = 50; RI = 90).

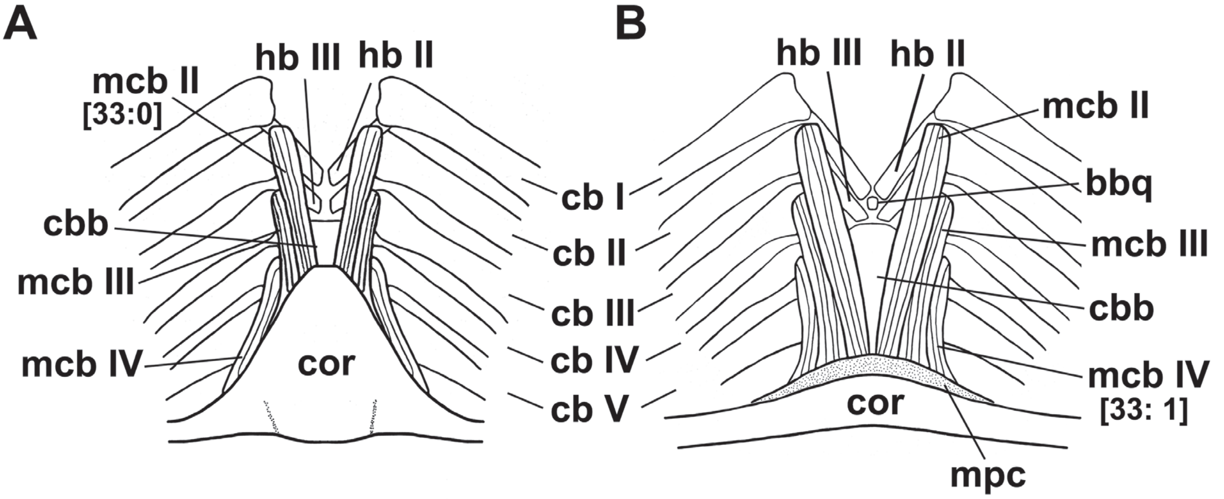

Figure 12. Detail of muscle *coracobranchialis*. A, *Cephaloscyllium umbratile*, USP uncatalogued, male, 409 mm TL; B, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL. **bbq**, basibranchial; **cb I–V**, ceratobranchials I–V; **cbb**, basibranchial copula; **cor**, coracoid bar; **hb II–III**, hypobranchials II–III; **mcb II–IV**, muscles *coracobranchialis* I–IV; **mpc**, pericardial membrane.

Nasal apertures may be positioned at the same level (*Cephaloscyllium*, *Poroderma*, *Schroederichthys* and *Scyliorhinus*; state 1, Fig. 15A–C) or at distinct levels with the incurrent aperture anterior to the excurrent one (most taxa examined; Fig. 15).

39 Fusion of the external nasal cartilage to the dorsal position of the nasal capsule: (0) present; (1) absent. (CI = 50; RI = 89).

The external nasal cartilage, situated anteriorly to the nasal apertures and ventrally to the nasal capsules, may or may not be fused to the anterodorsal portion of the nasal capsules (Goto 2001). The fusion is observed in *Apristurus*, *Asymbolus*, *Cephalurus*, *Figaro*, *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus* and *Proscyllium* (state 0; Fig. 15E–G). In scyliorhinines, *Atelomycterus*, *Aulohalaelurus* and *Schroederichthys*, the external nasal cartilage is not fused to the nasal capsules and a narrow strip of connective tissue separates the external cartilage from the dorsal portion of the nasal capsules (state 1; Fig. 15A–D).

40 Degree of development of the subnasal plate: (0) restricted to the medial portion of the nasal capsules and ventral to the internasal septum; (1) laterally expanded and united to the lateral border of the nasal capsule. (CI = 33; RI = 0).

The subnasal plate is the ventral floor of the nasal capsules, generally associated with a cavity posteromedial to the incurrent aperture and covered by a layer of connective tissue (nasal fontanelle of Compagno 1988a, 1999). In most taxa examined, the subnasal plate is restricted to the medial portion of the nasal capsules and ventral to the internasal septum and the nasal fontanelle occupies the entire region posterior to the excurrent aperture (state 0; Fig. 15). In *Apristurus*, *Galeus* and *Proscyllium*, the subnasal plate is laterally expanded, occupying almost the entire region posterior to the excurrent aperture and the nasal fontanelle is reduced to a narrow strip at the posterior border of the excurrent aperture, divided into two portions (state 1; Fig. 15G). Compagno (1988a) suggested a tendency concerning the enlargement of the subnasal plate in derived taxa and consequent substitution of the nasal fontanelle by cartilage.

41 Epiphyseal notch: (0) absent; (1) present. (CI = 25; RI = 79).

The anterior fontanelle, the anterodorsal aperture of the neurocranium covered by a layer of connective tissue, presents different shapes amongst species and also varies between sexes (Soares et al. 2015, 2016). This fontanelle may present a notch or an indentation on its posterior border, the epiphyseal notch to the pineal body, as observed in *Atelomycterus*, *Halaelurus*, *Holohalaelurus*, *Schroederichthys* and *Scyliorhinus* (state 1; Figs 13A, C, D, 14) or a straight and continuous border, as in *Cephaloscyllium*, *Poroderma* and in the other taxa examined (state 0; Figs 13B, E and G). In *Holohalaelurus*, this notch is well developed, corresponding to two thirds of the length of the anterior fontanelle (Fig. 14).

42 Supraorbital crest: (0) present; (1) absent. (CI = 50; RI = 87.

The occurrence of a supraorbital crest on the neurocranium is widely used for identification and separation of shark genera and families. The presence of this crest is considered primitive for elasmobranchs and its absence secondary in some sharks and rays (Compagno 1988a). This

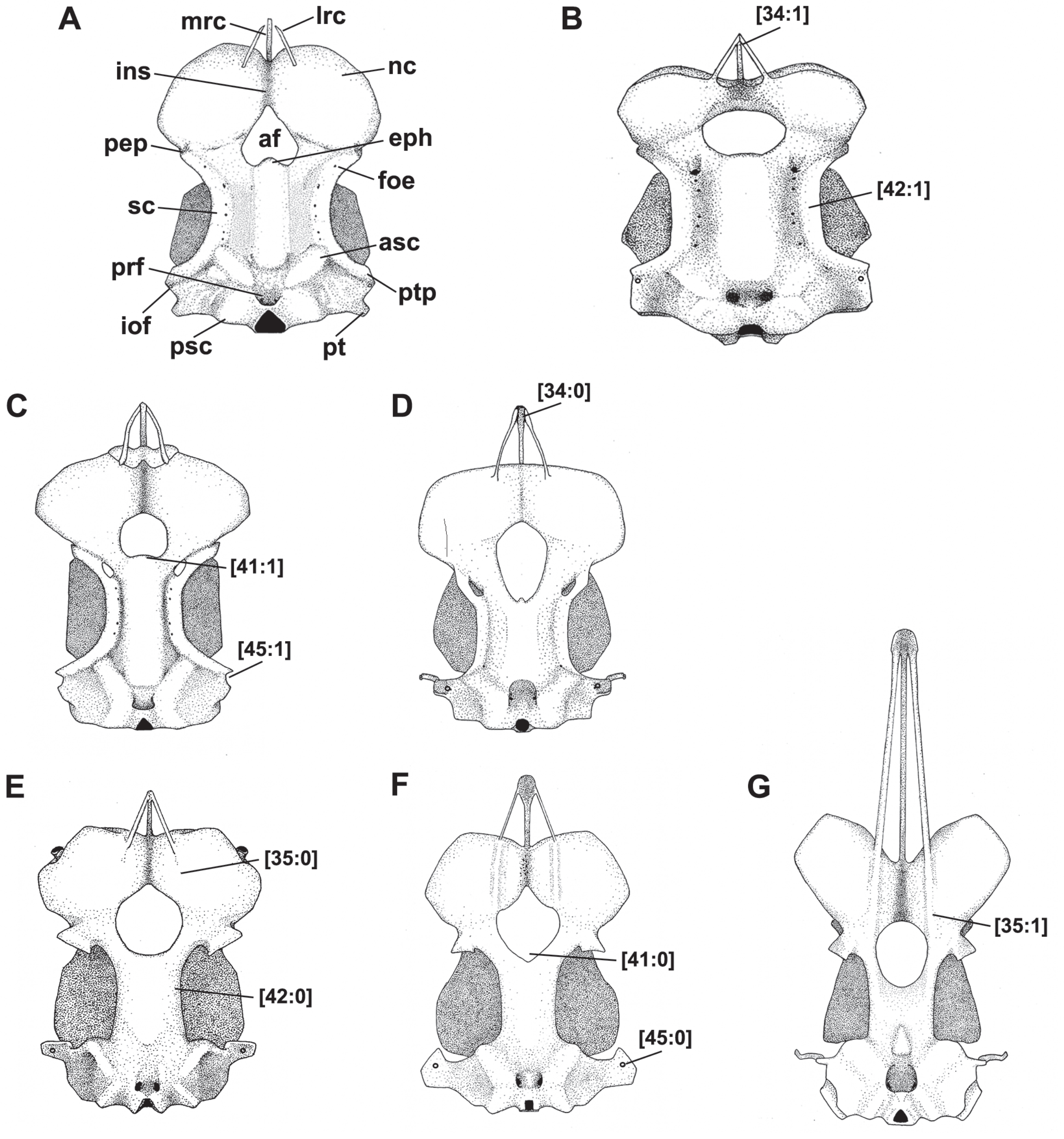

Figure 13. Neurocranium; dorsal view. A, *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, *Cephaloscyllium variegatum*, AMS I.43762-001, female, 670 mm TL; C, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL; D, *Atelomycterus fasciatus*, CSIRO H1298-7, male, 370 mm TL; E, *Asymbolus rubiginosus*, AMS I.30393-004, male, 527 mm TL; F, *Figaro boardmani*, CSIRO H989-5, female, 465 mm TL; G, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. **af**, anterior fontanelle; **asc**, anterior semicircular canal; **eph**, epiphyseal notch; **foe**, external foramen of preorbital canal; **ins**, internasal septum; **iof**, infraorbital canal of the lateral line; **lrc**, lateral rostral cartilage; **mrc**, medial rostral cartilage; **nc**, nasal capsule; **pep**, preorbital process; **prf**, parietal fossa; **psc**, posterior semicircular canal; **pt**, pterotic process; **ptp**, postorbital process; **sc**, supraorbital crest.

structure is situated dorsally to the orbits and continuous to pre- and postorbital processes in scyliorhinines, *Atelomycterus*, *Aulohalaelurus*, *Proscyllium* and *Schroederichthys* (state 1; Fig. 13 A–D). In scyliorhinids of the subfamily Pentanchinae (*sensu* Compagno, 1988a), the supraorbital crest is absent (state 0; Fig. 13E–G). Iglésias et al. (2005) used the occurrence of this crest to distinguish the families Scyliorhinidae and Pentanchidae (= subfamily Pentanchinae of Compagno 1988a), although these authors did not provide further information about the condition found in other families of carcharhiniforms. According to Compagno (1988a), the loss of the supraorbital crest in Hemigalei-

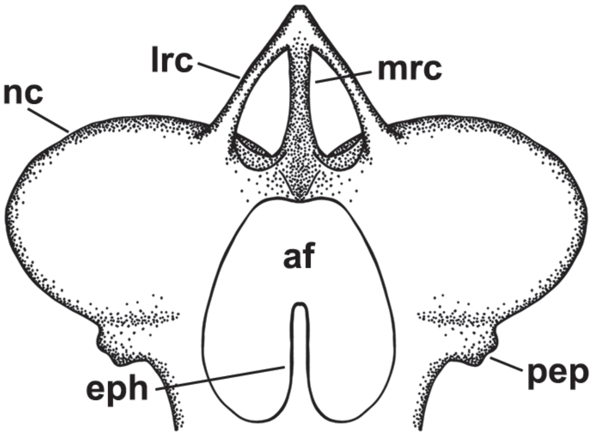

Figure 14. Detail of rostral region and anterior fontanelle of *Holohalaelurus regani*, SAIAB 25717, male, 610 mm TL. **af**, anterior fontanelle; **eph**, epiphyseal notch; **lrc**, lateral rostral cartilage; **mrc**, medial rostral cartilage; **nc**, nasal capsule; **pep**, preorbital process.

dae, Carcharhinidae and Sphyrnidae may be related to the anterior expansion of the muscle *levator palatoquadrati* dorsal to the orbital wall and neurocranial roof. However, in scyliorhinids without a crest, the muscle *levator palatoquadrati* originates in the ventral surface of the postorbital process and is situated entirely posterior to the orbit.

43 Distance between internal carotid foramina: (0) greater than the distance between internal carotid and stapedial foramina; (1) smaller than the distance between internal carotid and stapedial foramina; (2) equal to the distance between internal carotid and stapedial foramina. (ordered; CI = 20; RI = 27).

Four foramina are present on the posterior portion of the basal plate: two for the medial internal carotid arteries and two for the lateral stapedial arteries. Compagno (1988a) reported the median position of the foramina of the internal carotid artery on the basal plate in scyliorhinids, proscylliids and *Pseudotriakis*, but did not propose any distinction between the patterns observed. The distance between these foramina varies widely amongst scyliorhinids. In *Cephaloscyllium*, *Holohalaelurus*, *Proscyllium*, *Schroederichthys* and *Scyliorhinus*, foramina to the internal carotid artery are very close to each other and separated by a shorter distance than the distance between the internal carotid and stapedial foramina, which are fused in some cases (state 1; Fig. 15A–C). In *Atelomycterus*, *Aulohalaelurus*, *Cephalurus*, *Halaelurus* and *Parmaturus*, the internal carotid foramina are separated by a distance similar to that between internal carotid and stapedial foramina (state 2; Fig. 15D). In *Apristurus*, *Asymbolus*, *Figaro*, *Galeus*, *Haploblepharus* and *Poroderma*, the distance between the internal carotid foramina is greater than the distance between the internal carotid and stapedial foramina (state 0; Fig. 15E–G).

44 Relative size of postorbital groove: (0) groove corresponds to more than one-half the height of the hyomandibular facet; (1) groove corresponds to less than one-half the height of the hyomandibular facet. (CI = 33; RI = 0).

The postorbital groove is situated posteriorly to the orbits and ventral to the postorbital processes, limited dorsally by the opisthotic process and ventrally by the hyomandibular facet; the lateral vein of the head passes along this groove (Compagno 1988a). In most scyliorhinids, the postorbital groove corresponds to more than one-half of the height of the hyomandibular facet, resulting in a prominent and laterally visible structure (state 0; Fig. 16A, B). In *Apristurus*, *Aulohalaelurus* and *Cephalurus*, this groove is very narrow and shallow, corresponding to one-third or less of the height of the hyomandibular facet (state 1; Fig. 16C).

45 Fenestra for the infraorbital canal of the lateral line: (0) present; (1) absent. (CI = 50; RI = 0).

The pre- and postorbital processes are laterally expanded from the neurocranial roof, as wide as or wider than the nasal capsules. In most scyliorhinids, the distal tip of the postorbital process has a large fenestra through which passes the infraorbital canal of the lateral line (Compagno 1988a; state 0, Fig. 13). In *Apristurus* and *Schroederichthys*, this fenestra is absent. In the latter, the infraorbital canal passes through a bifurcation situated at the distal tip of the postorbital process (Fig. 13C). In *Apristurus*, the postorbital process is narrow and rod-like, not presenting any bifurcation or fenestra and the infraorbital canal of the lateral line passes posteriorly to it (Fig. 13G).

Jaws

46 Labial ridge of the quadrate process: (0) present; (1) absent. (CI = 17; RI = 17).

Compagno (1999) pointed out that, primitively, the palatoquadrate of sharks presents elevated quadrate processes with prominent ridges on the labial surface; this configuration was observed in *Notorynchus cepedianus* (Daniel 1934: fig. 48). The presence of a prominent ridge on the labial surface and about one-half the length of the quadrate process is found in some scyliorhinids (*Asymbolus*, *Atelomycterus*, *Cephalurus*, *Galeus*, *Halaelurus*, *Haploblepharus* and *Parmaturus*; state 0, Fig. 17B) and may be related to the region of insertion of the m. *preorbitalis* and the division between dorsal and ventral portions of the m. *adductor mandibulae*. This ridge is absent in scyliorhinines, *Apristurus*, *Figaro*, *Holohalaelurus*, *Proscyllium* and *Schroederichthys* (state 1; Fig. 17A).

47 Position of the orbital processes of the palatoquadrate: (0) at the anterior one-fourth of each antimere;

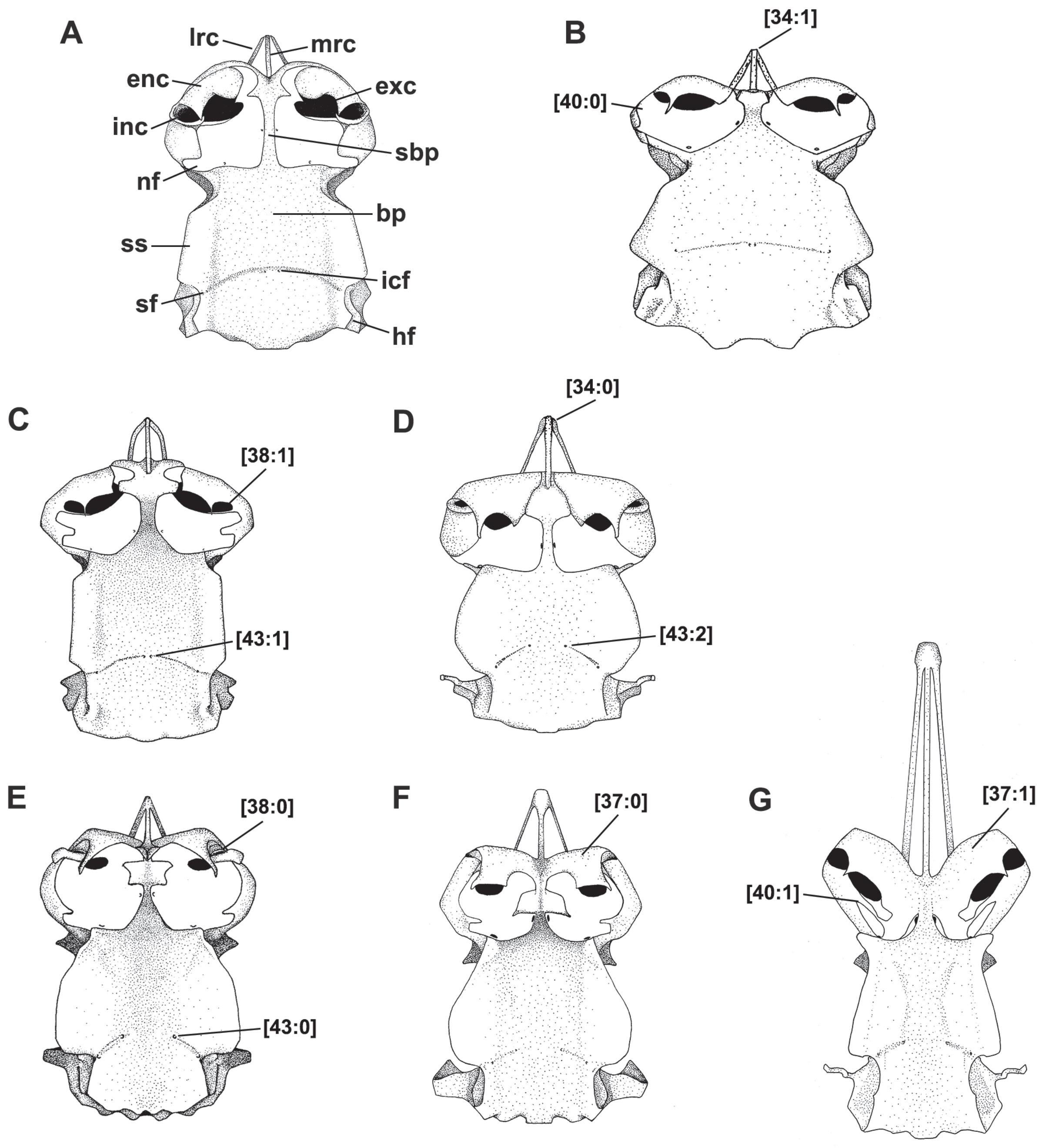

Figure 15. Neurocranium; ventral view. A, *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, *Cephaloscyllium variegatum*, AMS I.43762-001, female, 670 mm TL; C, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL; D, *Atelomycterus fasciatus*, CSIRO H1298-7, male, 370 mm TL; E, *Asymbolus rubiginosus*, AMS I.30393-004, male, 527 mm TL; F, *Figaro boardmani*, CSIRO H989-5, female, 465 mm TL; G, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. **bp**, basal plate; **enc**, external nasal cartilage; **exc**, excurrent aperture; **hf**, hyomandibular facet; **icf**, internal carotid foramen; **inc**, incurrent aperture; **lrc**, lateral rostral cartilage; **mrc**, medial rostral cartilage; **nf**, nasal fontanelle; **sbp**, subnasal plate; **sf**, stapedial foramen; **ss**, suborbital shelf.

(1) closer to the half-length of each antimere. (CI = 100; RI = 100).

The palatoquadrate articulates to the neurocranium by ethmopalatine ligaments, which are inserted on the postorbital processes of the palatoquadrates and originate from the orbital notches; these notches are situated between the posteroventral region of the nasal capsules and the preorbital wall. Orbital processes are situated in variable positions in the dorsal border of each antimere of the palatoquadrate, delimitating the extension of palatine and quadrate processes. In most scyliorhinids,

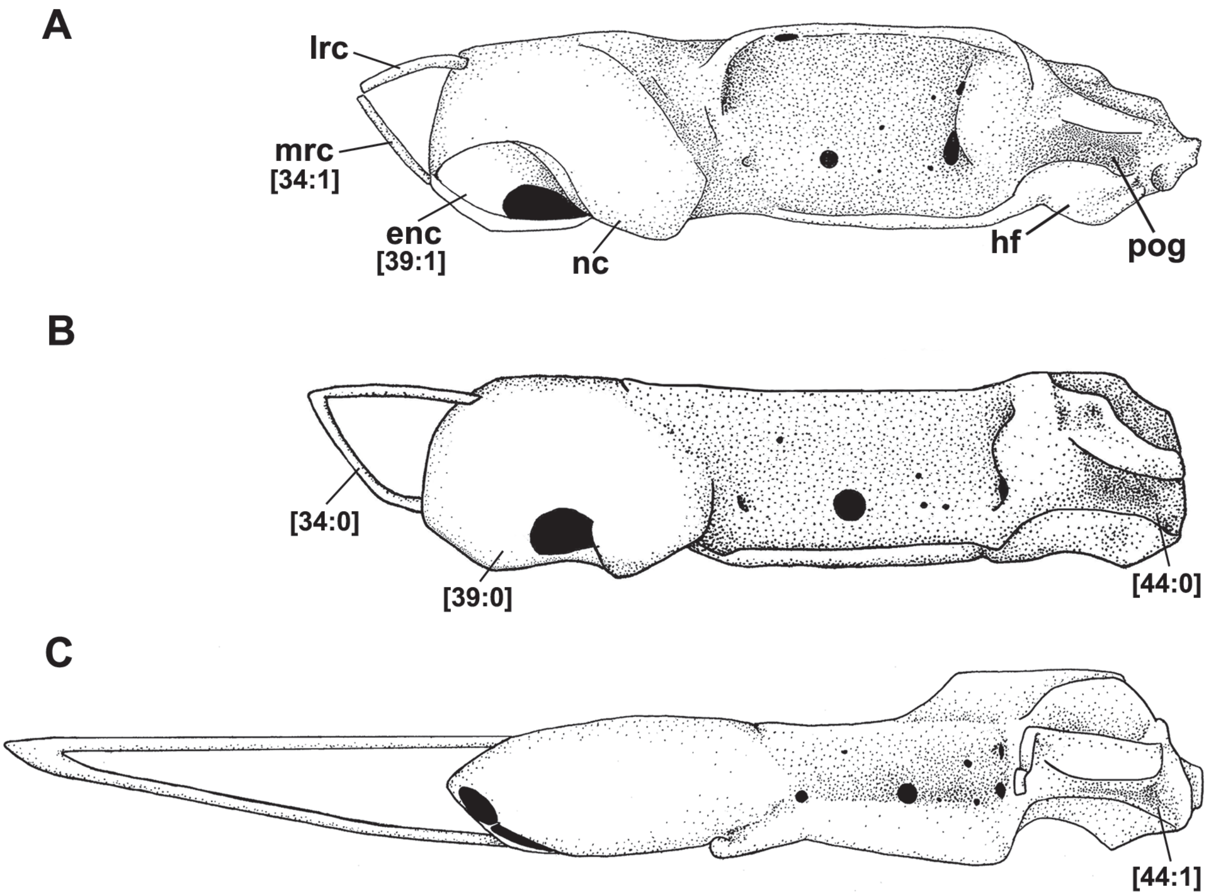

Figure 16. Neurocranium; lateral view. A, *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, *Figaro boardmani*, CSIRO H989-5, female, 465 mm TL; C, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. **enc**, external nasal cartilage; **hf**, hyomandibular facet; **lrc**, lateral rostral cartilage; **mrc**, medial rostral cartilage; **nc**, nasal capsule; **pog**, postorbital groove.

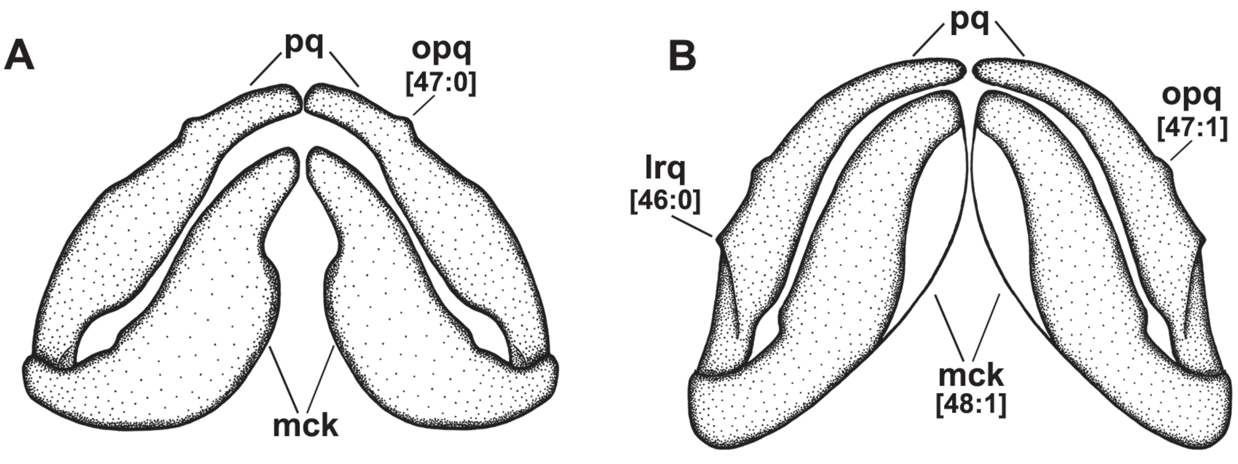

Figure 17. Detail of jaws; lighter portion of Meckel's cartilage is less calcified portion. A, *Scyliorhinus ugoi*, USNM 221611, male, 432 mm TL; B, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. **lrq**, labial ridge of the quadrate process; **mck**, Meckel's cartilage; **opq**, orbital process of the palatoquadrate; **pq**, palatoquadrate.

orbital processes are situated at the anterior one-fourth (state 0; Fig. 17A). In *Apristurus*, *Cephalurus*, *Galeus*, *Haploblepharus*, *Holohalaelurus* and *Parmaturus*, they are more posteriorly situated, close to one-half the length of the palatoquadrate (state 1; Fig. 17B). As described by Compagno (1988a), more posterior orbital processes are situated at a greater distance from the orbital notches and connected to them through elongated ethmopalatine ligaments (except in *Haploblepharus*); this arrangement is probably an adaptation to increase jaw protusibility. In *Haploblepharus*, a unique condition is found as the ethmopalatine ligaments are short and the articulation occurs directly between orbital processes and notches.

48 Degree of calcification of the medial portion of Meckel's cartilage: (0) similar calcification throughout; (1) medial portion less calcified than the rest of Meckel's cartilage. (CI = 100; RI = 100).

Meckel's cartilages present distinct degrees of calcification in some scyliorhinids. In *Apristurus*, *Cephalurus*, *Figaro*, *Galeus* and *Parmaturus*, the medial portion of the antimeres is less calcified than the rest of the cartilage (state 1; Fig. 17B). In the other taxa examined, the degree of calcification is equal throughout Meckel's cartilage (state 0; Fig. 17A).

49 Articular region of the quadratomandibular joint of Meckel's cartilage: (0) posterior lingual condyle situated between anterior labial condyle and facet; (1) anterior and posterior condyles forming a unit and distant from the facet; (2) posterior lingual condyle opposite to the facet. (ordered; CI = 50; RI = 60).

Moss (1972) described two articular regions between the jaws in carcharhinid sharks, relating that both regions correspond to the 'ball and socket' type of articulation: palatoquadrate with a convex posterior region and situated more laterally and Meckel's cartilage with a more anterior and medial condyle. Motta and Wilga (1995), describing the jaw anatomy of *Negaprion brevirostris*, proposed the terms 'medial quadratomandibular joint' (QJM) and 'lateral quadratomandibular joint' (QJL) to refer to the articular regions between palatoquadrate and Meckel's cartilage. We observed a greater complexity and wider variation in relation to the arrangement of condyles and facets of the quadratomandibular region of Meckel's cartilage; three patterns were identified: i) 'medial quadratomandibular joint' composed of two condyles (labial and lingual), forming a unit (state 1, Fig. 18A); ii) a lingual condyle situated posteriorly to the 'lateral quadratomandibular joint' (*Asymbolus*, *Atelomycterus*, *Figaro*, *Galeus*, *Halaelurus* and *Proscyllium*; state 0, Fig. 18B); iii) labial condyle more internally positioned and lingual condyle more posterior and opposite to the facet (*Apristurus*; state 2, Fig. 18C). The first pattern is found in scyliorhinines, *Cephalurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus* and *Schroederichthys*, in which the condyles are significantly separated from the facet. In relation to the articular region of the palatoquadrate, an anterior facet and a posterior condyle have the same morphology in all taxa examined.

Hyoid and gill arches

50 Thyroid foramen: (0) present; (1) absent. (CI = 33; RI = 60).

The basihyal cartilage, situated ventromedially to other components of the hyoid arch, is a structure that presents variable dimensions amongst taxa. This cartilage may or may not present an opening in its anterior portion, the thyroid foramen (de Beer 1937), which is the entrance to the duct of the thyroid gland. This foramen is present in scyliorhinines, *Asymbolus*, *Atelomycterus*, *Figaro*, *Halaelurus*, *Holohalaelurus* and *Schroederichthys* (state 0; Fig. 19), but absent in other scyliorhinids (state 1). In taxa without a thyroid foramen, the duct of the thyroid gland passes anteriorly to the anterior border of the basihyal cartilage.

51 Internal surface of the hyomandibular cartilage: (0) smooth; (1) concave. (CI = 50; RI = 0).

In *Apristurus* and *Parmaturus*, we observed a prominent concavity on the internal surface of the posterior region of the hyomandibular cartilage, close to the articular region between the ceratohyal and Meckel's cartilages (state 1; Fig. 20B). This concavity is situated in the region of the insertion of the muscles *constrictor superficialis dorsalis* and *levator hyomandibulae* in *Parmaturus*, but only of the m. *constrictor superficialis dorsalis* in *Apristurus*. In other examined taxa, the internal surface is smooth and no concavity is present (state 0; Fig. 20A).

52 Anterior border of the basihyal cartilage: (0) not bifurcated; (1) bifurcated. (CI = 33; RI = 33).

The occurrence of a bifurcation on the anterior border of the basihyal cartilage, anterior to the thyroid foramen and not confluent with it, was observed in *Atelomycterus*, *Halaelurus*, *Holohalaelurus* and *Schroederichthys* (state 1; Fig. 19B). This bifurcation was reported and illustrated for *Schroederichthys chilensis* by Leible et al. (1982). In scyliorhinines and other taxa examined, the basihyal cartilage has a smooth and slightly convex anterior border (state 0; Fig. 19A).

53 Lateral processi rastriformis: (0) present; (1) absent. (CI = 33; RI = 60).

Processi rastriformis were observed and illustrated in *Squalus acanthias* by Marinelli and Strenger (1959) and defined as anteriorly directed cartilaginous projections situated on the internal borders of the cerato- and epibranchial cartilages. Compagno (1988a; fig. 2.7) used the term 'dermal papillae' to refer to short structures without cartilaginous support observed in scyliorhinids, proscylliids and some carcharhinids, distinguishing these from the processi rastriformis found in squaliforms, hexanchiforms and *Megachasma pelagios*. The presence and distribution of these papillae vary widely in the taxa examined, whereas processi rastriformis *sensu strictu* were observed only in some taxa in which they occupy specific positions in relation to the gill arches. Processi rastriformis greater than the dermal papillae and situated

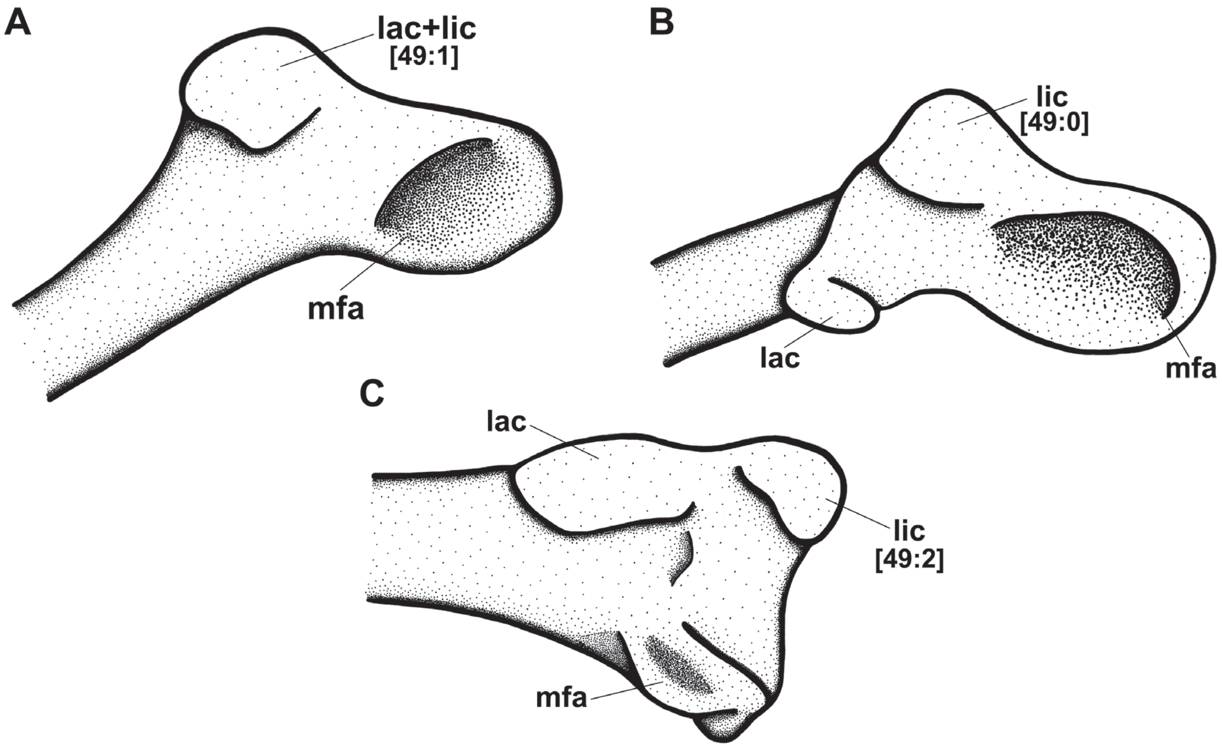

Figure 18. Detail of the articular region of the quadratomandibular joint of Meckel's cartilage. A, *Cephaloscyllium sufflans*, SAIAB 6242, male, 800 mm TL; *Galeus antillensis*, UF 77853, female, 370 mm TL; C, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. **lac**, labial condyle; **lic**, lingual condyle; **mfa**, mandibular facet.

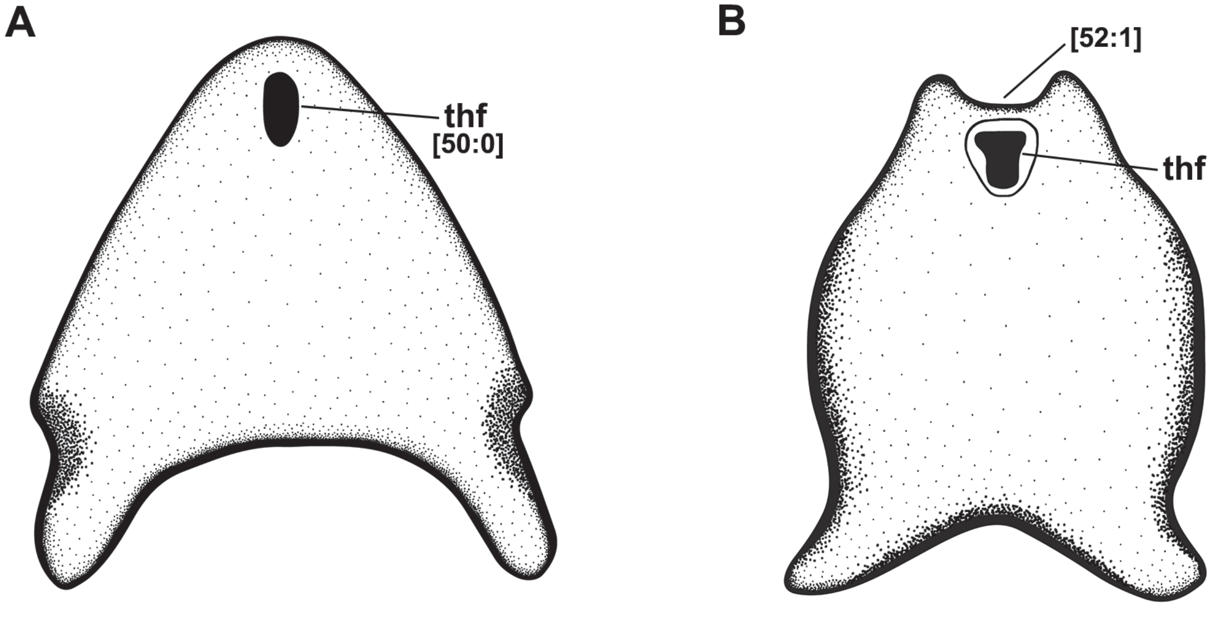

Figure 19. Detail of the basihyal cartilage. A, *Scyliorhinus haeckelii*, UERJ 1691, male, 522 mm TL; B, *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL. **thf**, thyroid foramen.

only on the anterior surface of the articular region between cerato- and epibranchial cartilages were observed in *Asymbolus*, *Atelomycterus*, *Halaelurus*, *Poroderma* and *Schroederichthys* (state 0; Fig. 21). In *Cephaloscyllium*, *Scyliorhinus* and other taxa examined, processi rastriformis are absent. The term 'gill rakers' used by Daniel (1934) and Compagno (1988a) is not used here, as the structures observed in elasmobranchs are formed by cartilage, whereas gill rakers of bony fishes have a dermal origin and are, therefore, not homologous to processi rastriformis.

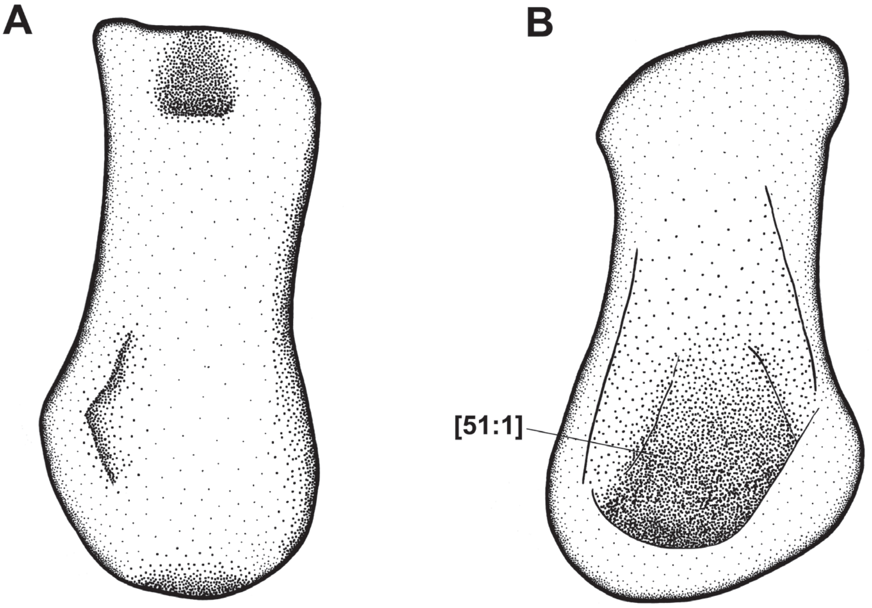

Figure 20. Detail of the hyomandibular cartilage; internal surface. A, *Scyliorhinus haeckelii*, UERJ 1691, male, 522 mm TL; B, *Apristurus longicephalus*, HUMZ 170382, male, 475 mm TL. 2358.

54 Oropharyngeal denticles: (0) small and not forming rows on internal face of gill components; (1) large and forming rows on internal face of gill components. (CI = 25; RI = 25).

Nelson (1970) described macroscopic features, such as shape, distribution and abundance of oropharyngeal denticles in *Rhizoprionodon terraenovae*. Later, Ciena et al. (2016) and Rangel et al. (2017) described the ultrastructure of oropharyngeal denticles and their disposition amongst dermal papillae in *Rhizoprionodon lalandii* and *Prionace glauca*, respectively. In all of these species, the denticles are distributed on the entire ventral surface of the oropharyngeal cavity. Heemstra (1997) observed rows of oropharyngeal denticles greater than the denticles around the fifth ceratobranchial of *Mustelus norrisi*. Here, we report a different condition for oropharyngeal denticles in *Apristurus longicephalus*, *Cephaloscyllium sufflans*, *C. variegatum*, *Halaelurus natalensis* and *Parmaturus xaniurus* (state 1; Fig. 22). Besides the denticles of the ventral surface, rows of denticles, greater than the surrounding ones and similar in shape and size to the dermal denticles of dorsolateral surfaces of the body, were found on the internal surface of gill components (cerato- and/or epibranchial) in these taxa. Two rows parallel to the gill arches and composed of 5 to 13 denticles were observed. In other taxa examined, these denticles were absent (state 0).

55 Shape of the gill pickax: (0) elongated and sling-like; (1) short and triangular. (CI = 50; RI = 80).

The fusion between the dorsal tips of gill arches IV and V, forming a unique plate known as the gill pickax (Shirai 1992a), is observed in many neoselachians, with the exception of some rays (Shirai 1996). Despite the presence of this structure having been listed by Shirai (1992a) as a diagnostic character for modern elasmobranchs (except *Heterodontus* and *Trigonognathus*), no mention of its morphological variations was provided. Amongst the taxa examined, we observed some differences regarding the shape of the gill pickax. In *Cephaloscyllium* and *Poroderma*, the gill pickax is short and triangular in shape (state 1; Fig. 23B). In *Proscyllium* and other scyliorhinids, this structure is distally elongated and sling-like (state 0; Fig. 23).

56 Ventral extrabranchial cartilages: (0) four; (1) three. (CI = 100; RI = 100).

Ventral extrabranchial cartilages are present amongst muscle bundles of the *coracobranchialis* and on the posterior border of the four anteriormost gill openings. In most taxa examined, four cartilages are observed, whereas in scyliorhinines only three are present (state 1). The number of ventral extrabranchial cartilages was listed by Compagno (1988a) as a diagnostic character of the subfamily Scyliorhininae.

Pectoral skeleton

57 Medial projection of the coracoid bar: (0) present; (1) absent. (CI = 50; RI = 0).

The presence of a medial projection on the coracoid bar was observed in many orders of elasmobranchs by Silva and de Carvalho (2015), who reported and illustrated its presence in the following galeomorph taxa: *Heterodontus*

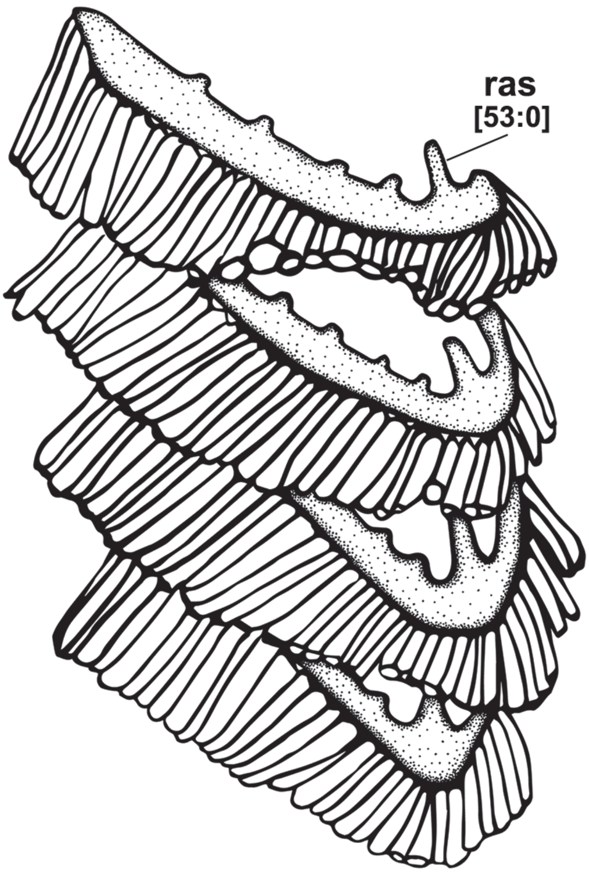

Figure 21. Detail of the lateral processi rastriformis (**ras**) in *Schroederichthys saurisqualus*, UERJ uncatalogued, female, 564 mm TL.

francisci (Heterodontiformes), *Ginglymostoma cirratum*, *Rhincodon typus*, *Stegostoma fasciatum* (Orectolobiformes), *Alopias superciliosus*, *Carcharias taurus*, *Isurus oxyrhinchus*, *Mitsukurina owstoni*, *Pseudocarcharias kamoharai* (Lamniformes), *Carcharhinus galapagensis* and *Mustelus canis* (Carcharhiniformes). This projection was observed in *Proscyllium* and most scyliorhinid taxa examined (state 0; Fig. 24A, B, D), except *Haploblepharus* and *Schroederichthys*. In these taxa, the coracoid bar has a straight anterior border with no projections (state 1; Fig. 24C).

58 Degree of development of the medial projection of the coracoid bar: (0) reduced to less than twice the size of the lateral portion of the coracoid bar; (1) well developed, more than twice the size of the lateral portion of the coracoid bar. (CI = 50; RI = 90).

In taxa in which a medial projection of the coracoid bar is present, differences concerning its shape and degree of development were observed. In *Asymbolus*, *Apristurus*, *Atelomycterus*, *Galeus*, *Halaelurus*, *Poroderma* and *Proscyllium*, the medial projection has an anterior border that is slightly convex and not very prominent (state 0; Fig. 24B). In *Cephalurus*, *Cephaloscyllium* and *Scyliorhinus*, the projection is well developed and corresponds to more than twice the lateral portion of the coracoid bar. In these taxa, the medial projection entirely covers the heart ventrally (state 1; Fig. 24A, D).

59 Lateral processes on pectoral girdle: (0) present; (1) absent. (CI = 25; RI = 57).

Lateral processes on the coracoid bar, medial to the articular region between pectoral girdle and fins, were observed in *Cephaloscyllium*, *Halaelurus*, *Haploblepharus*, *Schroederichthys* and *Scyliorhinus* (state 0; Fig. 24A, B). The processes observed in scyliorhinids correspond to two thirds of the length or similar in size to the medial projection of the coracoid bar. In the illustrations provided by Silva and de Carvalho (2015), projections similar to the lateral processes are present in *Alopias superciliosus* (p. 17; fig. 14) and *Pseudocarcharias kamoharai* (p. 30; fig. 27); the authors briefly mentioned the presence of these processes in the latter species.

Clasper

60 Dermal denticles on the dorsal surface of clasper glans: (0) present; (1) absent. (CI = 25; RI = 40).

Dermal denticles on the dorsal surface of clasper glans were observed in most taxa examined. In *Apristurus longicephalus*, *Cephalurus cephalus*, *Halaelurus natalensis*, *Haploblepharus edwardsii*, *Parmaturus xaniurus* and *Proscyllium habereri*, the dorsal surface is totally smooth (state 1). The absence of dermal denticles on the dorsal surface of clasper glans may be related to the degree of development of the cover rhipidion and/or the exorhipidion and the presence of an open clasper groove.

61 Distribution of dermal denticles on dorsal surface of clasper glans: (0) denticles present only on the exorhipidion; (1) denticles over all of the dorsal surface except on rhipidion and terminal dermal cover. (CI = 25; RI = 73).

Leigh-Sharpe (1926b) subdivided the genus *Scyliorhinus* (as *Scyllium*) into four ‘pseudogenera’ based on characters of the external morphology of the claspers, including the distribution of dermal denticles on dorsal surface of the clasper glans. Only two of the four groups proposed (*Alphascyllium* and *Betascyllium*) included species currently valid for *Scyliorhinus*. According to Leigh-Sharpe (1926b), species allocated to *Alphascyllium* presented claspers totally covered by dermal denticles, whereas in *Betascyllium* denticles are restricted to certain areas; no further details were provided by the author. In *Cephaloscyllium sufflans*, *C. ventriosum*, *Scyliorhinus* spp. (except *S. boa*, *S. cervigoni*, *S. hesperius* and *S. retifer*) and *Holohalaelurus regani*, the dermal denticles are present on most of the dorsal surface of the clasper glans with the exception of the rhipidion and the terminal dermal cover (state 1; Fig. 25B, C, E, F). In *S. boa*, *S. cervigoni*, *S. hes-*

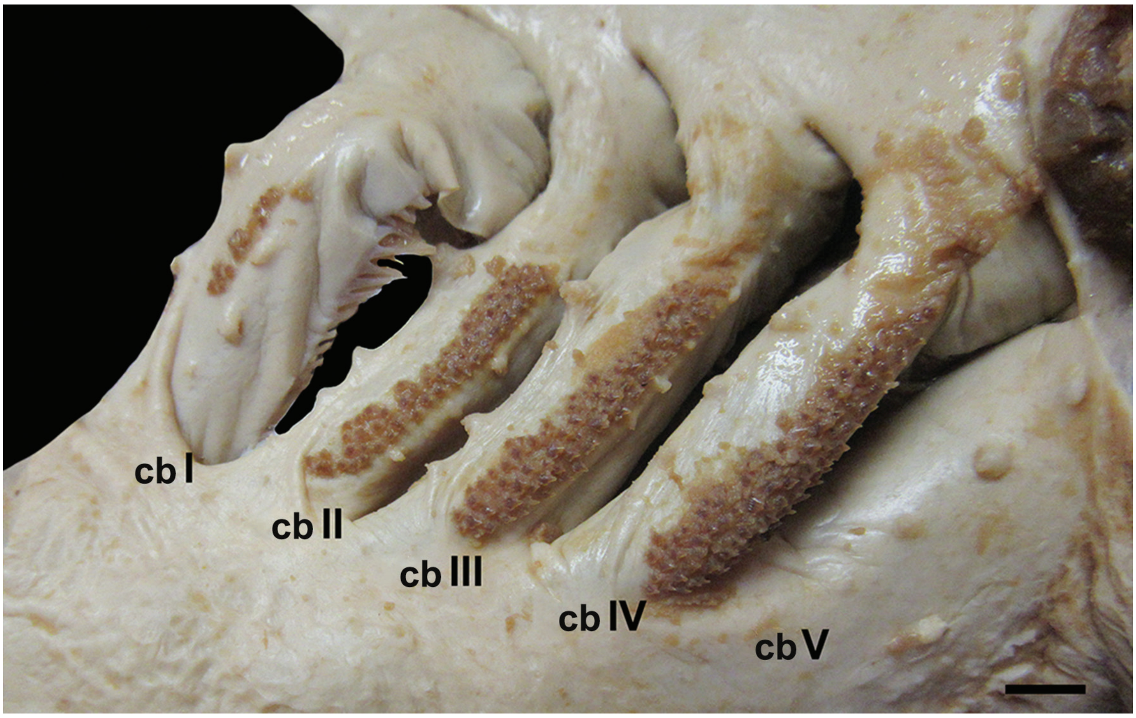

Figure 22. Detail of the oropharyngeal denticles in *Cephaloscyllium sufflans*, SAIAB 6242, male, 800 mm TL. **cb I–V**, ceratobranchials I–V.

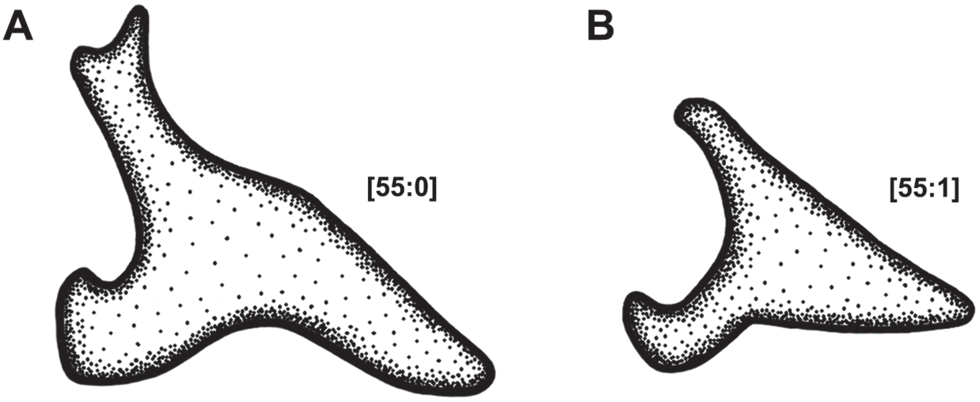

Figure 23. Detail of the gill pickax. A, *Scyliorhinus haeckelii*, UERJ 1691, male, 522 mm TL; B, *Cephaloscyllium sufflans*, SAIAB 6242, male, 800 mm TL.

perius and *S. retifer*, denticles are absent on cover rhipidion, rhipidion and the terminal dermal cover, as well as in *Asymbolus rubiginosus*, *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Figaro boardmani*, *Galeus antillensis* and *Schroederichthys saurisqualus* (state 0; Fig. 25A, D). In *Poroderma africanum* and *P. pantherinum*, dermal denticles are present only on the ventrolateral and posterior margins of the exorhipidion and medial to the rhipidion.

62 Dermal denticles on the medial border of the exorhipidion: (0) absent; (1) present. (CI = 25; RI = 25).

Compagno (1988a) mentioned the presence of hook-like dermal denticles arranged in rows on the ventral surface of the free margin of the exorhipidion in species of *Cephaloscyllium*, *Halaelurus*, *Parmaturus*, *Apristurus*, *Poroderma* and *Scyliorhinus*. Here, we observed specialised hooks in the claspers of *S. torazame* (Soares and de Carvalho 2019; Fig. 25F), *Figaro boardmani*, *Galeus antillensis*, *Halaelurus natalensis*, *Poroderma pantherinum* and *Proscyllium habereri*, slightly greater dermal denticles, on the ventral surface at the posterior border of the exorhipidion and on the medial margin of the cover rhipidion (state 1). These denticles were not observed in the other taxa examined (state 0).

63 Terminal dermal cover: (0) present; (1) absent. (CI = 50; RI = 0).

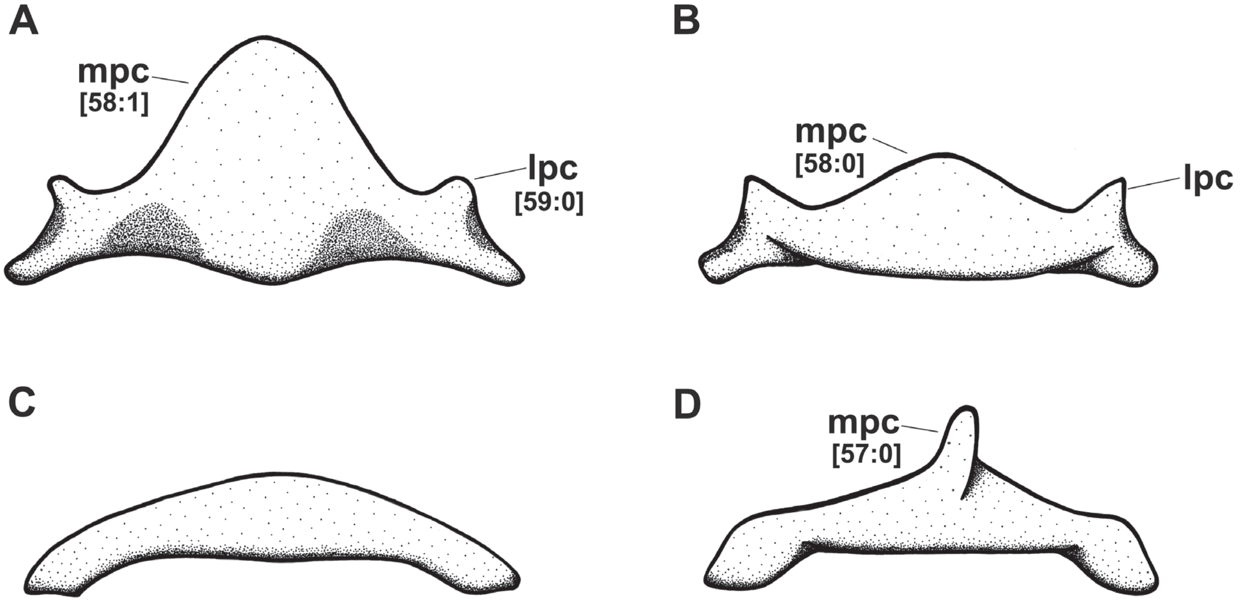

Figure 24. Coracoid bar; ventral view. A, *Scyliorhinus haeckelii*, UERJ 1691, male, 522 mm TL; B, *Halaelurus natalensis*, SAIAB 26951, male, 400 mm TL; C, *Holohalaelurus regani*, SAIAB 25717, male, 610 mm TL; D, *Cephalurus cephalus*, USNM 221527, female, 285 mm TL. **mpc**, medial projection of the coracoid bar; **lpc**, lateral processes on pectoral girdle.

Soares et al. (2015) described the terminal dermal cover in *Scyliorhinus ugoi*, which consists in a membrane situated on the posterior tip of the clasper glans, lacking denticles and in contact with the posterior borders of the cover rhipidion and exorhipidion. This structure was illustrated by Springer (1966) in *Scyliorhinus torrei* (p. 588, fig. 4a) and by Compagno (1988a) in *Holohalaelurus* cf. *punctatus* (fig. 13.14f–g), but they did not propose a name nor a definition for it. A terminal dermal cover is found in most taxa examined (state 0; Fig. 25), with the exception of *Apristurus longicephalus* and *Cephalurus* sp. In these taxa, the distal tips of the dorsal and ventral terminal cartilages are evident and uncovered (state 1).

64 Extension of the terminal dermal cover: (0) restricted to the distal tip of the clasper glans; (1) extending up to one-third of clasper glans. (CI = 33; RI = 71).

Regarding its extension, the terminal dermal cover may be restricted to the distal clasper tip or it extends up to one-third of the clasper glans, covering the posterior borders of the cover rhipidion and exorhipidion. The former condition was observed in *Asymbolus rubiginosus*, *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Halaelurus natalensis*, *Haploblepharus edwardsii*, *Parmaturus xaniurus*, *Proscyllium habereri* and *Schroederichthys saurisqualus*, in which the terminal dermal cover only reaches the posterior borders of the exorhipidion and cover rhipidion. In scyliorhinines, *Figaro boardmani*, *Galeus antillensis* and *Holohalaelurus regani*, a more developed terminal dermal cover was observed (state 1; Fig. 25).

65 Configuration of the terminal dermal cover: (0) smooth; (1) rough. (CI = 33; RI = 0).

Compagno (1988a) described and illustrated the presence of a 'brush-like papillose structure' on the distal tip of the clasper glans of *Holohalaelurus* cf. *punctatus*; this structure is here considered the terminal dermal cover (as per Soares et al. 2015). The adjective 'rough' is used as a substitute for 'papillose' by considering that the structure does not present papillae but rugosities. Additionally, we observe that, besides having a different texture, the terminal dermal cover projects posteriorly, corresponding to two-thirds of the clasper glans length in *Holohalaelurus* spp. A terminal dermal cover with similar texture was also observed in *Scyliorhinus canicula* and *S. capensis* (Soares and de Carvalho 2019; state 1, Fig. 25B). In the other taxa examined, this structure is smooth and without rugosities (state 0; Fig. 25).

66 Degree of development of the rhipidion: (0) well developed and presenting a prominent posterior margin; (1) reduced and consisting in a narrow strip. (CI = 25; RI = 77).

Some differences regarding the degree of development of the rhipidion were observed in taxa that have this structure (Leigh-Sharpe 1920, 1921, 1922a, 1922b, 1924a, 1924b, 1924c, 1926a, 1926b). In *Cephaloscyllium sufflans*, *Scyliorhinus* spp. (except *S. canicula*, *S. duhamelii* and *S. torazame*), *Asymbolus rubiginosus*, *Halaelurus natalensis*, *Holohalaelurus regani* and *Schroederichthys saurisqualus*, a well-developed rhipidion with a prominent posterior margin was observed (state 0; Fig. 26A). In

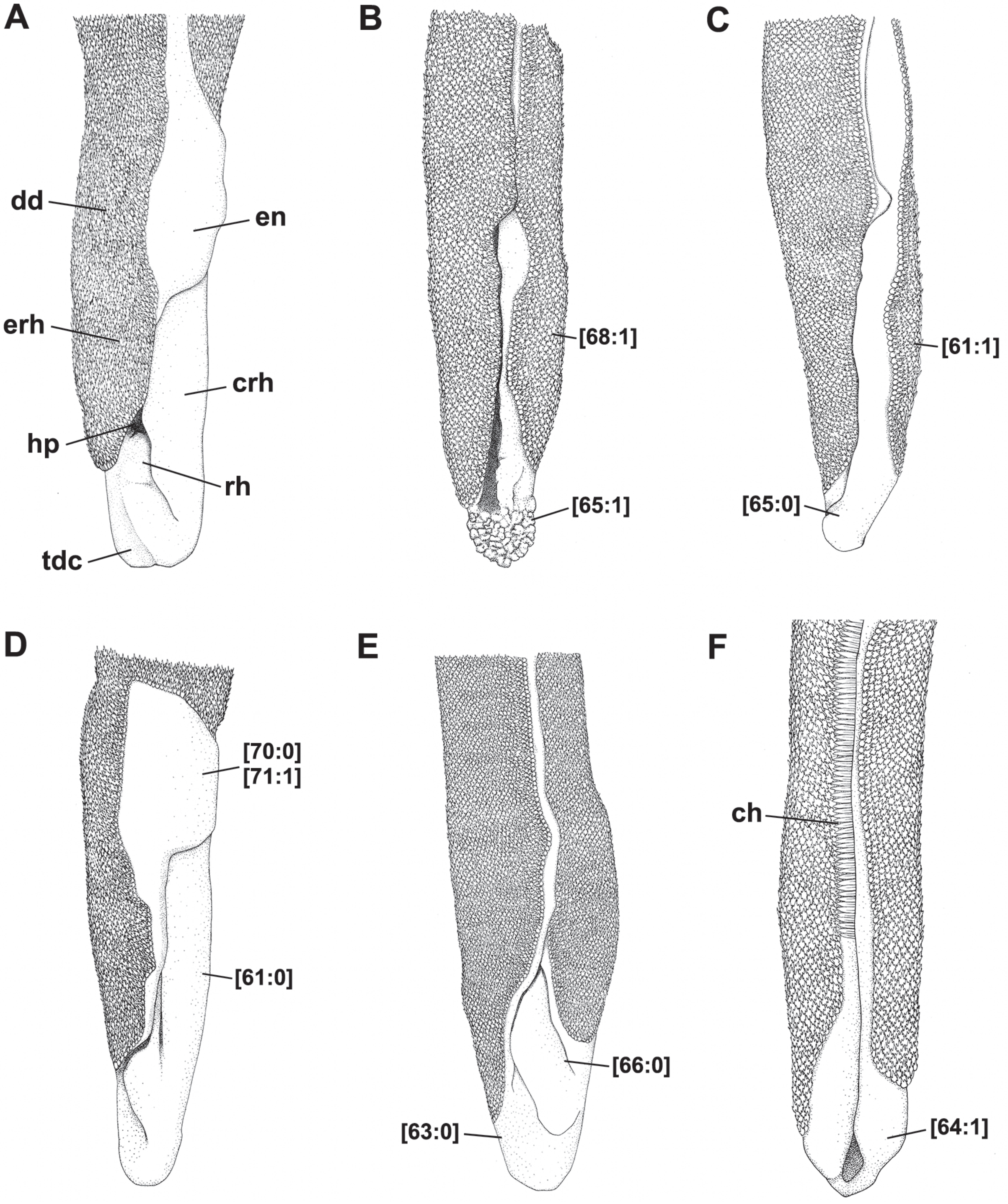

Figure 25. Clasper; external morphology. A, *Scyliorhinus boa*, USNM 221563, 348 mm TL; B, *Scyliorhinus canicula*, BMNH 1983.8.3.1–4, 585.7 mm TL; C, *Scyliorhinus duhamelii*, MCZ S-63, 338.7 mm TL; D, *Scyliorhinus retifer*, UF 36359, 372 mm TL; E, *Scyliorhinus stellaris*, BMNH 1976.7.30.10, 476 mm TL; F, *Scyliorhinus torazame*, NSMT 50632, 427.9 mm TL. **ch**, clasper hooks; **crh**, cover rhipidion; **dd**, dermal denticles; **en**, envelope; **erh**, exorhipidion; **hp**, hypopyle; **rh**, rhipidion; **tdc**, terminal dermal cover. Modified from Soares and de Carvalho (2019).

Scyliorhinus canicula, *S. duhamelii* and *S. torazame*, the rhipidion is narrow and not prominent, similar to *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Poroderma* spp., *Figaro boardmani*, *Galeus antillensis*, *Haploblepharus edwardsii*, *Parmaturus xaniurus* and *Proscyllium habereri* (state 1; Fig. 26B).

67 Extension of the rhipidion: (0) extending throughout the clasper glans; (1) extending up to one-third of the clasper glans. (CI = 25; RI = 73).

The extension of the rhipidion varies, depending on the species examined. In *Scyliorhinus* spp. (except *S. ca-*

nicula, *S. duhamelii* and *S. torazame*), *Cephaloscyllium sufflans*, *Asymbolus rubiginosus*, *Halaelurus natalensis*, *Holohalaelurus regani* and *Schroederichthys saurisqualus*, the rhipidion extends throughout the clasper glans, reaching the posterior border of the cover rhipidion (state 0; Fig. 26A). In *Scyliorhinus canicula*, *S. duhamelii*, *S. torazame*, *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Poroderma* spp., *Figaro boardmani*, *Galeus antillensis*, *Haploblepharus edwardsii*, *Parmaturus xaniurus* and *Proscyllium habereri*, the rhipidion extends up to the posterior one-third of the clasper glans, anterior to the posterior border of the cover rhipidion (state 1; Fig. 26B).

68 Cover rhipidion: (0) poorly developed; (1) well developed and medially expanded. (CI = 100; RI = 100).

Compagno (1988a) pointed out that the condition 'clasper groove closed and covered' would be a primitive character for Carcharhiniformes related to the absence or presence of a poorly developed cover rhipidion on claspers. He reported the presence of a slightly differentiated and short cover rhipidion, well anterior to the clasper glans, in scyliorhinines, *Galeus* and *Holohalaelurus* spp. In this study, we observed some differences amongst scyliorhinines and the other scyliorhinids, regarding the degree of development of the cover rhipidion. In scyliorhinines, *Atelomycterus fasciatus* and *Aulohalaelurus labiosus* (Soares 2020), the cover rhipidion is medially expanded and reaches the exorhipidion and is sometimes covered by it anteriorly and both cover the clasper groove (state 1; Fig. 25). In the other taxa examined, the cover rhipidion is nearly straight and restricted to the dorsolateral margin of claspers, lateral to the dorsal terminal 2 cartilage and not covering it (state 0).

69 Exorhipidion: (0) medially expanded; (1) poorly developed. (CI = 50; RI = 75).

The exorhipidion is a ventromedially situated flap, covering totally or partially the ventral terminal cartilage. In all species of *Scyliorhinus*, *Cephaloscyllium sufflans*, *Asymbolus rubiginosus*, *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Figaro boardmani*, *Galeus antillensis*, *Halaelurus natalensis*, *Parmaturus xaniurus* and *Poroderma* spp., we observed a well-developed exorhipidion totally covering the ventral terminal cartilage and extending to the end of the glans (state 0; Fig. 25). In the other taxa examined, a poorly-developed exorhipidion is observed (state 1) corresponding to a narrow strip restricted to the posterior portion of the ventral terminal 2 cartilage and not reaching the cover rhipidion medially.

70 Envelope: (0) present; (1) absent. (CI = 14; RI = 54).

The envelope is a distinct projection anterior to the exorhipidion, which covers the accessory terminal cartilage, posterior border of the ventral marginal cartilage and anterior border of the ventral terminal cartilage. According to our observations, this structure is present in *Scyliorhinus boa*, *S. cervigoni*, *S. haeckelii*, *S. retifer*, *S. torrei* and *S. ugoi* (Soares and de Carvalho 2019), as well as in *Apristurus longicephalus*, *Asymbolus rubiginosus*, *Figaro boardmani*, *Halaelurus natalensis*, *Parmaturus xaniurus* and *Schroederichthys saurisqualus* (state 0; Fig. 25). In *Haploblepharus edwardsii*, the accessory terminal cartilage is covered by a thin membrane, separated from the exorhipidion and the rest of the clasper cover; this membrane is not considered a true envelope. An envelope is also absent in *Atelomycterus fasciatus*, *Aulohalaelurus labiosus*, *Cephaloscyllium* spp., *Galeus antillensis*, *Holohalaelurus regani*, *Poroderma* spp., *Proscyllium* and other species of *Scyliorhinus* (state 1).

71 Degree of development of the envelope: (0) poorly developed; (1) medially expanded. (CI = 100; RI = 100).

A well-developed envelope, projecting medially and covering the anterior border of the cover rhipidion is observed in *Scyliorhinus boa* and *S. retifer* (state 1; Fig. 25A, D). In *S. cervigoni*, *S. haeckelii*, *S. torrei* and *S. ugoi*, we observed a discrete and poorly-developed envelope, not covering the cover rhipidion; this condition is also present in *Apristurus longicephalus*, *Asymbolus rubiginosus*, *Figaro boardmani*, *Halaelurus natalensis*, *Parmaturus xaniurus* and *Schroederichthys saurisqualus* (state 0).

72 Accessory terminal cartilage: (0) present; (1) absent. (CI = 20; RI = 60).

Jungersen (1899) described this cartilage as a structure situated between the ventral terminal cartilage and the posterior border of the ventral marginal cartilage. In taxa of Rajiformes, the accessory terminal cartilage presents a dorsal extension external to the integument, forming a protractile spine (Compagno 1988a). None of the taxa examined here presented such an extension. Soares (2020) pointed out that this cartilage is usually adjacent to the medial surface of ventral terminal cartilage. In *Scyliorhinus*, only the species *S. boa*, *S. canicula*, *S. capensis*, *S. retifer* and *S. torazame* have an accessory terminal cartilage (state 0; Fig. 27A, B, D, F). This cartilage is also present in *Proscyllium* and other scyliorhinids, except *Holohalaelurus regani* and *Poroderma* spp. (state 1).

73 Accessory dorsal marginal cartilage: (0) present; (1) absent. (CI = 33; RI = 80).

Jungersen (1899) described a mobile cartilage situated in the posterior border of the dorsal marginal cartilage (and continuous with it) in *Pristiurus melastomus* (= *Galeus melastomus*), naming it the 'accessory dorsal marginal cartilage'. According to this author, this cartilage is absent in *Scyliorhinus canicula* and *S. stellaris*. Soares et al. (2015, 2016) misidentified the dorsal terminal 2 cartilage as the accessory dorsal marginal cartilage

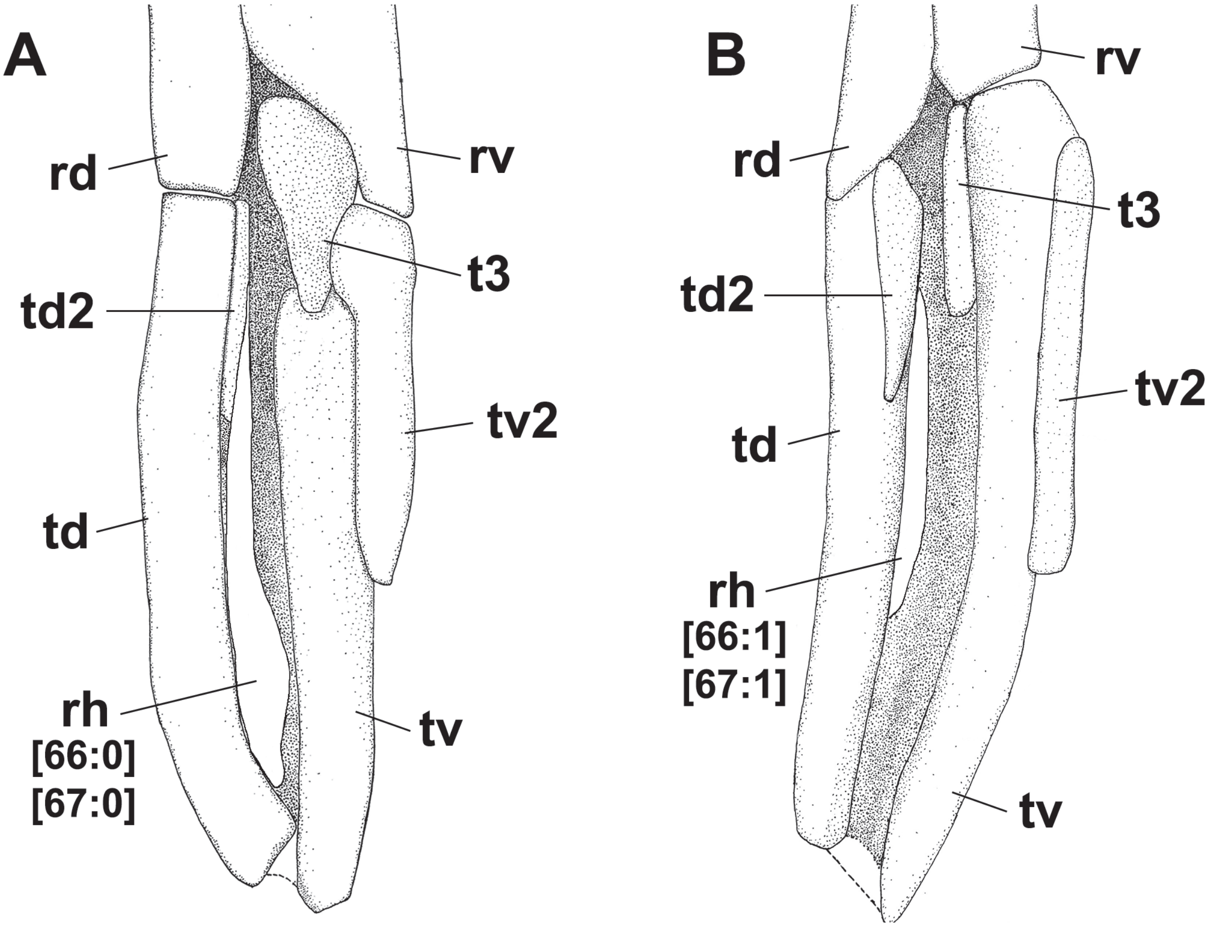

Figure 26. Detail of the rhipidion. A, *Scyliorhinus boa*, USNM 221563, 348 mm TL; B, *Scyliorhinus canicula*, BMNH 1983.8.3.1–4, 585.7 mm TL. Modified from Soares & de Carvalho (2019). **rd**, dorsal marginal cartilage; **rh**, rhipidion; **rv**, ventral marginal cartilage; **t3**, accessory terminal cartilage; **td**, dorsal terminal cartilage; **td2**, dorsal terminal 2 cartilage; **tv**, ventral terminal cartilage; **tv2**, ventral terminal 2 cartilage.

in *S. cabofriensis*, *S. haeckelii* and *S. ugoi*, because it is situated between the dorsal marginal and terminal cartilages; however, it is medial to these and is not a prolongation of the dorsal marginal cartilage. Thus, we verified for the present study that the accessory dorsal marginal cartilage is indeed absent in *Scyliorhinus* spp. (Soares and de Carvalho 2019; Soares 2020), as well as in other scyliorhinines (state 1; Fig. 27). This structure, however, is present in other taxa examined, except *Galeus antillensis* (state 0).

74 Dorsal marginal 3 cartilage: (0) absent; (1) present. (CI = 25; RI = 0).

The dorsal marginal 3 cartilage is situated dorsally and external to the accessory dorsal marginal cartilage or posterior to it. A dorsal marginal 3 cartilage is absent in scyliorhinines and most of the scyliorhinids examined (state 0). In *Haploblepharus edwardsii*, *Halaelurus natalensis* and *Holohalaelurus regani*, this cartilage is present and is very slender, resembling a shell dorsal to the accessory dorsal marginal cartilage (state 1).

75 Ventral marginal 2 cartilage: (0) present; (1) absent. (CI = 20; RI = 56).

The presence of a ventral marginal 2 cartilage was reported for *Sphyrna* by Compagno (1988a), opposite to the accessory dorsal marginal cartilage. This cartilage was observed in *Apristurus longicephalus*, *Halaelurus natalensis*, *Haploblepharus edwardsii*, *Parmaturus xaniurus*, *Poroderma* spp., and *Proscyllium* (state 0). A ventral marginal 2 cartilage is absent in *Scyliorhinus* spp., *Cephaloscyllium* spp., *Asymbolus rubiginosus*, *Aulohalaelurus labiosus*, *Atelomycterus fasciatus*, *Cephalurus cephalus*, *Figaro boardmani*, *Galeus* spp., *Holohalaelurus regani* and *Schroederichthys saurisqualus* (state 1).

76 Position of the ventral marginal 2 cartilage: (0) continuous to the posterior border of the ventral marginal cartilage; (1) lateral to the posterior border of the ventral marginal cartilage. (CI = 100; RI = 100).

Compagno (1988a) described the ventral marginal 2 cartilage as a structure situated posteriorly to the ventral marginal cartilage, but continuous to it. In *Apristurus longicephalus*, *Halaelurus natalensis*, *Haploblepharus edwardsii* and *Parmaturus xaniurus*, this cartilage presented the same condition described by Compagno (1988a), with a trapezoidal shape and covering the ventral terminal 2 cartilage (state 0). A different condition regarding the position of the ventral marginal 2 cartilage was found in *Poroderma* spp.; in these species, this cartilage is situated laterally to the ventral marginal cartilage and not continuous to it (state 1).

77 Dorsal terminal 2 cartilage: (0) present; (1) absent. (CI = 33; RI = 0).

The dorsal terminal 2 cartilage was described by Jungersen (1899) and consists of a narrow piece situated in the lateral border of the dorsal terminal cartilage that extends posteromedially to the posterior border of the dorsal marginal cartilage. White (1937) did not include the dorsal terminal 2 cartilage in her illustration of the clasper of *Scyliorhinus torazame* (pl. 47) and Compagno (1988a) reported its absence in *Scyliorhinus*. However, a dorsal terminal 2 cartilage was observed in all species of *Scyliorhinus* (state 0; Fig. 27), except *S. garmani*, *S. hesperius* and *S. meadi* (in these species adult males were not available for dissection). This cartilage was observed in *Proscyllium* and most scyliorhinids examined with the exception of *Halaelurus natalensis* (state 1).

78 Shape of the dorsal terminal 2 cartilage: (0) elongated and rod-like; (1) rhomboidal. (CI = 50; RI = 75).

Variations in the shape of the dorsal terminal 2 cartilage were observed amongst the taxa examined. In *Proscyllium* and most scyliorhinids, the dorsal terminal 2 cartilage is a rod-like structure (state 0; Fig. 27), while, in some species of *Scyliorhinus* (*S. cabofriensis*, *S. capensis*, *S. cervigoni*, *S. haeckelii* and *S. ugoi*), the dorsal terminal 2 cartilage is poorly developed and has a rhomboidal shape (state 1; Fig. 27C).

79 Ventral terminal 2 cartilage: (0) present; (1) absent. (CI = 25; RI = 0).

Jungersen (1899) reported the presence of an elongated element connected to the anterior tip of the ventral terminal cartilage and situated above it in claspers of *Lamna cornubica* (= *Lamna nasus*); this element was named the ventral terminal 2 cartilage. Jungersen (1899) did not describe this cartilage in *Galeus melastomus*, *Scyliorhinus canicula* and *S. stellaris*, the scyliorhinids he observed. However, a ventral terminal 2 cartilage is present in most species of *Scyliorhinus*, except *S. comoroensis* (Compagno 1988b; Soares and de Carvalho 2019). According to our observations, this cartilage is present in most taxa examined (state 0; Fig. 27) except *Cephaloscyllium sufflans*, *Cephalurus cephalus*, *Figaro boardmani*, *Halaelurus natalensis* and *Proscyllium habereri*.

80 Position of the ventral terminal 2 cartilage: (0) anteriorly situated and sometimes attached to the anterior tip of the ventral terminal cartilage; (1) posteriorly situated, posterior to the half-length of the ventral terminal cartilage. (CI = 50; RI = 50).

A different condition from the one described by Jungersen (1899) concerning the position of the ventral terminal 2 cartilage was observed in *Aulohalaelurus labiosus* and *Poroderma* spp. In these species, this cartilage is more posteriorly situated, posterior to the half-length of the ventral terminal 2 cartilage and not attached to the anterior tip of the ventral terminal cartilage (state 1). In the other taxa examined, the ventral terminal 2 cartilage presents the same condition described by Jungersen (1899) (state 0).

81 Extension of the clasper siphon: (0) extending beyond the half distance between the coracoid and cloaca; (1) shorter than the coracoid-cloaca half distance. (CI = 33; RI = 78).

Leigh-Sharpe (1920) proposed the term ‘siphon’ for ‘a sac with extremely muscular walls, situated immediately below the corium of the ventral surface of the abdomen, close to the median line and ending blindly, having no communication with the coelom’ (1920, p. 246). Leigh-Sharpe (1924a) proposed a transformation series between Scyliorhinidae and Carcharhinidae, with *Triakis* as an intermediate link, on the basis of siphon length: Scyliorhinidae presenting a short siphon and slightly anterior to the pelvic girdle and Carcharhinidae with extremely long siphons reaching the insertion of the pectoral fin in some taxa. Gilbert and Gordon (1972) suggested a relationship between siphon extension and reproductive mode, with oviparous sharks presenting short siphons and viviparous sharks long siphons. However, a great variation in siphon length was observed herein amongst scyliorhinids, which are reported as oviparous with several descriptions of egg capsules in literature (Springer 1979; Compagno 1988a; Gomes and de Carvalho 1995; Flammang et al. 2007; Flammang et al. 2008; Castro 2011; Ebert and Stehman 2013; Gordon et al. 2016; Silva and Soares 2017; Soares and de Carvalho 2019). Two conditions were observed in the present study: i) long siphons, extending beyond the coracoid-cloaca half distance; and ii) short siphons, shorter than the coracoid-cloaca half distance. In *Proscyllium* and most scyliorhinids, the longer condition was observed (state 0; Fig. 28A–C), similar to the siphons of *Mustelus* and *Carcharhinus* (Leigh-Sharpe 1924a). Short siphons were observed in scyliorhinines, *Apristurus longicephalus*, *Galeus antillensis* and *Holohalaelurus regani* (state 1; Fig. 28D, E, F).

Colouration

82 Colour pattern composed of saddles: (0) present; (1) absent. (CI = 25; RI = 50).

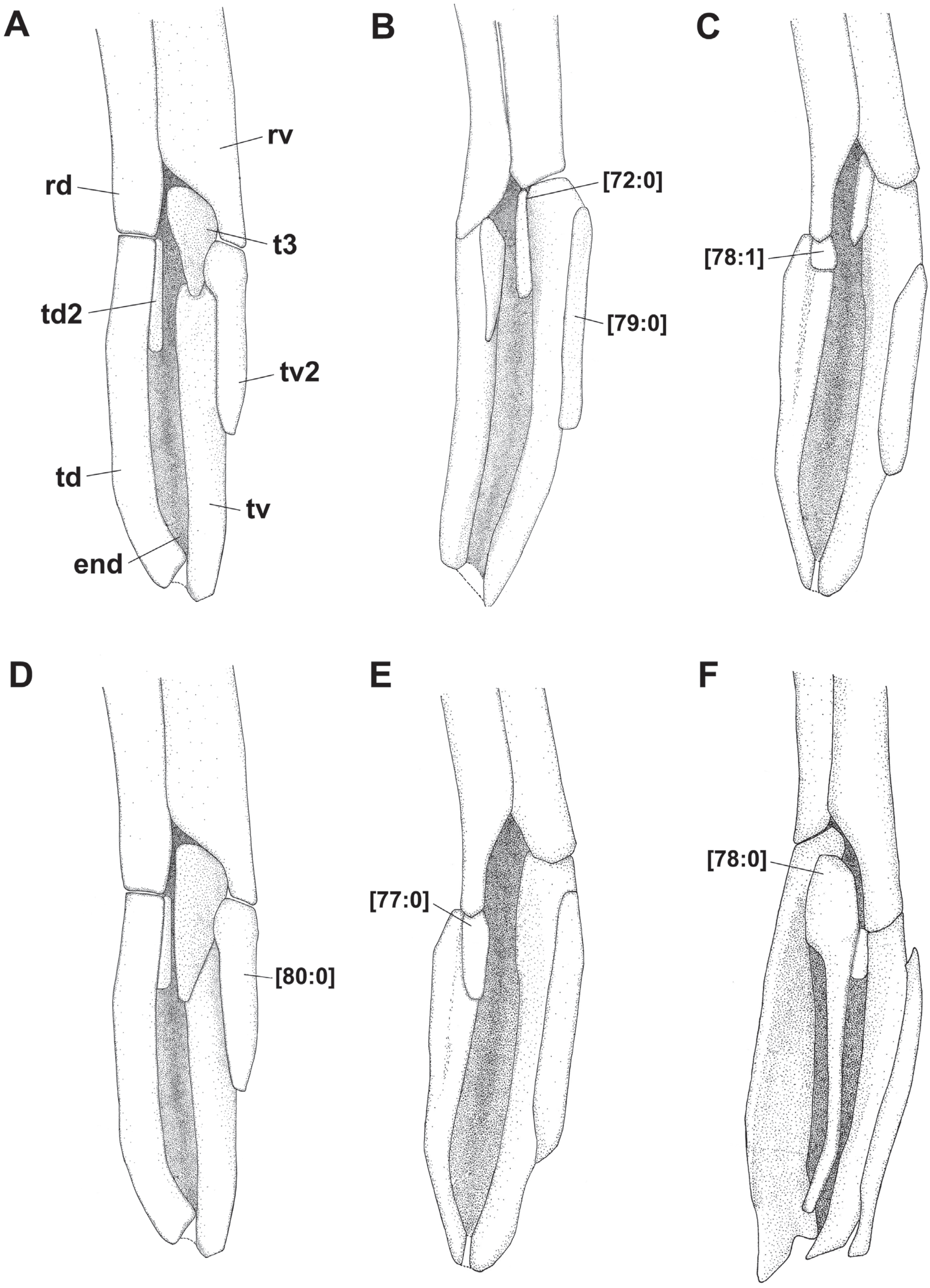

Figure 27. Clasper; skeleton. A, *Scyliorhinus boa*, USNM 221563, 348 mm TL; B, *Scyliorhinus canicula*, BMNH 1983.8.3.1–4, 585.7 mm TL; C, *Scyliorhinus capensis*, SAIAB 27577, 863 mm TL; D, *Scyliorhinus retifer*, UF 36359, 372 mm TL; E, *Scyliorhinus stellaris*, BMNH 1976.7.30.10, 476 mm TL; F, *Scyliorhinus torazame*, NSMT 50632, 427.9 mm TL. **end**, endstyle; **rd**, dorsal marginal cartilage; **rv**, ventral marginal cartilage; **t3**, accessory terminal cartilage; **td**, dorsal terminal cartilage; **td2**, dorsal terminal 2 cartilage; **tv**, ventral terminal cartilage; **tv2**, ventral terminal 2 cartilage. Modified from Soares and de Carvalho (2019).

The presence of transverse bands darker than the background colour over most of the body, known as 'saddles', is widespread amongst catsharks. Gomes et al. (2006), in their re-description of *Schroederichthys tenuis*, proposed three types of saddles: primary saddles, secondary saddles and subsaddles; these latter are situated ventrally to the lateral line. Primary saddles, more prominent in relation to the background colour, were observed in most species of *Scyliorhinus* (Soares and de Carvalho 2019; Fig. 29), except in *S. duhamelii* and *S. garmani*. In *S. torrei*, these saddles are found only in juvenile specimens. In *S. boa* and *S. retifer*, spots and dark lines, slightly darker than the background colour, are bordering the saddles (Fig. 29B). In *Asymbolus* spp., *Atelomycterus* spp., *Cephaloscyllium* spp., *Halaelurus* spp., *Haploblepharus* spp., *Proscyllium habereri* and *Schroederichthys* spp., saddles were also observed, varying in number and position (state 0; Fig. 29E). In *Apristurus* spp., *Cephalurus* spp., *Galeus* spp., *Holohalaelurus regani*, *Parmaturus* spp., and *Poroderma* spp., saddles are absent (state 1; Fig. 29F).

83 Dark spots: (0) present; (1) absent. (CI = 20; RI = 50).

Springer (1979) pointed out the relevance of colouration for identification of *Scyliorhinus* species to the detriment of other features, such as morphometric data and internal morphology. In *Scyliorhinus*, we observed some differences amongst species regarding the occurrence of dark spots. Dark spots are present in *S. boa*, *S. cabofriensis*, *S. canicula* (Fig. 29A), *S. cervigoni*, *S. duhamelii*, *S. garmani*, *S. haeckelii*, *S. stellaris* and *S. ugoi*, whereas they are absent in *S. capensis*, *S. comoroensis*, *S. hesperius*, *S. meadi*, *S. torazame* (Fig. 29C) and *S. torrei* (Fig. 29D; Soares and de Carvalho 2019). In *Cephaloscyllium* spp., *Poroderma pantherinum* (Fig. 29H), *Proscyllium habereri* and most scyliorhinids, dark spots were observed, with the exception of *Apristurus longicephalus*, *Cephalurus cephalus* and *Parmaturus* spp.

84 Dark stripes: (0) absent; (1) present. (CI = 50; RI = 0).

A colour pattern, composed of dark stripes running in different directions, was observed in *Scyliorhinus retifer* (Fig. 29B) and *Poroderma africanum* (state 1; Fig. 29G), differing from all other scyliorhinid species examined. In *Scyliorhinus retifer*, stripes form polygons and are bordering saddles, while in *Poroderma africanum*, stripes are parallel to the anteroposterior axis and do not form saddles, extending throughout the body.

Non-informative (autapomorphic) characters

Anterior nasal flaps in *Haploblepharus*

Bell (1993) described anterior nasal flaps as expanded and medially fused, forming a nasal curtain that covers the upper lip, in *Haploblepharus*. However, according to our observations, nasal flaps in *Haploblepharus* (Fig. 3C) are not fused, but present the same point of origin, medially; this pattern is unique amongst carcharhiniforms.

Muscle *preorbitalis* originating from the posterolateral wall of the nasal capsules

The muscle *preorbitalis* is situated anteriorly to the m. *adductor mandibulae* and limited posteriorly by the mandibular ramus of the nerve V (Huber et al. 2011). This muscle originates from the posteroventral wall of the nasal capsules and extends to the orbital notch in most taxa examined. In *Holohalaelurus regani*, a unique condition was observed; m. *preorbitalis* originates from the posterolateral surface of the nasal capsules. In all other scyliorhinid species, insertion of these muscles is on the muscle *adductor mandibulae*.

Muscle *levator hyomandibulae* with undifferentiated muscle fibres

Shirai (1992b) described the muscle *levator hyomandibulae* as united to the m. *constrictor hyoideus dorsalis* in Carcharhiniformes and separated from it in batoids. In Orectolobiformes and *Heterodontus*, the muscle *levator hyomandibulae* is situated internally to the m. *constrictor hyoideus dorsalis*, with its ventral portion laterally exposed (Goto 2001). In most of the examined taxa, muscle fibres are differentiated in m. *levator hyomandibulae*, internally to the m. *constrictor hyoideus dorsalis*, originating on the pterotic process of the neurocranium and inserting in the distal tip of the hyomandibular cartilage. In *Apristurus longicephalus*, the m. *levator hiomandibulae* seems to be fused to the m. *constrictor hyoideus dorsalis* or is absent; the same condition is also observed in *Squalus acanthias* (Marinelli and Strenger 1959; Huber et al. 2011).

Origin of the muscle *coracomandibularis* on the lateral borders of the coracoid bar

The m. *coracomandibularis* is dorsally situated to the muscles *intermandibularis* and *interhyoideus*, consisting of a median bundle originating from the m. *coracoarcualis* (most taxa examined) or from the medial surface of the coracoid bar (*Apristurus longicephalus*; Fig. 11D). According to Shirai (1992b), the first condition is widely distributed amongst neoselachians. Association of the m. *coracomandibularis* directly with the coracoid bar was reported by Shirai (1992a) for *Centroscyllium* and *Rhina* and by Goto (2001) for *Brachaelurus*, *Ginglymostoma* and *Stegostoma*. Shirai (1996) coded in his character matrix the origin of the m. *coracomandibularis* on the fascia of the m. *coracoarcualis* for all carcharhiniforms (his character 51), differing from what we observed in *Apristurus longicephalus*. Shirai (1996) also coded the origin of this muscle on the coracoid bar or pericardial membrane for *Heterodontus*, *Hexanchus*, *Heptranchias*, *Squatina*, Squaliformes and some rays.

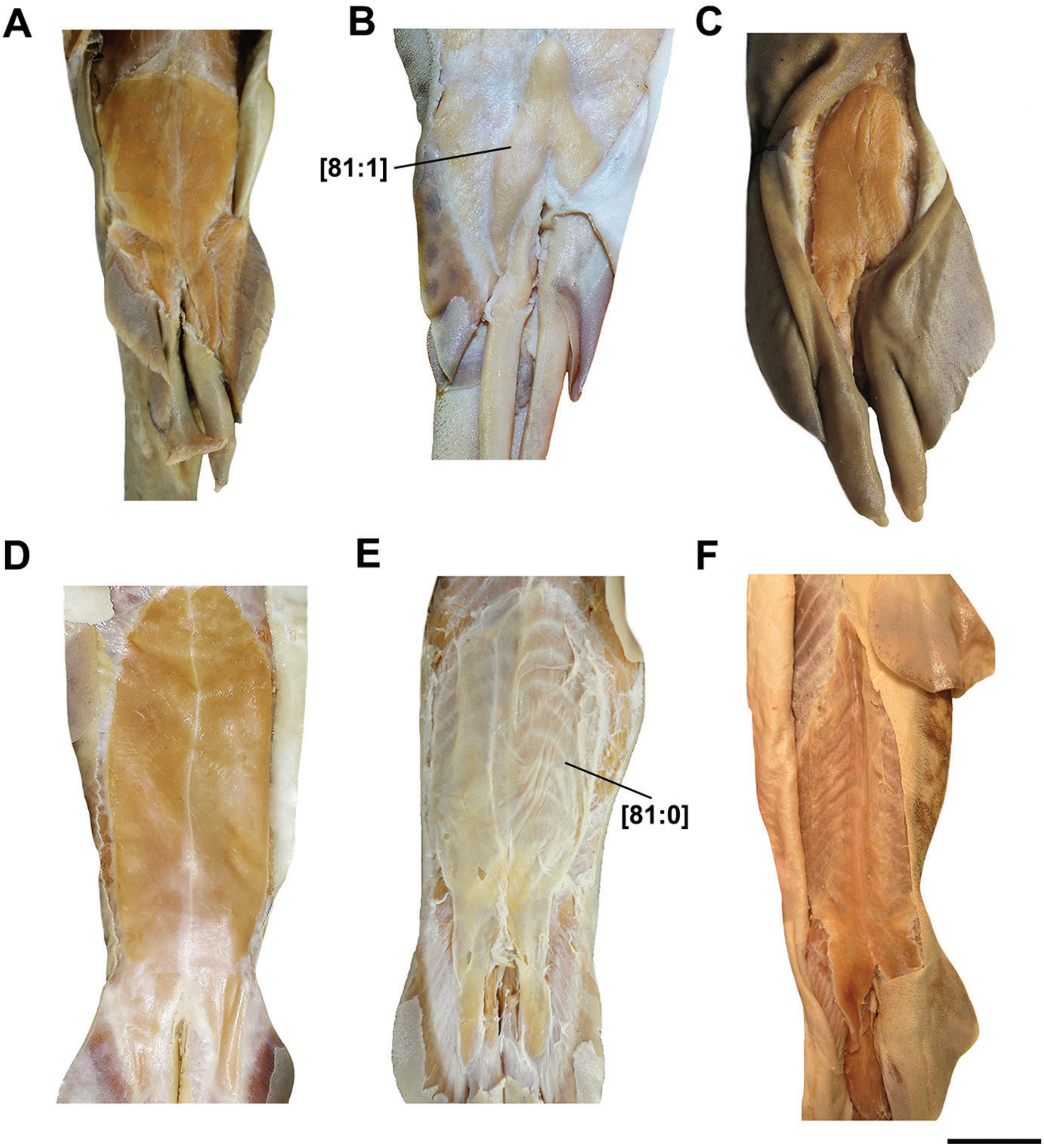

Figure 28. Detail of the clasper siphon. A, *Apristurus longicephalus*, HUMZ 170382, 475 mm TL; B, *Holohalaelurus regani*, SAIAB 25717, 610 mm TL; C, *Poroderma africanum*, SAIAB 25343, 920 mm TL; D, *Asymbolus rubiginosus*, AMS I.30393-004, 527 mm TL; E, *Halaelurus natalen*sis, SAIAB 26951, 400 mm TL; F, *Haploblepharus edwardsii*, AMNH 40988, 480 mm TL. Scale bar: 20 mm.

Clasper hooks

In *Scyliorhinus torazame*, we observed specialised hooks in the claspers forming a row that extends from the beginning of the ventral marginal cartilage to the terminal dermal cover and running along the medial margin of the exorhipidion (Schimidt 1930; Soares and de Carvalho 2019; Fig. 24F). This arrangement is unique amongst the taxa examined.

Phylogenetic reconstruction

The phylogenetic analysis of the data matrix (Appendix 2) including 84 morphological characters (five quantitative and 79 qualitative) and 35 terminal taxa and the use of implied weighting (k = 3) resulted in three equally most-parsimonious trees with 233 steps, CI = 0.37 and RI = 0.69. A strict consensus was generated and is presented in Figure 30 and its analysis is detailed below. The char-

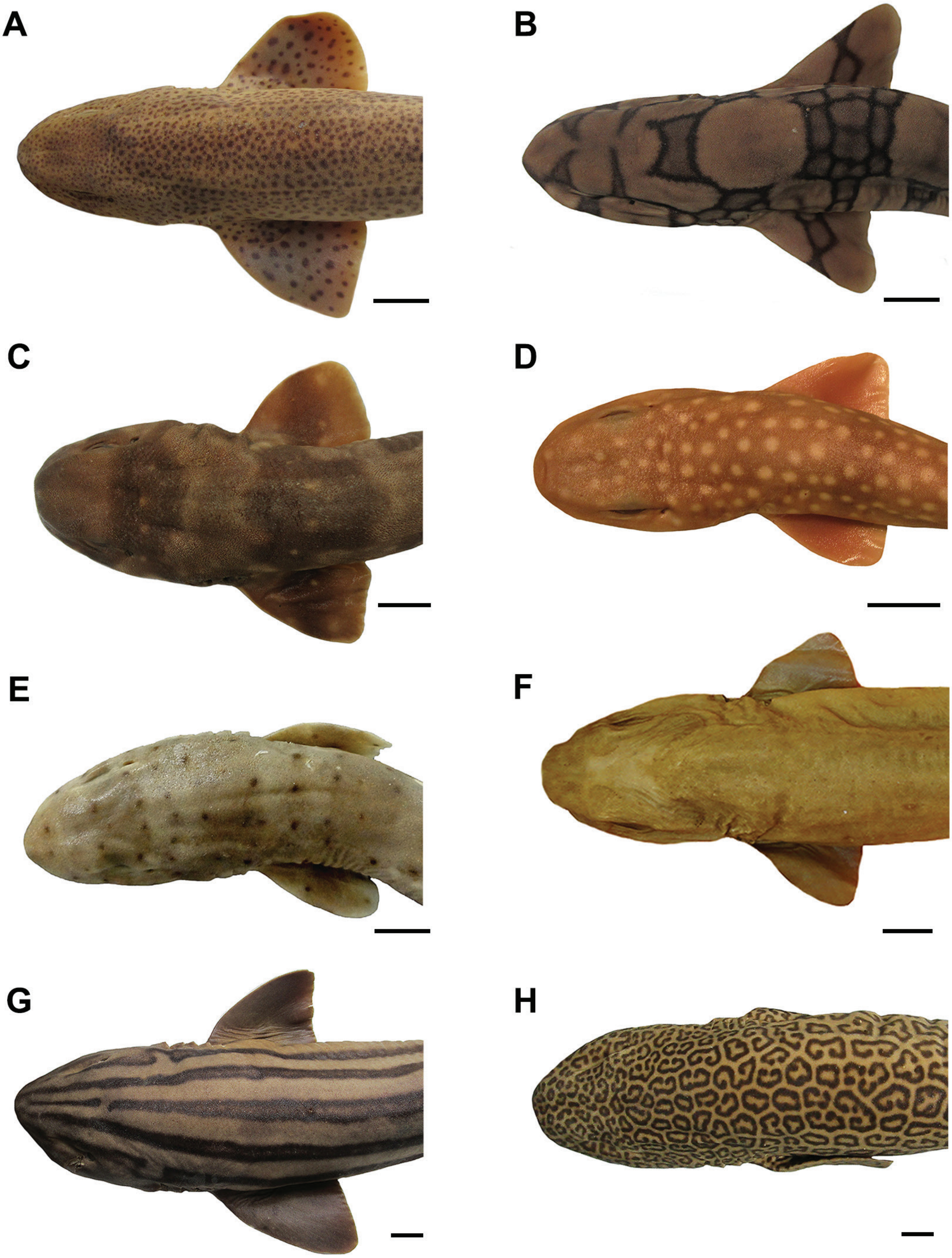

Figure 29. Color patterns. A, *Scyliorhinus canicula*, MNHN 1999–1732, female, 418.5 mm TL; B, *Scyliorhinus retifer*, UF 36359, male, 372 mm TL; C, *Scyliorhinus torazame*, NSMT 50632, male, 427.9 mm TL; D, *Scyliorhinus torrei*, USNM 157852, male, 285 mm TL; E, *Atelomycterus fasciatus*, CSIRO H1298-7, male, 370 mm TL; F, *Parmaturus angelae*, MZUSP 124001, female, 425 mm TL; G, *Poroderma pantherinum*, SAIAB 34577, male, 640 mm TL; H, *Poroderma africanum*, SAIAB 25343, male, 920 mm TL. Scale bar: 20 mm.

acter matrix was divided into two datasets: in Appendix 2, quantitative characters with absolute and normalised values for each terminal are presented, whereas in Appendix 3 only qualitative characters are included.

Character listings for clades numbered in Figure 30 are summarised in Appendix 4. The list of synapomorphies, presented below, begins in Scyliorhininae and progressively continues to less inclusive clades within this family. For each clade, only non-ambiguous synapomorphies are listed. After each synapomorphy, the number of the referred character and its state changes are shown in brackets. Synapomorphies followed by an asterisk represent unique transformations in the present analysis. A complete list of character transformations is presented in Appendix 5. Relative Bremer support values are shown in Figure 30 below each node.

Monophyly of clade 1

The hypothesis of the monophyly of the Scyliorhininae is supported by eight synapomorphies, four of them proposed for the first time herein. This clade is composed of *Scyliorhinus*, *Cephaloscyllium* and *Poroderma*. Monophyly of the Scyliorhininae was previously proposed by Compagno (1998a), who listed loss of the *depressor palpebrae nictitantis* muscle and loss of the fourth ventral extrabranchial cartilage as synapomorphies for the subfamily (both corroborated herein). However, no cladistic analysis was performed by this author. Later, Iglésias et al. (2005), Human et al. (2006) and Naylor et al. (2012a, 2012b) corroborated the monophyly of this clade using molecular data.

1. Lower diplospondylous vertebral count [char. 2, 0.520–0.660 > 0.280–0.310].
2. Muscle *depressor palpebrae nictitantis* absent [char. 29, 0 > 1].
3. Nasal apertures at the same level in nasal capsules [char. 38, 0 > 1].
4. Articular region of the quadratomandibular joint of Meckel's cartilage composed by a posterior lingual condyle opposite to the facet [char. 49, 0 > 1].
5. Three ventral extrabranchial cartilages [char. 56, 0 > 1].
6. Terminal dermal cover extending up to one-third of the clasper glans [char. 64, 0 > 1].
7. Accessory dorsal marginal cartilage absent [char. 73, 0 > 1].
8. Clasper siphon short and restricted to the pelvic region [char. 81, 0 > 1].

Monophyly of clade 2

The monophyly of *Poroderma* is supported by five synapomorphies.

1. Anterior nasal flap divided into two portions, medial and lateral [char. 8, 0 > 1].
2. Muscular nasal barbel present [char. 10, 0 > 1].
3. Accessory terminal cartilage absent [char. 72, 0 > 1].
4. Ventral terminal 2 cartilage posteriorly situated, posterior to the half-length of the ventral terminal cartilage [char. 80, 0 > 1].
5. Colour pattern not composed of transverse saddles [char. 82, 0 > 1].

Poroderma africanum is characterised by the following autapomorphies:

1. Projected flap present on the upper lip margin [char. 17, 0 > 1]. Independently acquired in *Scyliorhinus* spp.
2. Muscle *coracomandibularis* inserting on the medial aspect of antimeres of Meckel's cartilage [char. 30, 0 > 1].
3. Colour pattern composed of stripes [char. 84, 0 > 1].

Poroderma pantherinum is characterised by the following autapomorphy:

1. Dermal denticles present on the medial border of the exorhipidion [char. 62, 0 > 1].

Monophyly of clade 3

The monophyly of the clade formed by *Scyliorhinus* and *Cephaloscyllium* is supported by seven synapomorphies. Compagno (1988a) already had proposed a close relationship between both genera, listing the loss of upper labial furrows and pseudopera rudimentary and absent as synapomorphies. Here, absence of the upper labial furrows is not considered a synapomorphy for this clade and features of the pseudopera were not included in the present analysis as this structure is poorly defined.

1. Mesonarial crest prominent [char. 9, 0 > 1].
2. One upper labial cartilage [char. 19, 0 > 1].
3. Lateral processi rastriformis similar to dermal papillae in length [char. 53, 0 > 1].
4. Coracoid bar with a well-developed medial projection, more than twice the size of its lateral portion [char. 58, 0 > 1].
5. Rhipidion well-developed and presenting a prominent posterior margin [char. 66, 1 > 0].
6. Rhipidion extending throughout the clasper glans [char. 67, 1 > 0].
7. Ventral marginal 2 cartilage absent [char. 75, 0 > 1].

Monophyly of clade 4

The monophyly of *Cephaloscyllium* is supported by the following synapomorphies:

1. Higher monospondylous vertebral count [char. 1, 0.540–0.650 > 0.730].
2. Higher upper tooth row count [char. 3, 0.230–0.350 > 0.450–0.480].

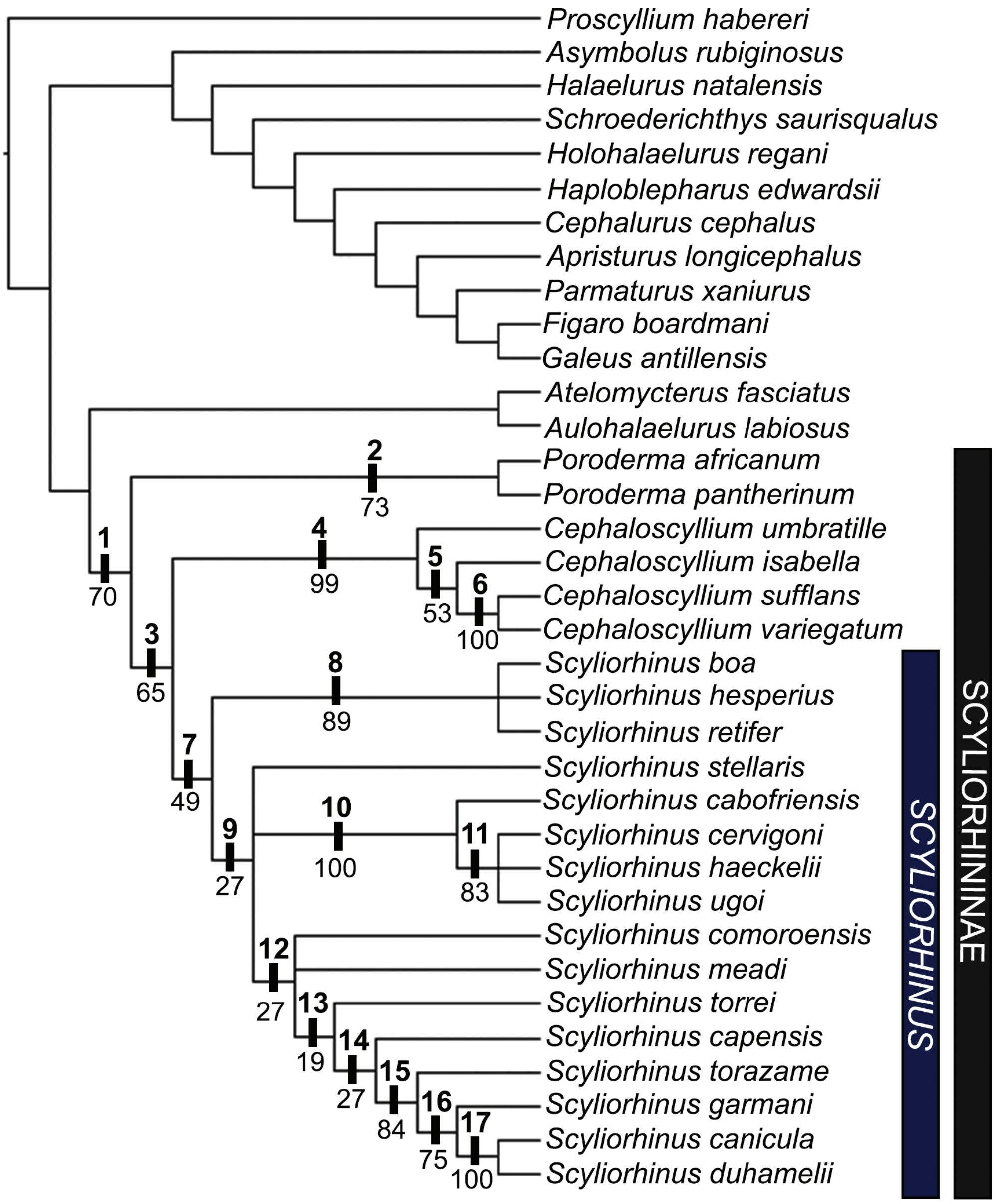

Figure 30. Strict consensus cladogram of the three equally most-parsimonious trees (L = 233, CI = 0.37, RI = 0.69). Number of clades shown above branches. Values of relative Bremer support shown below branches.

3. Higher lower tooth row count [char. 4, 0.230–0.370 > 0.490–0.530].
4. Lower labial furrow absent [char. 16, 0 > 1].
5. Postoral grooves present [char. 20, 0 > 1].
6. Origin of second dorsal fin anterior to half-length of the anal-fin base [char. 24, 0 > 1].
7. Muscle bundles of muscle *coracohyoideus* separated by at least one-half the width of each bundle [char. 32, 0 > 1].

Cephaloscyllium umbratile is hypothesised as sister group of the clade formed by the species *C. isabella*, *C. sufflans* and *C. variegatum* (clade 5) and characterised by the following autapomorphies:

1. Higher diplospondylous vertebral count [char. 2, 0.280–0.310 > 0.670–1.00].
2. Higher upper tooth row count [char. 3, 0.450–0.480 > 0.570–1.00].
3. Higher lower tooth row count [char. 4, 0.490–0.530 > 0.580–1.00].

Monophyly of clade 5

The clade, formed by species *Cephaloscyllium isabella*, *C. sufflans* and *C. variegatum*, is characterised by the following synapomorphy:

1. Lower diplospondylous vertebral count [char. 2, 0.280–0.310 > 0.130–0.170].

Cephaloscyllium isabella is hypothesised as the sister group of the clade formed by the species *C. sufflans* and *C. variegatum* (clade 6) and characterised by the following autapomorphy:

1. Lower diplospondylous vertebral count [char. 2, 0.130–0.170 > 0.060–0.080].

Monophyly of clade 6

This clade is formed by *Cephaloscyllium sufflans* and *C. variegatum* and is characterised by the following synapomorphy:

1. Oropharyngeal denticles large and forming rows on internal face of gill components [char. 54, 0 > 1].

No unique autapomorphies were found for *Cephaloscyllium variegatum*. *Cephaloscyllium sufflans* is characterised by the following autapomorphy:

1. Higher monospondylous vertebral count [char. 1, 0.730 > 0.810].

Monophyly of clade 7

The monophyly of *Scyliorhinus* is supported by five synapomorphies in all equally most-parsimonious trees. The genus is divided into two main clades: *S. boa*, *S. hesperius* and *S. retifer* (clade 8) and a clade for all remaining species.

1. Lower values for upper tooth row count [char. 3, [0.230–0.350 > 0.210–0.220].
2. Lower values for lower tooth row count [char. 4, 0.230–0.370 > 0.220].
3. Projected flap present on the upper lip margin [char. 17, 0 > 1].
4. Pelvic apron present [char. 21, 1 > 0].
5. Ephyseal notch present [char. 41, 0 > 1].

Monophyly of clade 8

This clade is formed by the species *Scyliorhinus boa*, *S. hesperius* and *S. retifer* and is characterised by the following synapomorphies:

1. Envelope present on clasper [char. 70, 1 > 0].
2. Envelope medially expanded [char. 71, 0 > 1].

No unique autapomorphies were found in the present analysis for *Scyliorhinus boa*. *Scyliorhinus hesperius* is characterised by the following autapomorphy:

1. Colour pattern without dark spots [char. 83, 0 > 1].

Scyliorhinus retifer is characterised by the following autapomorphy:

1. Colour pattern composed of dark stripes [char. 84, 0 > 1].

Monophyly of clade 9

The monophyly of the clade, formed by *S. stellaris*, *S. cabofriensis*, *S. canicula*, *S. capensis*, *S. comoroensis*, *S. cervigoni*, *S. duhamelii*, *S. garmani*, *S. haeckelii*, *S. meadi*, *S. torazame*, *S. torrei* and *S. ugoi*, is supported by the following synapomorphy:

1. Accessory terminal cartilage absent [char. 72, 0 > 1].

Scyliorhinus stellaris is hypothesised as the sister group of all remaining species of *Scyliorhinus* (cited above) and characterised by the following autapomorphy:

1. Higher intestinal valve count [char. 5, 0.420 > 0.670–0.750].

In some trees:

1. Higher monospondylous vertebral count [char. 1, 0.460–0.540 > 0.580–0.690].

Monophyly of clade 10

This clade is formed by *S. cabofriensis*, *S. cervigoni*, *S. haeckelii* and *S. ugoi* and characterised by the following synapomorphy:

1. Terminal dorsal 2 cartilage rhomboidal [char. 78, 0 > 1].

In some trees:

1. Lower monospondylous vertebral count [char. 1, 0.540–0.580 > 0.420–0.460].
2. Higher intestinal valve count [char. 5, 0.420 > 0.250].

Scyliorhinus cabofriensis is hypothesised as the sister group of *S. haeckelii*, *S. cervigoni* and *S. ugoi*, but no unique autapomorphies were found for this species.

Monophyly of clade 11

The monophyly of the clade formed by *S. cervigoni*, *S. haeckelii* and *S. ugoi* is supported by the following synapomorphy:

1. Envelope present on clasper [char. 70, 1 > 0].

No unique autapomorphies were found in the present analysis for *S. haeckelii* and *S. ugoi*. *Scyliorhinus cervigoni* is characterised by the following autapomorphy:

1. Dermal denticles restricted to the exorhipidion on dorsal surface of clasper glans [char. 61, 1 > 0].

Monophyly of clade 12

The monophyly of the clade, formed by *S. canicula*, *S. capensis*, *S. comoroensis*, *S. duhamelii*, *S. garmani*, *S. meadi*, *S. torazame* and *S. torrei*, is supported by the following synapomorphy:

1. Colour pattern without dark spots [char. 83, 0 > 1].

Scyliorhinus comoroensis and *S. meadi* are hypothesised as the sister group of the remaining species. *Scyliorhinus comoroensis* is characterised by the following synapomorphies:

1. Higher upper tooth row count [char. 3, 0.280–0.310 > 0.470].
2. Ventral terminal 2 cartilage absent [char. 79, 0 > 1].

Scyliorhinus meadi is characterised by the following autapomorphy:

1. Higher monospondylous vertebral count [char. 1, 0.460 > 0.540–0.770].

Monophyly of clade 13

The monophyly of the clade, formed by *S. canicula*, *S. capensis*, *S. duhamelii*, *S. garmani*, *S. torazame* and *S. torrei*, is supported by the following synapomorphy:

1. Pelvic inner margins almost entirely fused. [char. 22, 1 > 2].

Scyliorhinus torrei is hypothesised as sister group of clade 14 (see below) and is characterised by the following autapomorphies:

1. Lower monospondylous vertebral count [char. 1, 0.350–0.540 > 0.080–0.270].
2. Lower upper tooth row count [char. 3, 0.170–0.220 > 0.00–0.120].
3. Lower values for lower tooth row count [char. 4, 0.190–0.220 > 0.010–0.180].
4. Envelope present on clasper [char. 70, 1 > 0].

Monophyly of clade 14

This clade is formed by *S. canicula*, *S. capensis*, *S. duhamelii*, *S. garmani* and *S. torazame* and is characterised by the following synapomorphy:

1. Accessory terminal cartilage present [char. 72, 1 > 0].

Scyliorhinus capensis is hypothesised as sister group of the clade 15 (see below) and is characterised by the following autapomorphies:

1. Higher monospondylous vertebral count [char. 1, 0.350–0.540 > 0.620–0.690].
2. Lower values for lower tooth row count [char. 4, 0.210–0.220 > 0.260–0.770].
3. Terminal dermal cover rough [char. 65, 0 > 1].
4. Dorsal terminal 2 cartilage rhomboidal [char. 78, 0 > 1].

Monophyly of clade 15

The monophyly of the clade, formed by *S. canicula*, *S. duhamelii*, *S. garmani* and *S. torazame*, is supported by the following synapomorphies:

1. Rhipidion reduced and consisting of a narrow strip [char. 66, 0 > 1].
2. Rhipidion extending up to 1/3 of the clasper glans length [char. 67, 0 > 1].

Scyliorhinus torazame is hypothesised as the sister group of the clade formed by *S. canicula*, *S. duhamelii* and *S. garmani*, but no unique autapomorphies were found for this species.

Monophyly of clade 16

The monophyly of the clade, formed by *S. canicula*, *S. duhamelii* and *S. garmani*, is supported by the following synapomorphies:

1. Anterior nasal flap entirely covering excurrent aperture, posterior nasal flap and upper lip [char. 6, 0 > 2].
2. Colour pattern composed of dark spots [char. 83, 1 > 0].

Scyliorhinus garmani is hypothesised as the sister group of the clade formed by *S. canicula* and *S. duhamelii* and this species is characterised by the following autapomorphy:

1. Higher monospondylous vertebral count [char. 1, 0.350–0.540 > 0.770].

Monophyly of clade 17

Monophyly of the clade, formed by *S. canicula* and *S. duhamelii*, is supported by:

1. Anterior nasal flaps distant from each other by less than half of their length [char. 7, 0 > 1].
2. Posterior nasal flap laterally situated to the excurrent aperture [char. 13, 0 > 1].
3. Nasoral groove present [char. 14, 0 > 1].

Scyliorhinus canicula is characterised by the following autapomorphy:

1. Terminal dermal cover rough [char. 65, 0 > 1].

Scyliorhinus duhamelii is characterised by the following autapomorphies:

1. Lower intestinal valve counts [char. 5, 0.420 > 0.250].
2. Accessory terminal cartilage absent [char. 72, 0 > 1].

Discussion

Phylogeny of *Scyliorhinus* species

The phylogenetic relationships of species of the subfamily Scyliorhininae on the basis of morphological data and inferred from a numerical cladistic study including all *Scyliorhinus* species, are here presented for the first time. The monophyly of Scyliorhininae is supported by the absence of the muscle *depressor palpebrae nictitantis*, nasal apertures at the same level on nasal capsules, articular region of the quadratomandibular joint of Meckel's cartilage, characterised by a posterior lingual condyle opposite to the facet, three ventral extrabranchial cartilages, terminal dermal cover extending to one-third of the clasper glans, absence of accessory dorsal marginal cartilage and clasper siphon short and restricted to the pelvic region.

Compagno (1988a) listed the absence of the muscle *depressor palpebrae nictitantis* and the loss of the fourth ventral extrabranchial cartilage as synapomorphies for Scyliorhininae. He also mentioned the reduction of claspers components and of the second dorsal fin as diagnostic characters for this subfamily. However, Compagno (1988a) did not mention which parts of the clasper are reduced or absent in the subfamily and his descriptions of carcharhiniform genera did not present detailed information on the skeletal anatomy of the copulatory organs. Soares (2020) reported the presence of an accessory dorsal marginal cartilage in many scyliorhinid taxa, but not in species of *Cephaloscyllium* and *Poroderma*. Regarding the great variability of sizes and position between dorsal fins, their relative sizes were not included in the present analysis as they are highly influenced by ontogeny and preservation, especially in specimens of *Apristurus* and *Cephalurus*.

Scyliorhinus is hypothesised to be the sister group of *Cephaloscyllium*, sharing with it the presence of only one upper labial cartilage, lateral processi rastriformis similar in size to the dermal papillae, coracoid bar with a well-developed medial projection corresponding to more than twice the size of its lateral portion, a well-developed rhipidion presenting a prominent posterior margin and extending throughout the clasper glans and the absence of the ventral marginal 2 cartilage. A closer relationship between *Scyliorhinus* and *Cephaloscyllium* was also proposed by Compagno (1988a) who listed the absence of upper labial furrows and pseudopera absent or rudimentary in claspers as diagnostic characters.

The monophyly of *Scyliorhinus* is supported by the presence of a projected flap on the upper lip margin, of a pelvic apron and an ephyseal notch at the posterior border of the anterior fontanelle on the neurocranium. The presence of a pelvic apron is observed in *Scyliorhinus*, *Asymbolus* and *Holohalaelurus*, being more developed and extending to at least two thirds or almost the entire length of pelvic inner margins in *Scyliorhinus* species. The presence of an ephyseal notch on the neurocranium of Scyliorhinus species is unique amongst scyliorhinines. The presence of a projected flap is the main character used by many authors to identify species of *Scyliorhinus* (Garman 1913; Bigelow and Schroeder 1948; Springer 1966, 1979; Compagno 1988a; Compagno et al. 2005; Ebert et al. 2013), but is proposed as a synapomorphy for these species for the first time herein. This flap is also present in *Poroderma africanum*, but this species is hypothesised as the sister group of *P. pantherinum*, sharing with it the following characters: anterior nasal flap divided into two portions (medial and lateral), presence of a muscular nasal barbel, distance between internal carotid foramina greater than the distance between internal carotid and stapedial foramina, absence of an accessory terminal cartilage, ventral terminal cartilage posteriorly situated (posterior to the half-length of the ventral terminal cartilage) and colour pattern not composed of transverse saddles. Additionally, *Poroderma* is hypothesised as sister group of the clade formed by *Cephaloscyllium* + *Scyliorhinus*.

Springer (1979) pointed out that the unique configuration of the nasoral region of *S. canicula* would be sufficient to guarantee the allocation of all other species of the genus in a distinct taxon; we note here that the same configuration is present in *S. duhamelii*. Some authors also made comments on the similarities observed in the nasoral region of *Scyliorhinus canicula* and species of *Atelomycterus* and *Haploblepharus*, highlighting the need of a more detailed examination and the investigation of phylogenetic relationships amongst these taxa (Compagno 1988a; Bell 1993). According to our results, *S. canicula* and *S. duhamelii* are distinguished from species of *Atelomycterus* and *Haploblepharus* by the absence of upper labial furrows and the presence of posterior nasal flaps (vs. upper furrows present and posterior flaps absent in *Atelomycterus* and *Haploblepharus*). Additionally, *S. canicula* and *S. duhamelii* share with their congeners the presence of a flap on the upper lip that projects laterally, covering the lower labial furrows and the presence of a pelvic apron in males. Similarities amongst *S. canicula* and *S. duhamelii* and species of *Atelomycterus* and *Haploblepharus* have been suggested as being the result of adaptative convergence to benthic habits (Bell 1993). However, these characters are not present in other demersal scyliorhinids.

Species of *Cephaloscyllium*, here examined, shared the following synapomorphies: absence of an upper labial furrow, presence of a postoral groove, origin of a second dorsal fin anterior to the half-length of the anal fin, muscle bundles of muscle *coracohyoideus* well separated along all their extension and higher values for monospondylous vertebrae, upper and lower tooth row counts. Postoral grooves are observed in all species of *Cephaloscyllium* with varied extensions, but no flap or labial furrow is found in any of them (17 species are considered valid; Fricke et al. 2020). Notches near the lower edge of the mouth are observed and illustrated for specimens of *C. signorum* (Last et al. 2008), *C. variegatum* and *C. zebrum* (Last and White 2008) and can be confused with lower labial furrows without a detailed examination.

Clasper morphology contributed important characters that helped elucidate the phylogenetic relationships among species of *Scyliorhinus* and other scyliorhinines (21 characters from the clasper were included in the present analysis). Amongst the most relevant characters are the following: dermal denticles along the dorsal surface of the clasper, degree of development of the envelope, configuration of terminal dermal cover, occurrence of accessory terminal and ventral terminal 2 cartilages and shape of dorsal terminal 2 cartilage. A closer relationship between *S. boa* and *S. retifer* was proposed by Goode and Bean (1896) and Garman (1913), based on colour pattern of both species, which is corroborated here by clasper morphology. Both species share the presence of a well-developed and medially-expanded envelope that lacks dermal denticles, covering the anterior portion of the cover rhipidion; this condition is also observed in *S. hesperius*. The clade, formed by *Scyliorhinus cabofriensis*, *S. cervigoni*, *S. haeckelii* and *S. ugoi*, is supported by the presence of a reduced dorsal terminal 2 cartilage. These species are distributed in the Southern Atlantic Ocean, off the eastern coast of Brazil (*S. cabofriensis*, *S. haeckelii* and *S. ugoi*) and west coast of Africa (*S. cervigoni*), with records in similar latitudes, suggesting a common evolutionary history that may date from the formation of the Atlantic Ocean.

According to Springer (1966: p. 597), species of *Scyliorhinus* distributed in the Western Central Atlantic may form a 'compact infrageneric group', as they are more similar to each other than they are to species in the Eastern Atlantic and Western Pacific. According to our results, however, this hypothesis is not corroborated because of the closer phylogenetic relationships of species from the Western Central Atlantic with those from other regions. *Scyliorhinus torrei* is hypothesised here to being more closely related to *S. capensis* (Southeastern Atlantic), *S. torazame* (Western Pacific), *S. canicula* and *S. duhamelii* (North-eastern Atlantic and Mediterranean Sea) by sharing a well-developed pelvic apron with pelvic inner margins almost entirely fused. *Scyliorhinus boa*, *S. hesperius* and *S. retifer* form a clade hypothesised as the sister group of all species of *Scyliorhinus*.

The impact of morphological characters

Characters from the nasoral region, dermal denticles, claspers, vertebrae and intestinal counts were revealed to be extremely important to shed light on the phylogenetic relationships amongst scyliorhinines and may contribute to future phylogenetic analyses concerning scyliorhinids. A more detailed examination of the nasal flaps and labial furrows allows for the identification of differences amongst the genera *Atelomycterus*, *Haploblepharus* and *Scyliorhinus* and clarifies questions related to the distribution and variation of characters amongst species of *Scyliorhinus* (e.g. *S. canicula* and *S. duhamelii*).

Data from tooth morphology of catsharks are scarce and the only study that reported tooth characters for Scyliorhinidae is Herman et al. (1990). Besides this study, information on sexual and ontogenetic heterodonty are found only for a few species (Brough 1937; Nakaya 1975; Springer 1966; Compagno 1988a; Gomes and Tomás 1991; Litvinov 2003; Soares and de Carvalho 2019) and for some scyliorhinid species, heterodonty seems to be absent (Weigmann et al. 2018). In this study, males and females, adults and juveniles were not available for some species and, thus, it was not possible to investigate the influence of sexual dimorphism and ontogeny in tooth characters (mainly regarding the number of cusplets and degree of development of striae). As a consequence, characters of tooth morphology were not included in the present analysis.

Despite the relevance of characters associated to claspers in species identification and phylogenetic analyses, information on the internal anatomy of these organs are found only for some species and mainly in classical works about clasper morphology (Jungersen 1899; Leigh-Sharpe 1920, 1921, 1922, 1924a, b; Compagno 1988a), being absent in most species descriptions and taxonomic reviews (Human 2006b; Séret and Last 2007; Last et al. 2008; Last and White 2008; Nakaya et al. 2013; amongst others). Soares (2020) provided detailed descriptions of clasper structures in almost all catshark genera and demonstrated the uselfulness of claspers for taxonomic and systematic purposes. We highlight here the importance of including clasper descriptions in taxonomic studies.

Morphology and molecular data

The monophyly of the subfamily Scyliorhininae is corroborated by the present study, as well as by phylogenetic analyses, based on molecular data (Iglésias et al. 2005; Human et al. 2006; Naylor et al. 2012a, 2012b). However, morphology and molecular-based studies diverge on the hypotheses of relationships amongst *Scyliorhinus*, *Cephaloscyllium* and *Poroderma* (Fig. 31). In this study, *Cephaloscyllium* is hypothesised as the sister group of *Scyliorhinus*, based on clasper and skeletal characters.

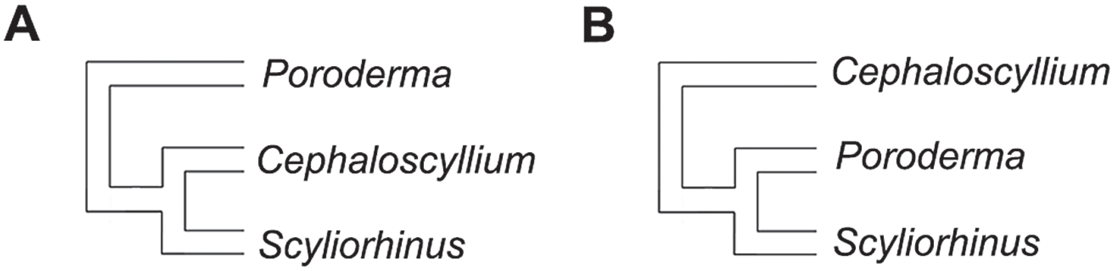

Figure 31. Phylogenetic hypotheses of the subfamily Scyliorhininae. A, morphology- based hypothesis (present work; Compagno, 1988a); B, molecular-based hypothesis (Naylor et al., 2012a, 2012b).

Naylor et al. (2012a, 2012b) hypothesised a closer relationship between *Poroderma* and *Scyliorhinus*, analysing the NADH2 mitochondrial gene and conducting a model-Bayesian phylogenetic analysis.

The monophyly of the genus *Scyliorhinus* is supported here and also by Human et al. (2006) and Naylor et al. (2012a, 2012b). The phylogeny of Iglésias et al. (2005) resolved *Scyliorhinus* as paraphyletic, with a weakly-supported relationship between *S. torazame* and *Cephaloscyllium umbratile*. These authors analysed only few species of *Scyliorhinus* and no species of *Poroderma* was included in the analysis (Iglésias et al. 2005).

In the present study, we contribute to the understanding of the phylogenetic relationships amongst *Scyliorhinus* species. In recent molecular studies, only few species of *Scyliorhinus* were included and, therefore, little information on infrageneric relationships could be obtained (Iglésias et al. 2005; Naylor et al. 2012a, 2012b). Nevertheless, a closer relationship between *S. retifer* and *S. stellaris* was recovered by Naylor et al. (2012a), which agrees with the results presented here.

Despite the contributions presented here for the phylogeny of Scyliorhininae, there is a great need to review the taxonomy of *Cephaloscyllium*, including the examination of clasper morphology in its species. Deeper considerations on the monophyly of Scyliorhinidae and the phylogenetic relationships amongst scyliorhinids and other taxa were not performed here, since additional taxa of other carcharhiniform families should be included in a broader phylogenetic analysis. Taxonomic reviews, detailed morphological studies and cladistic analyses, based on morphological and molecular data, are necessary to improve our understanding of the phylogenetic relationships amongst scyliorhinids and other carcharhiniforms.

Conclusions

- The monophyly of Scyliorhininae is supported by four characters proposed by Compagno (1988a) and other four proposed for the first time;
- *Scyliorhinus* is hypothesised to be the sister group of *Cephaloscyllium*, sharing with it the presence of only one upper labial cartilage, lateral processi rastriformis similar in size to the dermal papillae, coracoid bar with a well-developed medial projection corresponding to more than twice the size of its lateral portion, a well-developed rhipidion presenting a prominent posterior margin and extending throughout the clasper glans and the absence of the ventral marginal 2 cartilage.
- The monophyly of *Scyliorhinus* is supported by the presence of a projected flap on the upper lip margin, of a pelvic apron and an ephyseal notch at the posterior border of the anterior fontanelle on the neurocranium.
- Characters from the nasoral region, dermal denticles, claspers, vertebrae and intestinal counts were revealed to be extremely important to shed light on the phylogenetic relationships amongst scyliorhinines and may contribute to future phylogenetic analyses concerning scyliorhinids and carcharhiniforms.
- Results presented here mostly agree with those obtained in recent phylogenetic analyses, but further work integrating molecular and morphological data is still needed.

Acknowledgements

The authors wish to acknowledge Barbara Brown (AMNH), David Catania (CAS), Rob Robbins (FLMNH), Toshio Kawai (HUMZ), Karsten Hartel and Andrew Williston (MCZ), Patrice Pruvost (MNHN), Marcelo Brito (MN/UFRJ), Alessio Datovo (MZUSP), Oliver Crimmen and Ralf Britz (BMNH), Sven Kullander (NRM), Masanori Nakae and Gento Shinohara (NSMT), Ofer Gon and Nkosinathi Mazungula (SAIAB), Albe Bosman (SAM), Ulisses Gomes and Hugo Santos (UERJ), Ricardo Rosa (UFPB), Otto Gadig (UNESP, São Vicente), José Ortiz (USAC), Lynne Parenti, Jeffrey Williams, Kris Murphy and Sandra Raredon (USNM), Peter Bartsch (ZMB), Ralf Thiel (ZMH), and Marcus Krag (ZMUC) for permission to visit the collections and examine the specimens under their care. José Ortiz (USAC) for sending photos of specimens of *Scyliorhinus hesperius*. Mônica de Toledo-Piza (USP), Otto Gadig (UNESP, São Vicente), Ulisses Gomes (UERJ), Alessio Datovo (MZUSP) and Rodrigo Caires for their comments and contributions on the writing of this paper. Ênio Matos and Phillip Lentitakis (IBUSP) for the SEM images and Giulia Baldaconi for the neurocranium illustrations. The first author was supported by CAPES (Código de Financiamento 001) and FAPESP (processes 2014/20316-5, 2015/21314-9, 2016/22214-0); the second author by a grant from CNPq (304615/2011-0).

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Appendix 1

List of examined material

Apristurus longicephalus. HUMZ 170382, male, 475 mm TL (Japan).

Asymbolus rubiginosus. AMS I.30393-004, male, 527 mm TL (Australia), AMS I.34899-002, female, 390 mm TL (Australia).

Atelomycterus fasciatus. CSIRO H1298-7, male, 370 mm TL (Australia), MZUSP 118095, female, 363 mm TL (western Australia).

Aulohalaelurus labiosus. ZMH 2-1989, female, 480 mm TL, male, 572 mm TL (32°S, 115°30'E).

Cephaloscyllium isabella. AMNH 59832, male, 370 mm TL (Sagami, Japan), USNM 320594, female, 390 mm TL (New Zealand); *C. sufflans*. SAIAB 6242, male, 800 mm TL (South Africa); *C. umbratile*. USP uncatalogued, male, 409 mm TL (Taiwan); *C. variegatum*. AMS I.43762-001, female, 670 mm TL (Australia), AMS I.24039-007, male, 235 mm TL (Australia).

Cephalurus cephalus. USNM 221527, female, 285 mm TL (15°4.30'S, 75°45'W); HUMZ 174830, male, 230 mm TL (no locality data).

Figaro boardmani. CSIRO H989-5, female, 465 mm TL (northern Australia), MZUSP 118096, male, 486 mm TL (35°55.6'S, 150°1.9'E).

Galeus antillensis. UF 77853, female, 370 mm TL, male, 385 mm TL (18°33'N, 65°25'W).

Halaelurus natalensis. SAIAB 26951, male, 400 mm TL (South Africa).

Haploblepharus edwardsii. AMNH 40988, male, 480 mm TL (6°S, 12°40'E); BMNH 1953.5.10.3, male, 720 mm TL (Cape of Good Hope, South Africa).

Holohalaelurus regani. SAIAB 25717, male, 610 mm TL (South Africa).

Parmaturus xaniurus. CAS 232152, female, 450 mm TL (California, United States).

Proscyllium habereri. CAS 57189, male, 410 mm TL (27°30'N, 121°30'E).

Poroderma africanum. SAIAB 25343, male, 920 mm TL (Cape Town, South Africa); *P. pantherinum*. SAIAB 34577, male, 640 mm TL (Cape Town, South Africa).

Schroederichthys saurisqualus. UERJ uncatalogued, female, 564 mm TL, male, 580 mm TL (no locality data), ZMH 106492, female, 577 mm TL (30°7'S, 47°58'W, 520 m depth).

Scyliorhinus boa. NSMT 30514, male, 179.9 mm TL (7°36'N, 52°26'W, 33 m depth); NSMT 30516A, male, 210.1 mm (7°33'N, 54°10'W); USNM 221532, male, 500 mm TL (11°09'N, 74°26'W); USNM 221562, female, 185 mm TL (15°36'N, 61°13'W); USNM 221563, male, 348 mm TL (12°17'N, 72°40'W); USNM 221564, male, 488 mm TL (17°17'N, 62°23'W).

Scyliorhinus cabofriensis. UERJ 1425, female, 319 mm TL (Cabo Frio, Rio de Janeiro, south-eastern Brazil); UERJ 1427, female, 446 mm TL (Cabo Frio, Rio de Janeiro, south-eastern Brazil), UERJ 1582, female, 415 mm TL (Cabo Frio, Rio de Janeiro, south-eastern Brazil); UERJ 1694, male, 412 mm TL (Cabo Frio, Rio de Janeiro, south-eastern Brazil); UERJ 1702, male, 468 mm TL (Cabo Frio, Rio de Janeiro, south-eastern Brazil).

Scyliorhinus canicula. BMNH 1860.4.22.36-37, male, 512 mm TL, male, 374.7 mm TL (Lisbon, Portugal); BMNH 1888.5.23.48, female, 673.9 mm TL (Kerrera, United Kingdom); BMNH 1983.8.3.1-4, male, 585.7 mm TL (Dale Roads, Pembrokeshire, United Kingdom); CAS 20612, female, 354 mm TL, female, 361 mm TL, male, 439 mm TL (Naples, Italy); MNHN 1997-0450, female, 575 mm TL (Pas-de-Calais, France, 50°1'N, 1°6'E); NRM 7550, female, 227.2 mm TL (37°57.2'N, 21°4.13'E), NRM 7551, male, 248.7 mm TL (37°57.2'N, 21°4.13'E); NRM 7552, male, 286.3 mm TL (37°57.2'N, 21°4.13'E); NRM 7553, female, 342.4 mm TL (37°57.2'N, 21°4.13'E); NRM 21745, female, 591.3 mm TL (Bohüslan, Sweden); NRM 46988, female, 662 mm TL (Skagerrak,B Sweden); NRM 49164, male, 677.4 mm TL (Skagerrak, Sweden); NRM 50183, male, 582.4 mm TL (Southern Bohüslan, Sweden); NRM 50450, female, 468.6 mm TL (Skagerrak, Sweden); USNM 221218, female, 334 mm TL, female, 399 mm TL, male, 388 mm TL, male, 383 mm TL (35°41'N, 5°13'W); USNM 221464, male, 345 mm TL, male, 403 mm TL (37°17'N, 10°29'E); USNM 221470, female, 438 mm TL (38°8'N, 10°23.30'E); USNM 221509, female, 317 mm TL, female, 687 mm TL, male, 434 mm TL, male, 419 mm TL (25°28'N, 06°29'E); USNM 221600, male, 459 mm TL, female, 254 mm TL, female, 189 mm TL (35°28'N, 6°31'E); USNM 221601, female, 229 mm TL, male, 247 mm TL (35°12.50'N, 6°33.30'E); USM 221602, female, 258 mm TL (35°09'N, 6°32.20'W); USNM 221603, male, 207 mm TL (35°12.50'N, 6°33.30'W); USNM 221604, male, 306 mm TL (35°12.50'N, 6°33.30'W); USNM 221605, female, 350 mm TL, female, 308 mm TL, male, 346 mm TL (35°41'N, 12°30'W); USNM 221615, female, 354 mm

TL (37°21.30'N, 10°43'E); USNM 221616, female, 367 mm TL (37°7.30'N, 10°41'E).

Scyliorhinus capensis. BMNH 1900.11.6.18, female, 898 mm TL (Cape Town, South Africa); BMNH 1935.5.2.54, female, 558.8 mm TL (Cape Town, South Africa); CAS 31455, female, 382 mm TL (Cape of Good Hope, South Africa); SAIAB 12159, female, 224 mm TL (East London, 33°S, 27°9'E); SAIAB 26440, female, 843 mm TL (35°23'6"S, 22°4'E); SAIAB 27577, male, 863 mm TL (35°37'12"S, 15°23'42"E); SAM 38774, female, 670 mm TL, male, 686 mm TL (Eastern Cape, South Africa); SAM 38775, male, (Eastern Cape, South Africa).

Scyliorhinus cervigoni. USNM 221596, female, 251 mm (10°36'S, 13°12'E); USNM 221598, male, 333 mm TL (11°25'N, 17°21'W); USNM 221599, male, 283 mm TL (10°44'N, 17°06'W); USNM 221617, female, 337 mm TL (6°31'N, 11°29'W).

Scyliorhinus comoroensis. MNHN 1984–0701, male, 457.2 mm TL (Moroni, Comoro Islands, 400 m depth); MNHN 1991–0420, male, 175 mm TL, female, 181.5 mm TL (Madagascar, 13°45.8'S, 47°38.5'E, 430–700 m depth).

Scyliorhinus duhamelii. USNM 203744, male, 399.6 mm TL (36°57'N, 10°28'E, 64–75 m depth); USNM 221645, male, 400 mm TL (42°42.48'N, 17°58.50'E).

Scyliorhinus garmani. USNM 43749, female, 267.2 mm TL (“East Indies”, probably Philippines).

Scyliorhinus haeckelii. AC.UERJ 1420, male, 365 mm TL (Cabo Frio, Rio de Janeiro, southeastern Brazil); AC.UERJ 1421, female, 412 mm TL (Cabo Frio, Rio de Janeiro, southeastern Brazil); AC.UERJ 1422, female, 379 mm TL (Cabo Frio, Rio de Janeiro, southeastern Brazil); AC.UERJ 1423, male, 478 mm TL (no locality data); UERJ 1496.1, female, 361 mm TL (Itajaí, Santa Catarina, Southern Brasil); UERJ 1496.2, female, 367 mm TL (Itajaí, Santa Catarina, Southern Brazil); UERJ 1573, female, 297 mm TL (Paraná, Southern Brazil); UERJ 1574, female, 371 mm TL (Paraná, Southern Brazil); UERJ 1689, male, 566 mm TL (Southern Brazil); UERJ 1690, female, 467 mm TL (Southern Brazil); UERJ 1691, male, 522 mm TL (Rio de Janeiro, Southern Brazil); UERJ 1695, female, 494 mm TL (Southern Brazil); UERJ 1696, female, 451 mm TL (Southern Brazil); UERJ 1697, male, 491 mm TL (Southern Brazil); UERJ 1698, male, 454 mm TL (Southern Brazil); UERJ 1704, male, 425 mm TL (Southern Brazil); UERJ 2202, male, 444 mm TL (Southern Brazil).

Scyliorhinus hesperius. CAS 65844, male, 354 mm TL (12°35'N, 82°21'W); USNM 187688, female, 288 mm TL, female, 316 mm TL (16°45'N, 81°27'W); USNM 187728, female, 338 mm TL (14°10'N, 81°55'W); USNM 187731, male, 305 mm TL (9°N, 81°23'W); USNM 188732, female, 425 mm TL (9°03'N, 81°22'W); USNM 402344, male, 290 mm TL (12°16'N, 72°40'W); USNM 405705, male, 348 mm TL (9°N, 81°23'W).

Scyliorhinus meadi. USNM 188049, male, 267 mm TL (28°21'N, 79°51'W); USNM 188050, female, 239 mm TL, male, 175 mm TL (28°31'N, 79°51'W); USNM 188051, male, 190 mm TL (29°44'N, 80°12'W); USNM 221570, male, 180 mm TL (29°1.5'N, 79°56.5'W); USNM 221571, male, 204 mm TL (29°23'N, 79°56.5'W); USNM 221594, male, 271 mm TL (24°48'N, 79°17'W).

Scyliorhinus retifer. AMNH 19453, female, 361 mm TL (United States); MCZ 125401, female, 381 mm TL (39°58'N, 70°54'W); UF 28525, female, 500 mm TL (20°43'N, 92°25.8'W); UF 36359, male, 372 mm TL (36°30'N, 74°45'W); UF 41734, female, 500 mm TL (Gulf of Mexico, 26°N); USNM 26745, male, 340 mm TL (37°26'N, 74°19'W); USNM 84501, male, 449 mm TL, male, 318 mm TL, female, 355 mm TL, female, 291 mm TL (37°03'N, 74°31.40'W); USNM 121954, male, 443 mm TL, male, 448 mm TL (Cape Henry, Virginia); USNM 157865, female, 475 mm TL (29°10'N, 88°13'W); USNM 158480, male, 428 mm TL, male, 319 mm TL, female, 297 mm TL (34°39'N, 75°05'W); USNM 187725, male, 465 mm TL, male, 415 mm TL (38°43'N, 73°08'W); USNM 188067, female, 537 mm TL, female, 374 mm TL, female, 241 mm TL (29°03.30'N, 88°28.30'W); USNM 188069, female, 451 mm TL, male, 374 mm TL (28°57.30'N, 88°39.30'W); USNM 188073, female, 298 mm TL, male, 261 mm TL, female, 287 mm TL, male, 242 mm TL (29°11'N, 88°07'W); USNM 188074, female, 513 mm TL (29°15'N, 87°45.30'W); USNM 188075, male, 440 mm TL, male, 437 mm TL (28°54'N, 88°51'W); USNM 221469, male, 410 mm TL, male, 420 mm TL (36°54'N, 74°39'W); USNM 221579, female, 200 mm TL (29°02'N, 88°34.5'W); USNM 221580, male, 252 mm TL, male, 298 mm TL (29°30'N, 87°10'W); 221593, male, 338 mm TL, male, 308 mm TL (29°58'N, 80°8.30'W); USNM 221606, female, 476 mm TL (29°25'N, 87°22'W); USNM 221644, female, 389 mm TL, female, 277 mm TL (24°23'N, 82°42'W); USNM 371557, female, 365 mm TL (27°53'N, 85°13'W); USNM 387819, male, 412 mm TL, male, 405 mm TL (38°24.10'N, 73°26.13'W).

Scyliorhinus stellaris. NRM 8989, female, 528.3 mm TL (Sicilia, Italy); NRM 8993, female, 236.3 mm TL, female, 174.6 mm TL (Nice, France); NRM 8995, male, 342.4 mm TL (Sicilia, Italy); USNM 28461, female, 317 mm TL (Livorno, Italy); USNM 34352, male, 358 mm TL (Venice, Italy); USNM 221693, female, 483 mm TL, female, 430 mm TL (45°30'N, 13°32'E).

Scyliorhinus torazame. HUMZ 117496, male, 401.6 mm TL (Shimoda, Shizuoka Prefecture, Japan); HUMZ 39459, male, 494.4 mm TL (Hakodate, Hokkaido, Japan); HUMZ 40047, male, 381.3 mm TL, male, 382 mm TL (no locality data); HUMZ 113575, female, 352.8 mm TL (Shimoda, Shizuoka Prefecture, Japan); MCZ 35309, male, 470 mm TL, male, 480 mm TL (Japan); MCZ 61163, female, 357 mm TL, male, 324 mm TL (South Korea); NSMT 66232, male, 246.1 mm TL (Sagami-nada, Tateyama, Japan); NSMT 66387, female, 297.3 mm TL, female, 289.7 mm TL (36°30.9'N, 140°59.6'E, 250 m depth); USNM 161525, female, 423 mm TL, female, 413 mm TL (Hakodate, Japan).

Scyliorhinus torrei. CAS 65845, female, 255 mm TL (23°34'N, 79°07'W); USNM 157845, male, 283 mm TL, female, 259 mm TL (22°59'N, 79°17'W); USNM 157852, male, 285 mm TL, female, 252 mm TL, male, 289 mm TL, male, 283 mm TL, male, 285 mm TL (22°55'N, 79°27'W); USNM 187685, female, 114 mm TL, male, 145 mm TL, female, 257 mm TL (23°05'N, 78°49'W); USNM 187713, female, 215 mm TL (23°34'N, 79°07'W); USNM 187940, female, 294 mm TL (28°08'N, 77°52'W); USNM 372729, male, 277 mm TL (Playa Santa, Porto Rico).

Scyliorhinus ugoi. UERJ 1426, female, 513 mm TL (Bahia, Brazil); UERJ 1722, female, 600 mm TL (Salvador, Bahia, Brazil); UERJ 1723, female, 427 mm TL (Brazil, between Pernambuco and Northern Rio de Janeiro); UERJ 1725, male, 530 mm TL (Brazil, between Southern Bahia and Northern Rio de Janeiro); UERJ 1726, female, 597 mm TL (Brazil, between Pernambuco and Northern Rio de Janeiro); UERJ 2179, male, 415 mm TL (Southern Bahia, north-eastern Brazil); USNM 221611, male, 432 mm TL (15°22'N, 61°27'W).

Appendix 2

Matrix summarising quantitative characters used in the phylogenetic study. 1, monospondylous vertebral counts; 2, diplospondylous vertebral counts; 3, upper tooth row counts; 4, lower tooth row counts; 5, intestinal valve counts. Absolute values and normalised ones (in parentheses) are given.

Terminal	**1**	**2**	**3**	**4**	**5**
Proscyllium habereri	38 (0.38)	118 (0.8)	47–62 (0.18–0.38)	49–59 (0.27–0.41)	10 (0.42)
Apristurus longicephalus	30–33(0.08–0.19)	?	35–45(0.03–0.16)	29–40(0–0.15)	15–17(0.83–1)
Asymbolus rubiginosus	?	?	61–62(0.35–0.37)	56–62(0.37–0.45)	?
Atelomycterus fasciatus	39–46(0.42–0.69)	110–115(0.67–0.75)	56–73(0.30–0.52)	50–59(0.29–0.41)	11–13(0.5–0.67)
Aulohalaelurus labiosus	45–46(0.65–0.69)	103–109(0.56–0.65)	50–70(0.22–0.48)	45–59(0.22–0.41)	16(0.92)
Cephaloscyllium isabella	45–48(0.65–0.77)	71–72(0.06–0.08)	50–70(0.22–0.48)	45–65(0.22–0.49)	?
C. sufflans	49(0.77)	75–91(0.12–0.37)	67–84(0.44–0.66)	67–87(0.52–0.79)	10(0.42)
C. umbratile	47–54(0.73–1)	110–131(0.67–1)	77–110(0.57–1.00)	71–102(0.57–1.00)	?
C. variegatum	44–47(0.61–0.73)	72–77(0.08–0.16)	68–82(0.45–0.63)	68–82(0.53–0.73)	?
Cephalurus cephalus	28–35(0–0.27)	67–71(0–0.06)	54–66(0.27–0.43)	54–68(0.34–0.53)	5–6(0–0.08)
Figaro boardmani	35–38(0.27–0.38)	105–111(0.59–0.68)	54–57(0.27–0.31)	54–62(0.34–0.45)	?
Galeus antillensis	33–39(0.19–0.42)	?	56(0.30)	52(0.31)	6–8(0.08–0.25)
Halaelurus natalensis	31–33(0.11–0.19)	92–100(0.39–0.51)	56(0.30)	47(0.25)	?
Haploblepharus edwardsii	33–40(0.19–0.46)	88–100(0.32–0.51)	66–75(0.43–0.54)	58–72(0.40–0.59)	6–7(0.08–0.17)
Holohalaelurus regani	28–33(0–0.19)	78–103(0.17–0.56)	60–70(0.35–0.48)	62–67(0.45–0.52)	7(0.17)
Parmaturus xaniurus	38–39(0.38–0.42)	71–108(0.06–0.64)	67–71(0.44–0.49)	78–82(0.67–0.73)	7–8(0.17–0.25)
Poroderma africanum	42–45(0.54–0.65)	73–92(0.07–0.39)	45–55(0.16–0.29)	42–49(0.18–0.27)	9–13(0.33–0.67)
P. pantherinum	32–46(0.15–0.69)	70–78(0.05–0.17)	45–51(0.16–0.23)	40–46(0.15–0.23)	8–13(0.25–0.67)
Schroederichthys saurisqualus	35–40(0.27–0.46)	80–129(0.20–0.96)	53–65(0.26–0.42)	41–56(0.16–0.37)	?
Scyliorhinus boa	39–42(0.42–0.54)	82–95(0.23–0.43)	39–49(0.08–0.21)	40–45(0.15–0.22)	?
S. cabofriensis	37–39(0.35–0.42)	83–85(0.25–0.28)	45–58(0.16–0.32)	44–50(0.20–0.29)	6–8(0.08–0.25)
S. canicula	35–40(0.27–0.46)	83–95(0.25–0.43)	40–61(0.09–0.36)	36–50(0.09–0.29)	10–11(0.42–0.5)
S. capensis	44–46(0.61–0.69)	78–88(0.17–0.32)	46–76(0.17–0.56)	48–85(0.26–0.77)	10–11(0.42–0.5)
S. cervigoni	40–45(0.46–0.65)	80–91(0.20–0.37)	44–58(0.14–0.32)	42–52(0.18–0.31)	?
S. comoroensis	40(0.46)	97(0.46)	50(0.22)	43(0.19)	?
S. duhamelii	35–37(0.27–0.35)	83–88(0.25–0.32)	42–48(0.04–0.19)	36–44(0.09–0.20)	8(0.25)
S. garmani	48(0.77)	83(0.25)	46(0.17)	44(0.20)	?
S. haeckelii	36–40(0.31–0.46)	81–87(0.21–0.31)	48–54(0.19–0.27)	42–53(0.18–0.33)	6–8(0.08–0.25)
S. hesperius	39–42(0.42–0.54)	85–96(0.28–0.45)	39–49(0.08–0.21)	38–46(0.12–0.23)	?
S. meadi	46–48(0.69–0.77)	84–90(0.26–0.35)	46–52(0.17–0.25)	43–50(0.19–0.29)	?
S. retifer	38–42(0.38–0.54)	84–93(0.26–0.40)	36–55(0.04–0.29)	34–50(0.07–0.29)	10–11(0.42–0.5)
S. stellaris	43–46(0.58–0.69)	87–89(0.31–0.34)	40–52(0.09–0.25)	33–50(0.05–0.29)	13–14(0.67–0.75)
S. torazame	32–37(0.15–0.35)	73–89(0.09–0.34)	50–76(0.22–0.56)	45–81(0.22–0.71)	10–11(0.42 –0.5)
S. torrei	30–35(0.08–0.27)	81–83(0.21–0.25)	33–42(0–0.04)	31–42(0.03–0.18)	6–8(0.08–0.25)
S. ugoi	38–39(0.38–0.42)	81–96(0.21–0.45)	47–56(0.18–0.30)	45–53(0.22–0.33)	6–8(0.08–0.25)

Appendix 3

Discrete morphological characters utilised in the phylogenetic analysis. Characters numbers correspond with those in the character descriptions (see text).

Terminal taxon	6–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–84
Proscyllium habereri	00000	0000000000	0?110??000	0000000001	0000010001	0010000011	?100011100	?00000001?	1000
Apristurus longicephalus	10000	1??0000000	0?00001000	1000101001	0001111121	1011000011	??1??1?010	0001000000	1110
Asymbolus rubiginosus	00000	0000000000	1000000000	0000000000	0000000000	0000000010	0000000000	0000000000	0000
Atelomycterus fasciatus	21000	1??1000000	0?00010000	0001000010	1120000000	0010000010	0000011101	?0011?0000	0000
Aulohalaelurus labiosus	00000	1??0000000	0?000?00??	???1000010	01210?????	?????0???0	0000011101	?000011?01	0000
Cephaloscyllium isabella	00010	0000110?11	0?01011010	0101000110	0110010010	001011010?	??????????	??????????	?000
C. sufflans	00010	0000110?11	0?01011010	0101000110	0110010010	0011110100	1001000101	?0101?001?	1000
C. umbratile	00010	0000110?11	0?01011010	0101000110	0110010010	001011010?	??????????	????????00	?000
C. variegatum	00010	0000110?11	0?01011010	0101000110	0110010010	001111010?	??????????	??????????	?000
Cephalurus cephalus	10100	0100000000	0?11111000	0110010000	0021001111	?010000111	??1??1?01?	?0001?001?	?110
Figaro boardmani	10000	0100000000	0?0000?100	0000100000	000001?100	00?0000010	0101011000	00001?0000	0000
Galeus antillensis	10000	0100000000	0?00001100	0000101001	0000001101	00100000?0	0101011001	?0101?1?00	1100
Halaelurus natalensis	00000	0000000000	0?00010000	0110000000	1020000000	0101000001	?100000000	0001001?00	0000
Haploblepharus edwardsii	21000	1??1000000	0?00010001	0010010000	0000001011	0010001?01	??00011011	?010000000	0000
Holohalaelurus regani	10000	0100110??0	1000001000	1010010000	1010011010	0110000010	1001100011	?1011?0000	1100
Parmaturus xaniurus	00000	0100000100	0?1110?100	0000100000	0020001111	1011000011	??00011000	0000000000	0110
Poroderma africanum	00101	0000101?00	0?0001?011	0001000110	0100010010	0000110000	0001011101	?110010001	11?1
P. pantherinum	00101	0000010000	0?0001?010	0001000110	0100010010	0000110000	0101011101	?110010001	1100
Schroederichthys saurisqualus	10110	0100000110	0?00111000	0010000110	1110110010	0100001?00	0001000100	0000000000	0000
Scyliorhinus boa	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000101	10101?0000	1000
S. cabofriensis	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001111101	?1101?0100	1000
S. canicula	21010	0011101?10	1200011010	0001000110	1110010010	0010010100	1001100101	?0101?0000	1000
S. capensis	00010	0000101?10	1200011010	0001000110	1110010010	0010010100	0001000100	?0101?0100	1010
S. cervigoni	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000101	01101?0100	1000
S. comoroensis	00010	0000101?10	11000110??	?????0????	??????????	?????????0	1001000101	?1101?0000	?010
S. duhamelii	21010	0011101?10	1200011010	0001000110	1110010010	0010010100	1001011101	?1101?001?	1000
S. garmani	20010	0000101?10	?000?10??	?????0????	?1????????	??????????	??????????	??????????	?000
S. haeckelii	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000100	01101?0100	1000
S. hesperius	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	00??00100	1?????????	?010
S. meadi	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000101	??????????	?010
S. retifer	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	0001000100	10101?0000	1001
S. stellaris	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000101	?1101?0000	1000
S. torazame	00010	0000101?10	1200011010	0001000110	1110010010	0010010100	1001011101	?0101?0000	1010
S. torrei	00010	0000101?10	1200011010	0001000110	1110010010	0010010100	1001000100	01101?0000	1010
S. ugoi	00010	0000101?10	1100011010	0001000110	1110010010	0010010100	1001000100	01101?0100	1000

Appendix 4

List of non-ambiguous synapomorphies of clades and terminal taxa based on the three most-parsimonious cladograms obtained. Synapomorphies followed by "!" appear only in some trees.

Clade 1
Char. 2: 0.52–0.66 > 0.28–0.31.
Char. 29: 0 > 1.
Char. 38: 0 > 1.
Char. 56: 0 > 1.
Char. 59: 0 > 1.
Char. 64: 0 > 1.
Char. 73: 0 > 1.
Char. 81: 0 > 1.
Clade 2
Char. 8: 0 > 1.
Char. 10: 0 > 1.
Char. 72: 0 > 1.
Char. 80: 0 > 1.
Char. 82: 0 > 1.
Clade 3
Char. 9: 0 > 1.
Char. 19: 0 > 1.
Char. 53: 0 > 1.
Char. 58: 0 > 1.
Char. 66: 1 > 0.
Char. 67: 1 > 0.
Char. 75: 0 > 1.
Clade 4
Char. 1: 0.54–0.65 > 0.73.
Char. 3: 0.23–0.35 > 0.45–0.48.
Char. 4: 0.23–0.37 > 0.49–0.53.
Char. 16: 0 > 1.
Char. 20: 0 > 1.
Char. 24: 0 > 1.

Char. 32: 0 > 1.
Clade 5
Char. 2: 0.28–0.31 > 0.13–0.17.
Clade 6
Char. 54: 0 > 1.
Clade 7
Char. 3: 0.23–0.35 > 0.21–0.22.
Char. 4: 0.23–0.37 > 0.22.
Char. 17: 0 > 1.
Char. 21: 1 > 0.
Char. 41: 0 > 1.
Clade 8
Char. 70: 1 > 0.
Char. 71: 0 > 1.
Clade 9
Char. 72: 0 > 1.
Clade 10
Char. 1: 0.54–0.58 > 0.42–0.46!
Char. 5: 0.42 > 0.25!
Char. 78: 0 > 1.
Clade 11
Char. 70: 1 > 0.
Clade 12
Char. 83: 0 > 1.
Clade 13
Char. 22: 1 > 2.
Clade 14
Char. 72: 1 > 0.
Clade 15
Char. 66: 0 > 1.
Char. 67: 0 > 1.
Clade 16
Char. 6: 0 > 2.
Char. 83: 1 > 0.
Clade 17
Char. 7: 0 > 1
Char. 13: 0 > 1.
Char. 14: 0 > 1.
C. isabella
Char. 2: 0.13–0.17 > 0.06–0.08.
C. sufflans
Char. 1: 0.73 > 0.81.
C. umbratile
Char. 2: 0.28–0.31 > 0.67–1.00.
Char. 3: 0.45–0.48 > 0.57–1.00.
Char. 4: 0.49–0.53 > 0.58–1.00.
C. variegatum
No autapomorphies.
P. africanum
Char. 17: 0 > 1.
Char. 30: 0 > 1.
Char. 84: 0 > 1.
P. pantherinum
Char. 62: 0 > 1.
S. boa
No autapomorphies.
S. cabofriensis
No autapomorphies.
S. canicula
Char. 65: 0 > 1.
S. capensis
Char. 1: 0.35–0.54 > 0.62–0.69.
Char. 4: 0.21–0.22 > 0.26–0.77.
Char. 65: 0 > 1.
Char. 78: 0 > 1.
S. cervigoni
Char. 61: 1 > 0.
S. comoroensis
Char. 3: 0.28–0.31 > 0.47.
Char. 79: 0 > 1.
S. duhamelii
Char. 5: 0.42 > 0.25.
Char. 72: 0 > 1.
S. garmani
Char. 1: 0.35–0.54 > 0.77.
S. haeckelii
No autapomorphies.
S. hesperius
Char. 83: 0 > 1.
S. meadi
Char. 1: 0.46–0.54 > 0.69–0.77.
S. retifer
Char. 84: 0 > 1.
S. stellaris
Char. 1: 0.46–0.54 > 0.58–0.69!
Char. 5: 0.42 > 0.67–0.75.
S. torazame
No autapomorphies.
S. torrei
Char. 1: 0.35–0.54 > 0.08–0.27.
Char. 3: 0.17–0.22 > 0.00–0.12.
Char. 4: 0.19–0.22 > 0.01–0.18.
Char. 5: 0.42 > 0.08–0.25.
Char. 70: 1 > 0.
S. ugoi
No autapomorphies.

Appendix 5

List of character transformation, based on the three most-parsimonious cladograms obtained.

Char. 1 (L = 2,345)
Clade 4: 0.54–0.65 > 0.73.
Clade 7: 0.54–0.65 > 0.46–0.58.
P. pantherinum: 0.54–0.65 > 0.15–0.69.
Clade 8: 0.46–0.58 > 0.46–0.54.
C. umbratile: 0.73 > 0.73–1.00.
Clade 10: 0.46–0.58 > 0.42–0.46.
C. isabella: 0.73 > 0.65–0.77.

S. boa: 0.46–0.54 > 0.42–0.54.
S. cabofriensis: 0.42–0.46 > 0.35–0.42.
S. hesperius: 0.46–0.54 > 0.42–0.54.
S. retifer: 0.46–0.54 > 0.38–0.54.
S. stellaris: 0.46–0.58 > 0.58–0.69.
Clade 13: 0.46–0.58 > 0.35–0.54.
C. sufflans: 0.73 > 0.81.
C. variegatum: 0.73 > 0.62–0.73.
S. capensis: 0.35–0.54 > 0.15–0.35.
S. cervigoni: 0.42–0.46 > 0.46–0.65.
S. comoroensis: 0.46–0.58 > 0.46.
S. garmani: 0.35–0.54 > 0.77.
S. haeckelii: 0.42–0.46 > 0.31–0.46.
S. meadi: 0.46–0.58 > 0.69–0.77.
S. torazame: 0.35–0.54 > 0.15–0.35.
S. torrei: 0.35–0.54 > 0.08–0.27.
S. ugoi: 0.42–0.46 > 0.38–0.42.
Clade 17: 0.35–0.54 > 0.35–0.46.
S. canicula: 0.35–0.46 > 0.27–0.46.
S. duhamelii: 0.35–0.46 > 0.27–0.35.
Char. 2 (L = 1,862)
Clade 1: 0.52–0.66 > 0.28–0.31.
Clade 2: 0.28–0.31 > 0.17–0.31.
P. africanum: 0.17–0.31 > 0.09–0.39.
P. pantherinum: 0.17–0.31 > 0.05–0.17.
Clade 5: 0.28–0.31 > 0.13–0.17.
C. isabella: 0.12–0.16 > 0.23–0.43.
C. umbratile: 0.28–0.31 > 0.67–1.00.
S. boa: 0.28–0.31 > 0.23–0.44.
S. cabofriensis: 0.28–0.31 > 0.25–0.28.
S. hesperius: 0.28–0.31 > 0.28–0.45.
S. retifer: 0.28–0.31 > 0.27–0.4.
S. stellaris: 0.28–0.31 > 0.31–0.34.
Clade 13: 0.28–0.31 > 0.25–0.31.
C. sufflans: 0.13–0.17 > 0.13–0.38.
C. variegatum: 0.13–0.17 > 0.08–0.17.
S. canicula: 0.25 > 0.25–0.43.
S. capensis: 0.25 > 0.17–0.32.
S. cervigoni: 0.28–0.31 > 0.20–0.37.
S. comoroensis: 0.28–0.31 > 0.46.
S. duhamelii: 0.25–0.31 > 0.25–0.33.
S. haeckelii: 0.28–0.31 > 0.22–0.31.
S. meadi: 0.28–0.31 > 0.27–0.36.
S. torazame: 0.25–0.31 > 0.09–0.34.
S. torrei: 0.25 > 0.21–0.25.
S. ugoi: 0.28–0.31 > 0.22–0.45.
Char. 3 (L=1,205)
Clade 1: 0.30–0.35 > 0.23–0.35.
Clade 2: 0.23–0.35 > 0.23–0.29.
Clade 4: 0.23–0.35 > 0.45–0.48.
P. africanum: 0.23–0.29 > 0.16–0.23.
P. pantherinum: 0.23–0.29 > 0.16–0.29.
Clade 7: 0.23–0.35 > 0.21–0.22.
Clade 8: 0.21–0.22 > 0.21.
C. isabella: 0.455–0.48 > 0.22–0.48.
C. umbratile: 0.45–0.48 > 0.57–1.00.
S. boa: 0.21 > 0.08–0.21.
S. cabofriensis: 0.21–0.22 > 0.16–0.32.
S. hesperius: 0.21 > 0.08–0.21.
S. retifer: 0.21 > 0.04–0.29.
S. stellaris: 0.21–0.22 > 0.09–0.25.
Clade 13: 0.21–0.22 > 0.17–0.22.
C. sufflans: 0.45–0.48 > 0.44–0.66.
C. variegatum: 0.45–0.48 > 0.45–0.64.
S. capensis: 0.17–0.22 > 0.17–0.56.
S. cervigoni: 0.21–0.22 > 0.14–0.32.
S. comoroensis: 0.21–0.22 > 0.22.
S. haeckelii: 0.21–0.22 > 0.19–0.27.
S. meadi: 0.21–0.22 > 0.17–0.25.
S. torazame: 0.17–0.22 > 0.22–0.56.
S. torrei: 0.17–0.22 > 0.22–0.56.
S. ugoi: 0.22–0.25 > 0.18–0.30.
Clade 16: 0.17–0.22 > 0.17–0.19.
S. canicula: 0.17 – 0.19 > 0.09–0.36.
S. duhamelii: 0.17–0.19 > 0.12–0.19.
S. garmani: 0.17–0.19 > 0.17.
Char. 4 (L=1,464)
Clade 1: 0.29–0.37 > 0.23–0.37.
Clade 2: 0.23–0.37 > 0.23–0.27.
Clade 7: 0.23–0.37 > 0.22.
Clade 4: 0.23–0.37 > 0.49–0.53.
P. africanum: 0.23–0.27 < 0.18–0.27.
P. pantherinum: 0.23–0.27 > 0.15–0.23.
Clade 6: 0.49–0.53 > 0.52–0.53.
C. isabella: 0.49–0.53 > 0.22–0.49.
C. sufflans: 0.52–0.53 > 0.52–0.79.
C. variegatum: 0.52–0.53 > 0.53–0.73.
S. cabofriensis: 0.22–0.25 > 0.21–0.29.
S. cervigoni: 0.22 > 0.18–0.32.
S. comoroensis: 0.19–0.22 > 0.19.
S. haeckelii: 0.22 > 0.18–0.33.
S. meadi: 0.19–0.22 > 0.19–0.29.
S. torrei: 0.19–0.22 > 0.10–0.18.
S. ugoi: 0.22 > 0.22–0.33.
Clade 12: 0.22–0.25 > 0.21.
S. boa: 0.21 > 0.08–0.21.
S. hesperius: 0.21 > 0.08–0.21.
S. retifer: 0.21 > 0.04–0.29.
S. stellaris: 0.22–0.25 > 0.09–0.25.
Clade 14: 0.19–0.22 > 0.21–0.22.
S. capensis: 0.20–0.22 > 0.26–0.77.
S. torazame: 0.20–0.22 > 0.22–0.71.
Clade 16: 0.20–0.22 > 0.21.
S. canicula: 0.21 > 0.10–0.29.
S. duhamelii: 0.20 > 0.10–0.21.
Char. 5 (L=2,251)
P. africanum: 0.42 > 0.33–0.67.
P. pantherinum: 0.42 > 0.25–0.67.
C. umbratile: 0.42 > ?
Clade 10: 0.42 > 0.25.
Clade 12: 0.42 > 0.25–0.42.
S. boa: 0.42 > ?
S. hesperius: 0.42 > ?
S. retifer: 0.42 > 0.42–0.50.
S. stellaris: 0.42 > 0.67–0.75.
C. isabella: 0.42 > ?

S. cabofriensis: 0.25 > 0.8–0.25.
S. meadi: 0.25–0.42 > ?
S. comoroensis: 0.25–0.42 > ?
C. variegatum: 0.42 > ?
S. ugoi: 0.25 > 0.08–0.25.
S. haeckelii: 0.25 > 0.08–0.25.
S. cervigoni: 0.25 > ?
S. torrei: 0.25–0.42 > 0.08–0.25.
Clade 14: 0.25–0.42 > 0.42.
S. canicula: 0.42 > 0.42–0.50.
S. capensis: 0.42 > 0.42–0.50.
S. duhamelii 0.42 > 0.25.
S. garmani: 0.42 > ?
S. torazame: 0.42 > 0.42–0.50.
Char. 6 (L = 8)
Clade 16: 0 > 2.
Char. 7 (L = 3)
Clade 17: 0 > 1.
Char. 8 (L = 3)
Clade 2: 0 > 1.
Char. 9 (L = 2)
Clade 3: 0 > 1.
Char. 10 (L = 1)
Clade 2: 0 > 1.
Char. 11 (L = 3)
No transformation in Scyliorhininae.
Char. 12 (L = 2)
No transformation in Scyliorhininae.
Char. 13 (L = 1)
Clade 17: 1 > 0.
Char. 14 (L = 3).
Clade 17: 0 > 1.
Char. 15 (L = 3)
Clade 1: 0 > 01.
Clade 3: 01 > 1.
P. africanum: 01 > 1.
P. pantherinum: 01 > 0.
Char. 16 (L =2)
Clade 4: 0 > 1.
Char. 17 (L = 2)
Clade 7: 0 > 1.
P. africanum: 0 > 1.
Char. 18 (L = 3)
Clade 1: 0 > 01.
P. pantherinum: 01 > 1.
Char. 19 (L = 2)
Clade 3: 0 > 1.
Char. 20 (L = 1)
Clade 4: 0 > 1.
Char. 21 (L = 3)
Clade 7: 1 > 0.
Char. 22 (L = 2)
Clade 7: 01 > 1.
Clade 13: 1 > 2.
Char. 23 (L = 1)
No transformation in Scyliorhininae.
Char. 24 (L = 2)
Clade 4: 0 > 1.
Char. 25 (L = 2)
No transformation in Scyliorhininae.
Char. 26 (L = 3)
No transformation in Scyliorhininae.
Char. 27 (L = 1)
Clade 1: 0 > 01.
Clade 3: 01 > 1.
Char. 28 (L = 2)
No transformation in Scyliorhininae.
Char. 29 (L = 2)
Clade 1: 0 > 1.
Char. 30 (L = 2)
P. africanum: 0 > 1.
Char. 31 (L = 2)
No transformation in Scyliorhininae.
Char. 32 (L = 3)
Clade 4: 0 > 1.
Char. 33 (L = 4)
No transformation in Scyliorhininae.
Char. 34 (L = 1)
No transformation in Scyliorhininae.
Char. 35 (L = 2)
No transformation in Scyliorhininae.
Char. 36 (L = 3)
No transformation in Scyliorhininae.
Char. 37 (L = 2)
No transformation in Scyliorhininae.
Char. 38 (L = 2)
Clade 1: 01 > 1.
Char. 39 (L = 1)
No transformation in Scyliorhininae.
Char. 40 (L = 2)
No transformation in Scyliorhininae.
Char. 41 (L = 5)
Clade 7: 01 > 1.
Char. 42 (L = 1)
No transformation in Scyliorhininae.
Char. 43 (L = 7)
Clade 2: 01 > 0.
Clade 3: 01 > 1.
Char. 44 (L = 3)
No transformation in Scyliorhininae.
Char. 45 (L = 2)
No transformation in Scyliorhininae.
Char. 46 (L = 5)
Clade 1: 01 > 1.
Char. 47 (L = 1)
No transformation in Scyliorhininae.
Char. 48 (L = 1)
No transformation in Scyliorhininae.
Char. 49 (L = 4)
Clade 1: 0 > 1.
Char. 50 (L = 2)
No transformation in Scyliorhininae.
Char. 51 (L = 1)
No transformation in Scyliorhininae.
Char. 52 (L = 3)
No transformation in Scyliorhininae.

Char. 53 (L = 2)
Clade 3: 0 > 1.
Char. 54 (L = 4)
Clade 6: 0 > 1.
Char. 55 (L = 2)
Clade 1: 0 > 01.
Clade 2: 01 > 1.
Clade 4: 01 > 1.
Clade 7: 01 > 0.
Char. 56 (L = 1)
Clade 1: 0 > 1.
Char. 57 (L = 2)
No transformation in Scyliorhininae.
Char. 58 (L = 2)
Clade 3: 0 > 1.
Char. 59 (L = 4)
Clade 1: 01 > 1.
Char. 60 (L = 3)
No transformation in Scyliorhininae.
Char. 61 (L = 4)
Clade 3: 0 > 01.
Clade 8: 01 > 0.
Clade 9: 01 > 1.
Char. 62 (L = 3)
P. pantherinum: 0 > 1.
Char. 63 (L = 2)
No transformation in Scyliorhininae.
Char. 64 (L = 3)
Clade 1: 0 > 1.
Char. 65 (L = 3)
S. canicula: 0 > 1.
S. capensis: 0 > 1.
Char. 66 (L = 4)
Clade 2: 01 > 1.
Clade 3: 01 > 0.
Clade 15: 0 > 1.
Char. 67 (L = 4)
Clade 3: 01 > 0.
Clade 15: 0 > 1.
Char. 68 (L = 1)
No transformation in Scyliorhininae.
Char. 69 (L = 4)
No transformation in Scyliorhininae.
Char. 70 (L = 7)
Clade 8: 1 > 0.
Clade 11: 1 > 0.
S. torrei: 1 > 0.
Char. 71 (L = 1)
Clade 8: 0 > 1.
Char. 72 (L = 5)
Clade 2: 0 > 1.
Clade 9: 0 > 1.
Clade 14: 1 > 0.
S. duhamelii: 0 > 1.
Char. 73 (L = 3)
Clade 1: 0 > 1.
Char. 74 (L = 4)
No transformation in Scyliorhininae.
Char. 75 (L = 5)
Clade 3: 0 > 1.
Char. 76 (L = 1)
No transformation in Scyliorhininae.
Char. 77 (L = 3)
No transformation in Scyliorhininae.
Char. 78 (L = 2)
Clade 10: 0 > 1.
S. capensis: 0 > 1.
Char. 79 (L = 3)
Clade 4: 0 > 01.
S. comoroensis: 0 > 1.
C. sufflans: 01 > 1.
Char. 80 (L = 2)
Clade 2: 0 > 1.
Char. 81 (L = 4)
Clade 1: 0 > 1.
Char. 82 (L = 4)
Clade 2: 0 > 1.
Char. 83 (L = 4)
Clade 12: 0 > 1.
Clade 16: 1 > 0.
Char. 84 (L = 2)
P. africanum: 0 > 1.
S. retifer: 0 > 1.

Zeitschrift/Journal: Zoosystematics and Evolution

Jahr/Year: 2020

Band/Volume: 96

Autor(en)/Author(s): Soares Karla D. A., Carvalho Marcelo R. de

Artikel/Article: Phylogenetic relationship of catshark species of the genus Scyliorhinus (Chondrichthyes, Carcharhiniformes, Scyliorhinidae) based on comparative morphology 345-395