Systematic implications of the caudal fin skeletal anatomy in ground sharks, order Carcharhiniformes (Chondrichthyes: Elasmobranchii)

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Sharks typically have a heterocercal tail, with both epaxial and hypaxial skeletal elements. The epaxial elements are composed of supraneural spines and neural arches (basidorsals and interdorsals); the hypaxial elements are basiventrals (forming the haemal arches) and haemal spines, as well as a series of prehypochordal cartilages found only in *Galeocerdo*. The tail of carcharhiniform sharks, except Scyliorhinidae, can be divided into anterior and posterior diplospondylic caudal regions. The anterior diplospondylic caudal region is characterized by haemal spines detached from basiventrals. The posterior diplospondylic caudal region has all haemal spines continuous with the basiventrals. In carcharhiniform sharks, the caudal fin skeleton can be divided into four main morphological types: scyliorhinoid (Scyliorhinidae), triakoid (Triakidae, *Chaenogaleus* and *Paragaleus*), carcharhinoid (*Hemipristis*, *Hemigaleus*, Carcharhinidae, *Sphyrna tiburo* and *Sphyrna tudes*) and eusphyrnoid (*Eusphyra*, *Sphyrna lewini* and *Sphyrna zygaena*). The carcharhinoid caudal fin type supports the monophyly of the clade Carcharhinidae and Sphyrnidae and is present in the hammerhead sharks with a relatively small cephalofoil that are phylogenetically basal within sphyrnids. The eusphyrnoid caudal fin type is the more derived pattern for Carcharhiniformes.

ADDITIONAL KEYWORDS: anatomy – caudal skeleton – morphological comparison.

INTRODUCTION

Carcharhiniformes is the most diverse shark order, with ~300 species placed in eight families (Compagno, 1988; Compagno, Dando & Fowler, 2005; Weigmann, 2016, 2017). Carcharhiniforms, popularly known as ground sharks, are considered to form a monophyletic group, but although there has been extensive research on the relationships within the order, systematic problems persist (Compagno, 1988; Shirai, 1992, 1996; Naylor *et al.*, 2012). The family Scyliorhinidae, for example, has been considered monophyletic and the most primitive carcharhiniform subgroup (White, 1937; Nakaya, 1975; Compagno, 1988), but divided into distict paraphyletic lineages interspersed among other ground shark clades (Iglésias, Lecointre & Sellos, 2005; Human *et al.* 2006; Naylor *et al.*, 2012). Compagno (1970, 1973, 1977, 1988) discussed the difficulty in separating the families Triakidae and Carcharhinidae and considered triakids as intermediates between the basal families Scyliorhinidae and Proscyllidae and the higher clade of carcharhiniforms composed of the families Hemigaleidae, Carcharhinidae and Sphyrnidae.

Carcharhinidae was supported as monophyletic by Compagno (1988), but the unique reproductive biology of *Galeocerdo* suggests that the tiger shark does not belong in this family (López *et al.*, 2006). Furthermore, molecular phylogenies have placed *Galeocerdo* as the sister group to a clade comprising the carcharhinids and hammerhead sharks (López *et al.*, 2006; Naylor *et al.*, 2012). The phylogenetic relationships among hammerhead shark species are still unclear and, according to

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Compagno (1988), the pelagic species (*Sphyrna mokarran*, *Sphyrna lewini*, *Sphyrna zygaena* and *Eusphyra*) are more derived within Sphyrnidae, whereas many authors (Gilbert, 1967; Martin, 1993; Cavalcanti, 2007; Naylor *et al.*, 2012) consider the pelagic hammerhead sharks more basal compared with demersal species with relatively smaller cephalofoils (*Sphyrna tiburo*, *Sphyrna media*, *Sphyrna corona* and *Sphyrna tudes*).

Sharks have an asymmetrical caudal fin commonly referred to as heterocercal, in which the dorsal lobe is internally supported by the vertebral column or notochord and is much larger than the ventral lobe. The term 'heterocercal' was proposed by Agassiz (1833), and the heterocercal caudal fin is believed to be primitive for sharks and ray-finned fishes (Moy-Thomas & Miles, 1971; Thomson, 1976; Lauder, 2000).

The vertebral column has been divided previously by Springer & Garrick (1964) into precaudal and caudal regions, demarcating the caudal fin origin from an internal anatomical standpoint. Compagno (1970, 1988) divided the posterior vertebral column into monospondylic precaudal, diplospondylic precaudal and diplospondylic caudal centra. The diplospondylic condition in the vertebral column was previously described by Ridewood (1899).

The biomechanical implications of a heterocercal tail and whether it delivers a symmetrical or asymmetrical thrust have been discussed in detail (e.g. Ferry & Lauder, 1996; Wilga & Lauder, 2002, 2004; Maia, Wilga & Lauder, 2012). However, anatomical studies of the caudal fin skeleton and its systematic patterns among elasmobranch lineages are less common, even though many morphological studies on the caudal fin skeleton of actinopterygians have been undertaken (e.g. Agassiz, 1833; Garman, 1913; Monod, 1968; Schultze & Arratia, 1986, 1988; Arratia, 1991).

Little & Bemis (2004) conduced morphological comparisons of the shark caudal skeleton. They found anatomical variations among taxa and that there is great phylogenetic potential in characters of the caudal fin skeleton. The aim of the present study was to describe the carcharhiniform shark caudal skeleton to improve our understanding of its morphology and systematic significance, thereby further elucidating the evolution of and intrarelationships between ground sharks (Carcharhiniformes).

MATERIAL AND METHODS

Gomes & Ficher (1993) and Little & Bemis (2004) consider the origin of the caudal fin to be at the first vertebral centrum that bears a haemal spine supporting the ventral caudal lobe. The caudal fin skeletal terminology used herein is based on Goodrich (1909, 1930), Shirai (1992), Gomes & Ficher (1993), Grande & Bemis (1998), Bemis & Grande (1999) and Little & Bemis (2004).

The dried skeletal caudal components were prepared with dermestid beetles or placed in hot water (at ~60 °C) with a tablespoon of potassium carbonate (K_2CO_3) to soften the skin and muscle tissue. Radiographs were taken at the Hospital Veterinário da Faculdade de Medicina Veterinária e Zootecnia da Universidade de São Paulo and analysed using Osirix. Radiographs provided by the Division of Fishes of the Smithsonian Institution (USNM) were also analysed. The material examined is from the following institutions: Universidade do Estado do Rio de Janeiro (AC. UERJ, anatomical collection; UERJ, ichthyological collection), Rio de Janeiro; Museu Nacional (MNRJ), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; American Museum of Natural History (AMNH), New York; National Museum of Marine Biology and Aquarium (NMMBP), Pingtung, Taiwan; and National Museum of Natural History, Smithsonian Institution (USNM), Washington, DC.

The figures are schematic and show the left side of the caudal fin. Skeletal structures are coloured for easy identification following Little & Bemis (2004). The material examined is listed in the Appendix. The cladograms were built with MESQUITE version 3.02 (Maddison & Maddison, 2011), in which the caudal skeletal characters uncovered in our study were mapped onto existing morphological (Shirai, 1996) and molecular (Naylor *et al.*, 2012) phylogenies. Character optimizations were carried out using the parsimony and unordered character options in MESQUITE.

RESULTS

GENERAL ANATOMY OF THE CAUDAL FIN OF SHARKS

The caudal fin skeleton of sharks is composed of epaxial and hypaxial elements. The epaxial elements are basidorsal, interdorsal and supraneural cartilages. The hypaxial elements comprise basiventral cartilages, haemal spines and prehypochordal cartilages (present only in the tiger shark, *Galeocerdo cuvier*). The basidorsal cartilages are above the vertebral centrum and the interdorsals are between each vertebra. The basidorsal and interdorsal cartilages are joined and form a neural arch where the caudal nerve extends towards the posterior tip of the caudal fin. Above the neural arches, on the upper margin of the dorsal lobe of the caudal fin, there is a series of flattened supraneural cartilages. The paired basiventral cartilages are situated below the vertebral centra and are joined distally to form the haemal arches, which enclose the caudal vein and artery almost to the posterior extremity of the caudal fin. The haemal spines are continuous or detached from the basiventral cartilages and can be divided into anterior

Table 1. Counts of vertebral centra

Species	ACD	PCD	Total
Atelomycterus marmoratus NMNBP 15349	–	–	55
Schroederichthys saurisqualus AC. UERJ 1285.1	–	–	51
Schroederichthys saurisqualus AC. UERJ 1285. 2	–	–	55
Galeus mincaronei AC. UERJ 1436	–	–	68
Apristurus parvipinnis UERJ 2056	–	–	71
Scyliorhinus haeckelii AC. UERJ 1420	–	–	43
Scyliorhinus haeckelii AC. UERJ 1423	–	–	51
Scyliorhinus haeckelii UERJ 1690	–	–	48
Scyliorhinus haeckelii UERJ 1496.2	–	–	52
Triakis semifasciata UERJ 1610.1	7	51	58
Triakis semifasciata UERJ uncatalogued	7	55	62
Mustelus canis UERJ 1678	7	55	62
Mustelus canis UERJ 1821	6	54	60
Mustelus schmitti UERJ 364	6	47	53
Galeorhinus galeus UERJ 291	6	49	55
Paragaleus tengi NMNBP 6452	8	48	56
Hemigaleus microstoma NMMBP uncatalogued	7	65	72
Chaenogaleus macrostoma NMBP 6414	7	56	63
Hemipristis elongata MZUSP uncatalogued	6	86	92
Galeocerdo cuvier UERJ 2184	8	111	119
Galeocerdo cuvier UERJ 2214	8	111	119
Isogomphodon oxyrhynchus UERJ 2215	7	80	87
Carcharhinus plumbeus UERJ 653	8	89	97
Carcharhinus melanopterus UERJ 2216	9	82	91
Carcharhinus brevipinna UERJ 2022	5	85	90
Carcharhinus acronotus UERJ 1117	6	84	90
Carcharhinus signatus UERJ 1680	7	82	89
Carcharhinus porosus UERJ 1124.3	4	62	66
Carcharhinus porosus UERJ 1124.5	7	68	75
Carcharhinus longimanus UERJ 1606	8	104	112
Prionace glauca UERJ 1866.1	8	99	107
Prionace glauca UERJ uncatalogued	7	92	99
Negaprion brevirostris MNRJ 16589	9	76	85
Rhizoprionodon lalandii AC. UERJ 285	8	72	80
Rhizoprionodon lalandii AC. UERJ 546	8	70	78
Rhizoprionodon porosus AC. UERJ 332	7	74	81
Rhizoprionodon porosus AC. UERJ 486	10	72	82
Rhizoprionodon porosus AC. UERJ 487	6	73	79
Rhizoprionodon porosus UERJ 371	7	75	82
Loxodon macrorhinus NMMBP uncatalogued	9	66	75
Sphyrna tiburo UERJ uncatalogued	5	79	84
Sphyrna tudes UERJ 1121.4	8	84	92
Sphyrna zygaena UERJ 1922	27	81	108
Sphyrna zygaena UERJ 2218	30	75	105
Sphyrna lewini AC. UERJ 915	25	87	112
Sphyrna lewini AC. UERJ 1463	29	77	106
Sphyrna lewini UERJ 2217	29	80	109
Eusphyra blochii CAS 88058	22	46	68
Eusphyra blochii USNM 195846	12	56	68
Eusphyra blochii USNM 197512	16	64	70

ACD, Anterior caudal diplospondylic region; PCD, Posterior caudal diplospondylic region.

and posterior diplospondylic caudal regions. The anterior diplospondylic caudal region comprises the haemal spines detached from basiventral cartilages, whereas the posterior diplospondylic caudal region is composed of haemal spines continuous to haemal arches. At the terminal tip of the caudal fin skeleton there are reduced haemal spines and no basiventral cartilages.

FAMILY SCYLIORHINIDAE

Externally, the scyliorhinid tail has a low ventral lobe, sometimes almost absent, and a triangular terminal lobe. Anterior to the caudal fin skeleton of *Scyliorhinus* and *Apristurus* there is a large fragmented plate, almost twice the usual basiventral length. The caudal fin skeleton of Scyliorhinidae has 43–71 vertebral centra (VC) (Table 1). In all examined species, the basidorsal and interdorsal cartilages are truncated, and most supraneural spines are slender and elongated (Figs 1, 2). The caudal fin skeletons of *Atelomycterus*, *Schroederichthys*, *Galeus*, *Apristurus* and *Scyliorhinus* are not divided into anterior and posterior diplospondylic regions (Table 2). In general, the haemal spines are flattened and stout (Figs 1, 2). The anteriormost spines can be fused together in *Apristurus* and *Scyliorhinus* (Figs 1, 2) and are slender in *Schroederichthys* and *Galeus*.

FAMILY TRIAKIDAE

The caudal fin has a distinct ventral lobe (however, almost absent in *Triakis*) and a large terminal dorsal lobe, especially in *Galeorhinus* (almost one-half of the entire caudal fin length) (Figs 3, 4). Preceding the caudal fin skeleton is a thin cartilaginous plate situated distally to the haemal arch (arrow in Figs 3, 4A). The caudal fin skeleton of examined triakids has ~53–62 VC (Table 1), the basidorsal and interdorsal cartilages are truncated, and the supraneural spines are elongated, curved and terminally tapering. The caudal fin skeletons of *Mustelus*, *Triakis* and *Galeorhinus* are divided into anterior and posterior diplospondylic caudal regions (Table 2). The anterior diplospondylic caudal region has six to seven VC (Table 1). The basiventral cartilages in this region are pentagonal in *Mustelus* and *Triakis* (Fig. 3) and have clear anterior apophyses (anterior prominences) in *Galeorhinus* (arrow in Fig. 4B). The first haemal spines are somewhat anteriorly concave. The haemal spines are slightly more slender in *Galeorhinus* than in *Mustelus* and *Triakis*. In the posterior diplospondylic caudal region, most of the haemal spines are anteriorly convex. At the posterior extremity of the caudal fin, in all examined genera of Triakidae, haemal spines are reduced and basiventral cartilages absent.
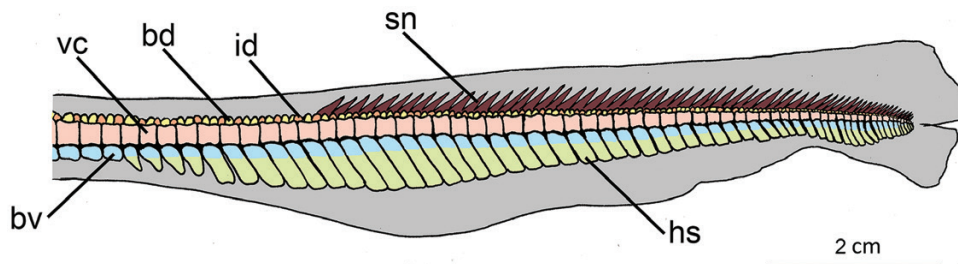
Figure 1. Left side of the caudal fin of *Schroederichthys saurisqualus* (UERJ 1285.1). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).
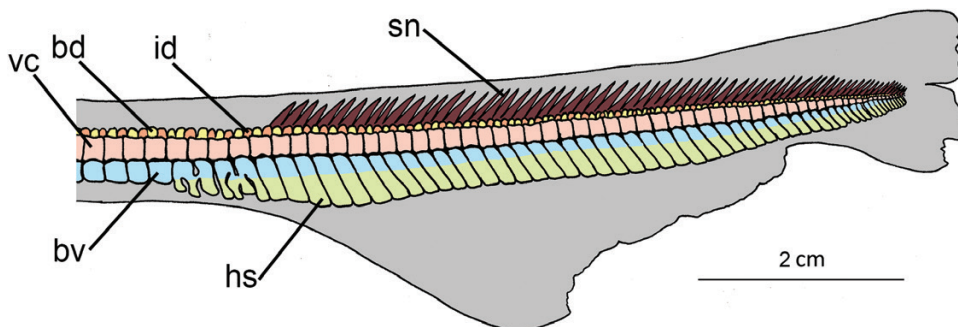
Figure 2. Left side of the caudal fin of *Scyliorhinus haeckelii* (AC. UERJ 1690). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).

Table 2. Anatomic regions of carcharhiniforms caudal fin

	DC	ACD	PCD	Haemal spine with >-shaped
Atelomycterus	X	–	–	–
Schroederichthys	X	–	–	–
Galeus	X	–	–	–
Apristurus	X	–	–	–
Scyliorhinus	X	–	–	–
Triakis	–	X	X	–
Mustelus	–	X	X	–
Galeorhinus	–	X	X	–
Paragaleus		X	X	X
Hemigaeus		X	X	X
Chaenogaleus		X	X	X
Hemipristis	–	X	X	X
Galeocerdo	–	X	X	X
Isogomphodon	–	X	X	X
Carcharhinus	–	X	X	X
Prionace	–	X	X	X
Negaprion	–	X	X	X
Rhizoprionodon	–	X	X	X
Loxodon	–	X	X	X
Sphyrna tiburo	–	X	X	X
Sphyrna tudes	–	X	X	X
Sphyrna zygaena	–	X	X	X
Sphyrna lewini	–	X	X	X
Eusphyra blochii	–	X	X	X

ACD, anterior caudal diplospondylic region; DC, diplospondylic caudal region; PCD, posterior caudal diplospondylic region.

FAMILY HEMIGALEIDAE

Externally, the hemigaleid caudal fin has a large dorsal lobe, elongated terminal lobe and falcate ventral lobe. The thin plate preceding the caudal fin skeleton is absent in Hemigaleidae (arrow in Figs 5A, 6A). The caudal fin skeleton of the examined species of Hemigaleidae has 56–92 VC (Table 1), rectangular basidorsal and interdorsal cartilages and elongated, slightly curved and tapering supraneural spines. The caudal fin skeletons of *Paragaleus*, *Chaenogaleus*, *Hemigaleus* and *Hemipristis* are divided into anterior and posterior diplospondylic caudal regions (Table 2). The anterior diplospondylic caudal region comprises six to eight VC (Table 1) and has basiventral cartilages with the anterior apophysis as a slight prominence (arrow in Figs 5B, 6B) and haemal spines slightly concave anteriorly. The posterior diplospondylic caudal region of *Paragaleus* and *Chaenogaleus* has all haemal spines anteriorly convex (Fig. 5A), whereas in *Hemigaleus* and *Hemipristis*, most haemal spines are weakly '>' shaped (Fig. 6A). In the terminal lobe, the haemal spines are straight and basiventral cartilages absent.

FAMILY CARCHARHINIDAE

The carcharhinid caudal fin has distinct dorsal and ventral lobes, with a thin cartilaginous plate preceding the caudal fin skeleton (arrow in Figs 7A, 8, 9, 10A). In all examined carcharhinids, the supraneural spines are elongated and tapering terminally (Figs 7–11) and the basidorsal and interdorsal cartilages are rectangular. The caudal fin has a wide range of VC (66–119), which are divided into anterior and posterior diplospondylic caudal regions (Tables 1, 2).

The anterior diplospondylic caudal region of *Isogomphodon* has seven VC, *Prionace* seven to eight VC, *Galeocerdo* eight VC, *Negaprion* nine VC and *Loxodon* nine VC. Among species of the genus *Carcharhinus*, this region is composed of four to nine VC and in *Rhizoprionodon* six to eight VC (Table 1). The basiventral cartilages have an apophysis as a slight prominence on the anterior margin in *Galeocerdo*, *Negaprion*, *Rhizoprionodon*, *Loxodon*, *Carcharhinus plumbeus* and *Carcharhinus porosus* (arrow in Figs 7B, 10B). The basiventrals of *Prionace*, *Isogomphodon*, *Carcharhinus acronotus*, *Carcharhinus brevipinna*, *Carcharhinus melanopterus*, *Carcharhinus longimanus* and *Carcharhinus signatus* are rectangular, slightly uniform and lack an anterior apophysis (Figs 8, 9, 11). In all carcharhinids, the first haemal spines are anteriorly concave, and only *Galeocerdo* has distal prehypochordal cartilages (Fig. 7A). This structure is absent in all other examined sharks.

Most of the haemal spines in the posterior diplospondylic caudal region are '>' shaped (Figs 7–11); however, in *Prionace*, close to the mid-length of the caudal fin, the haemal spines in the distal portion are posteriorly curved (Fig. 11A). The basiventrals are reduced or absent in the terminal caudal lobe.

FAMILY SPHYRNIDAE

Hammerhead sharks have a strong heterocercal caudal fin. A thin plate distal to the haemal arches precedes the caudal fin skeleton (arrow in Figs 12A, 13A, 14A) in all hammerhead shark species, including the winghead shark (*Eusphyra*). The caudal fin skeleton of examined hammerhead sharks has 84–112 VC, but the winghead shark has 68–70 VC (Table 1). Only *Eusphyra* has some vertebrae supporting up to two haemal arches and haemal spines. The basidorsal and interdorsal cartilages of *Sphyrna* and *Eusphyra* are rectangular, and the supraneural spines are elongated, slender and taper terminally. The caudal fin skeleton is divided into anterior and posterior diplospondylic caudal regions (Figs 12–14, Table 2).

The anterior diplospondylic caudal region of *S. lewini*, *S. zygaena* and *Eusphyra* is well developed
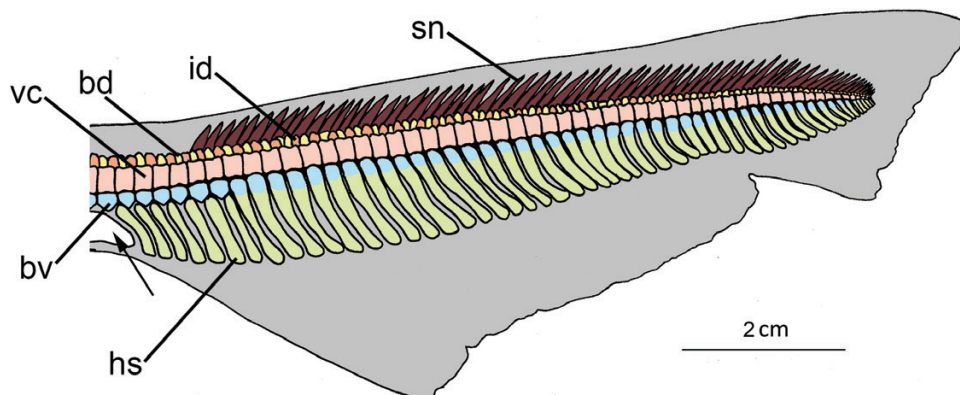
Figure 3. Left side of the caudal fin of *Triakis semifasciata* (UERJ 1610). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige). Arrow indicates the cartilaginous plate preceding the caudal fin.
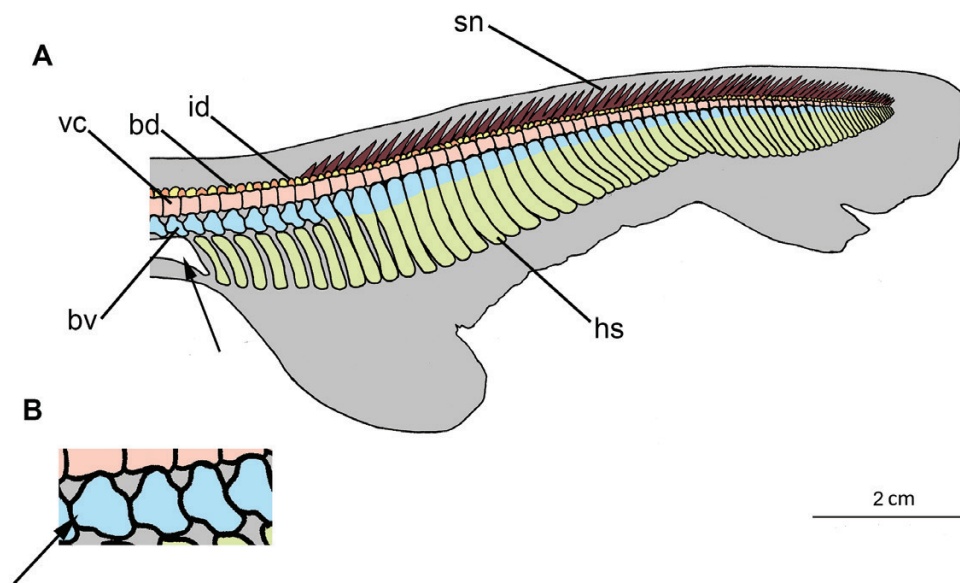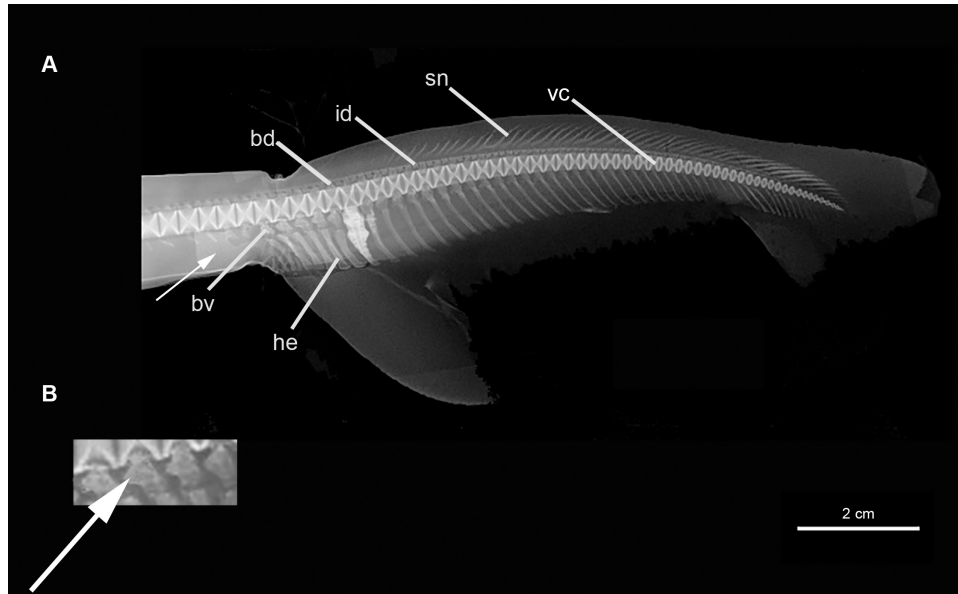

Figure 4. The caudal fin of *Galeorhinus galeus* (UERJ 291). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).

(~30% of the entire caudal fin vs. ~11% in *S. tiburo* and *S. tudes*). This region has five VC in *S. tiburo*, eight VC in *S. tudes*, 25–29 VC in *S. lewini*, 27–30 VC in *S. zygaena* and 16–22 VC in *Eusphyra* (Table 1). The basiventrals of *S. tudes*, *S. tiburo* and *Eusphyra* have apophyses similar to the prominence on the anterior margin of the cartilages (Figs 12B, 14B); the apophysis is more developed in *Eusphyra* (Fig. 14B). However, in *S. lewini* and *S. zygaena*, the anterior apophysis is present only in the most posterior basiventral cartilages, whereas the first basiventrals are rectangular and lack an apophysis (Fig. 13B). The haemal spines of *S. tudes* and *S. tiburo* are slightly concave anteriorly,

similar to the first haemal spines of *S. zygaena* and *S. lewini* (Figs 12A, 13A, 14A), and in *Eusphyra* the first spines are straight. The most posterior haemal spines of *S. zygaena*, *S. lewini* and *Eusphyra* are '>' shaped, with the distal portion more slender than the proximal portion (Figs 13A, 14A). In the terminal lobe, the haemal elements are reduced and the haemal arches absent in all sphyrnids.

SKELETON CAUDAL FIN TYPE

The carcharhiniform caudal fin skeleton is herein divided into four main morphological types, termed

Figure 5. Radiographic image of the caudal fin of *Paragaleus tengi* (NMMBP 6452). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses.
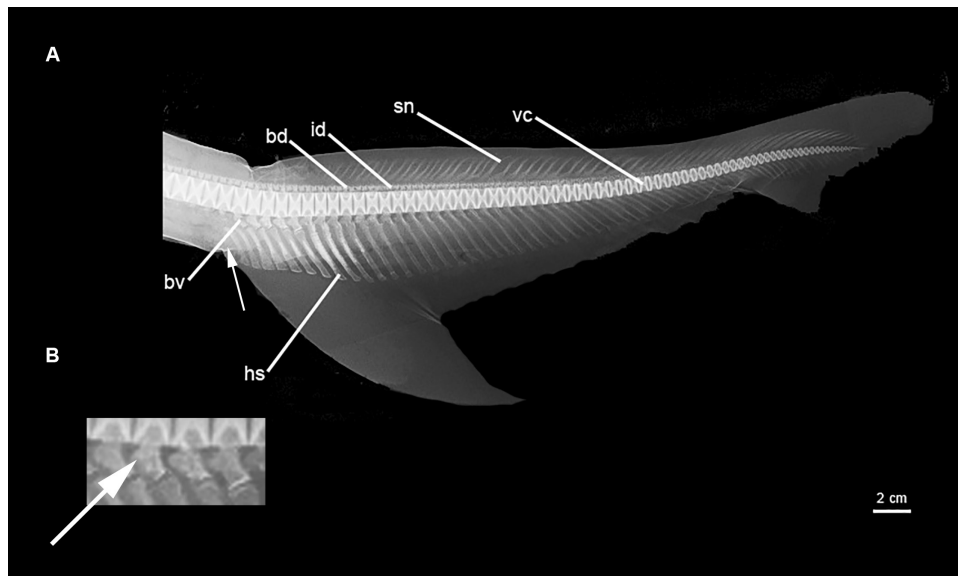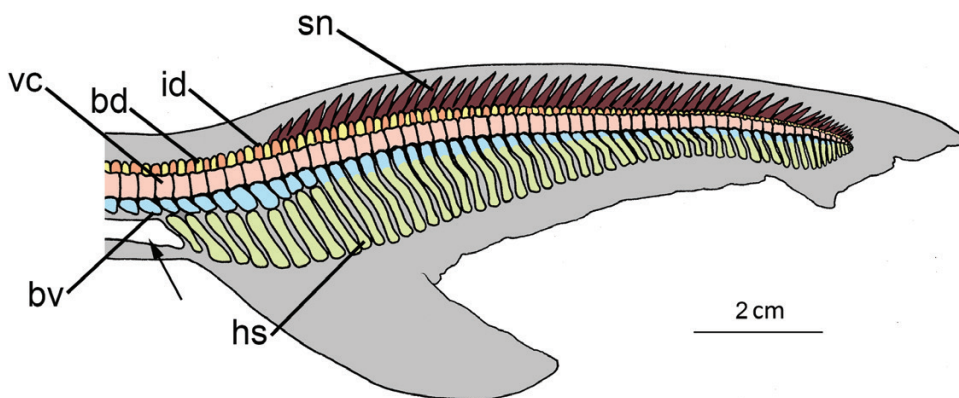

Figure 6. Radiographic image of the caudal fin of *Hemigaleus microstoma* (NMMBP, uncatalogued). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses.

scyliorhinoid, triakoid, carcharhinoid and eusphyrnoid. However, each main morphological type does not represent a monophyletic group. The scyliorhinoid type (family Scyliorhinidae) is characterized by all haemal spines continuous with the basiventrals (an undivided caudal fin skeleton, without a distinction between anterior and posterior diplospondylic regions). In the triakoid type (Triakidae, *Chaenogaleus* and *Paragaleus*), the caudal fin skeleton has anterior

haemal spines detached from basiventrals (anterior diplospondylic caudal region), and the entire posterior diplospondylic caudal region has slightly anteriorly convex haemal spines. In the carcharhinoid type (*Hemipristis*, *Hemigaleus*, Carcharhinidae, *S. tudes* and *S. tiburo*), the anterior haemal spines are detached from the basiventrals (forming the anterior diplospondylic caudal region), and the posterior diplospondylic caudal region has haemal spines that are '>' shaped
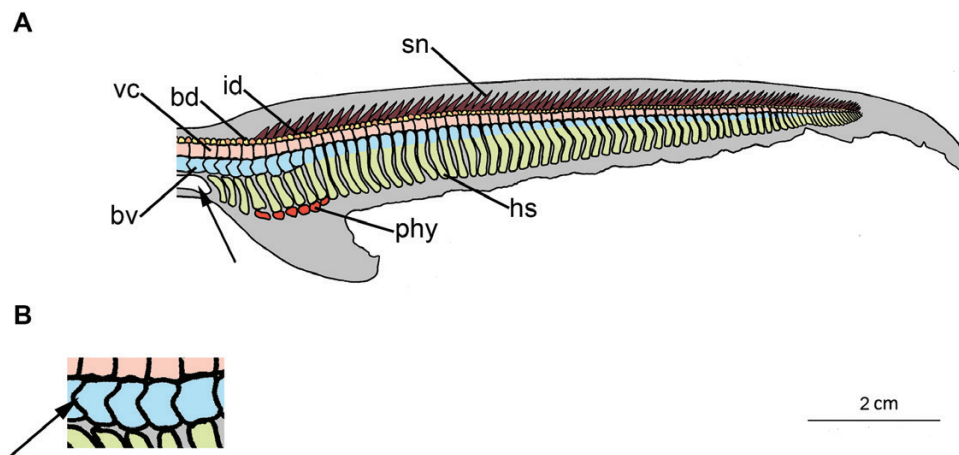
Figure 7. The caudal fin of *Galeocerdo cuvier* (UERJ 1821). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); phy, prehypochordal cartilages (red); sn, supraneural (brown); vc, vertebral centrum (beige).

Figure 8. Left side of the caudal fin of *Isogomphodon oxyrhynchus* (UERJ 2215). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneurals (brown); vc, vertebral centrum (beige). Arrow indicates the cartilaginous plate preceding the caudal fin.

in the mid-caudal fin. The eusphyrnoid caudal skeleton type (*S. zygaena*, *S. lewini* and *Eusphyra*) has a well-developed anterior diplospondylic caudal region (extending to close to the mid-length of the caudal fin), and most haemal spines are '>' shaped.

DISCUSSION

The caudal fin skeleton of extant sharks is composed of vertebral centra, basidorsals, interdorsals, basiventrals and haemal spines. In general, the supraneural spines of carcharhiniforms are slender, elongated and terminally tapered, resembling the same structures in *Heterodontus* (based on Whitehouse, 1910: fig. 1; Daniel, 1915: pl. 5, fig. 17; Daniel, 1934: fig. 78A),

Lamna (Mivart, 1879: pl. 75, fig. 6) and *Isurus* (Garman, 1913: pl. 63, fig. 5). Only *Alopias vulpinus* is set apart from other sharks by having rectangular supraneurals (Little & Bemis, 2004: fig. 5f, p. 571).

The pentagonal basiventrals in the anterior diplospondylic caudal region are diagnostic for *Triakis* and *Mustelus*. The anterior apophyses in the basiventral cartilages are clearly more developed in *Galeorhinus* and *Eusphyra* than in other carcharhiniforms. Only *Eusphyra* has some VC in the caudal fin supporting exclusive double haemal arches and haemal spines; this character is a synapomorphy for this genus. Prehypochordal cartilages situated distal to the anterior haemal spines in *Galeocerdo* are also reported in some non-carcharhiniform sharks, such as *Isurus* (Garman, 1913: pl. 63, fig. 5), some orectolobiforms
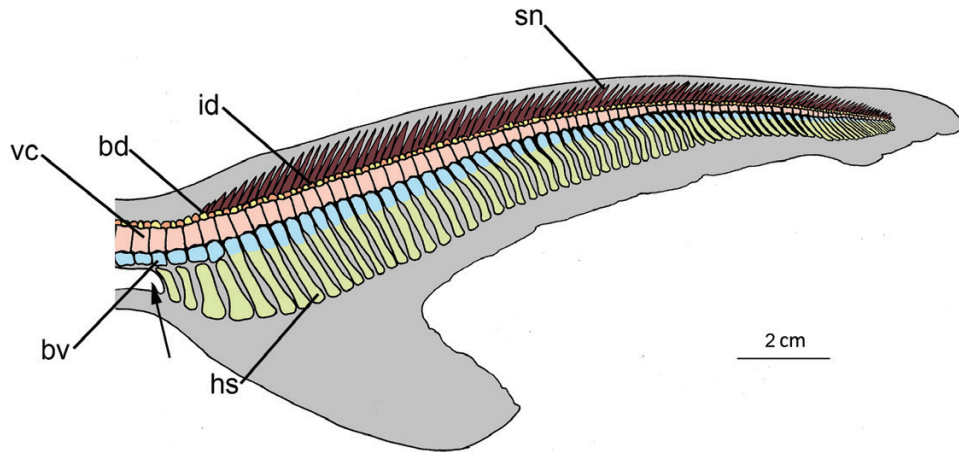
Figure 9. Left side of the caudal fin of *Carcharhinus melanopterus* (UERJ 2216). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige). Arrow indicates the cartilaginous plate preceding the caudal fin.
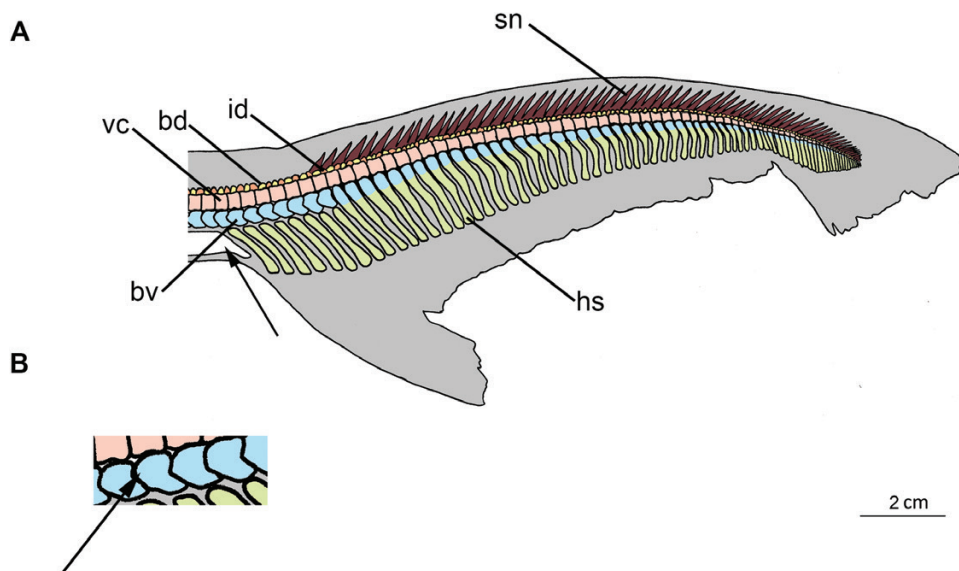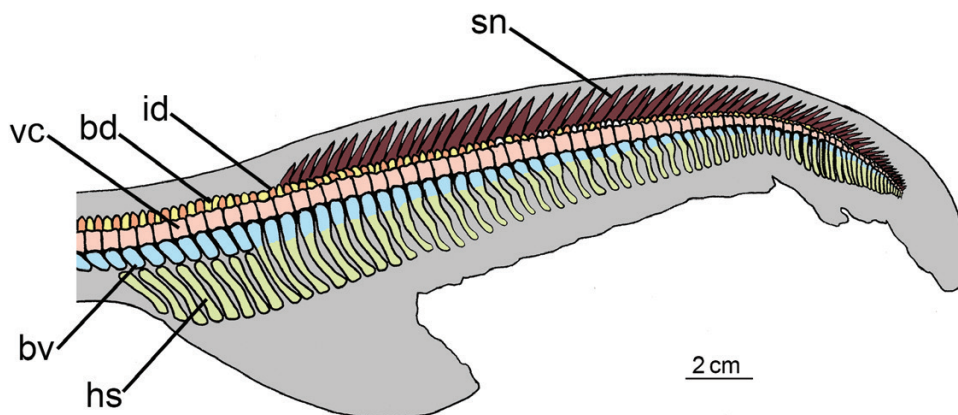
Figure 10. The caudal fin of *Carcharhinus brevipinna* (UERJ 2022). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).

(*Hemiscyllium*, *Parascyllium*, *Cirrhoscyllium* and *Rhincodon*; Goto, 2001; Goto & Nishida, 2001), and squalomorphs of the clade uniting *Centroscymnus*, *Scymnodon*, *Zameus* and *Somniosus* (Shirai, 1992). Therefore, the prehypochordal cartilages evolved independently at least once in galeomorphs and squalomorphs, and probably more than once in galeomorphs.

Information on the caudal fin skeleton in basal, fossil shark lineages is somewhat equivocal. For example, in hybodonts the caudal skeleton may be variable, as this group has been restored as having both a subdivided caudal fin (Coates & Gess, 2007) and an undivided one (*Hamiltonichthys*; Maisey, 1989). Hybodontiforms have been regarded as either the sister group to neoselachians (Compagno, 1977; Schaeffer, 1981; Maisey, 1982, 1986; de Carvalho, 1996) or very closely related to them (e.g. Janvier & Pradel, 2015). Additionally, the pattern of haemal spines detached from the basiventral cartilages has also been reported in the caudal fin skeleton of

Figure 11. Left side of the caudal fin of *Prionace glauca* (UERJ 1866). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).
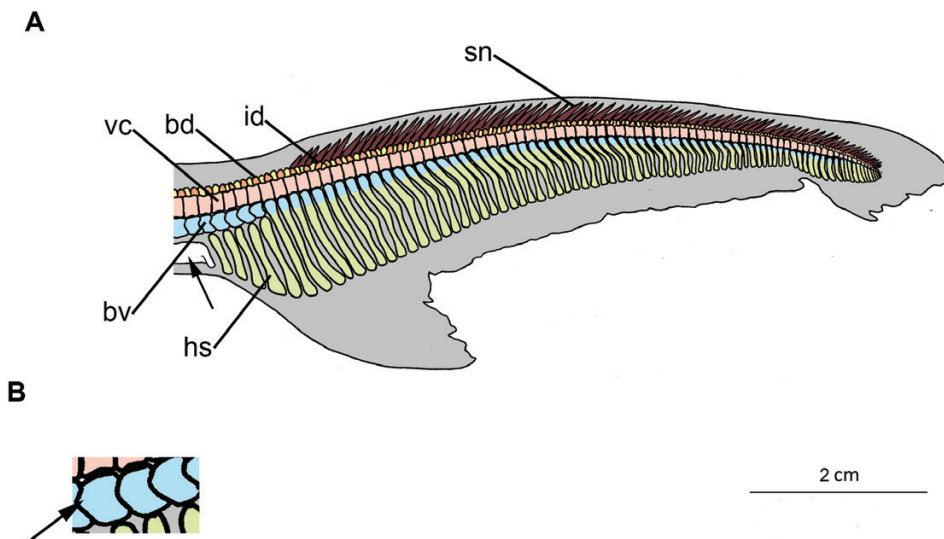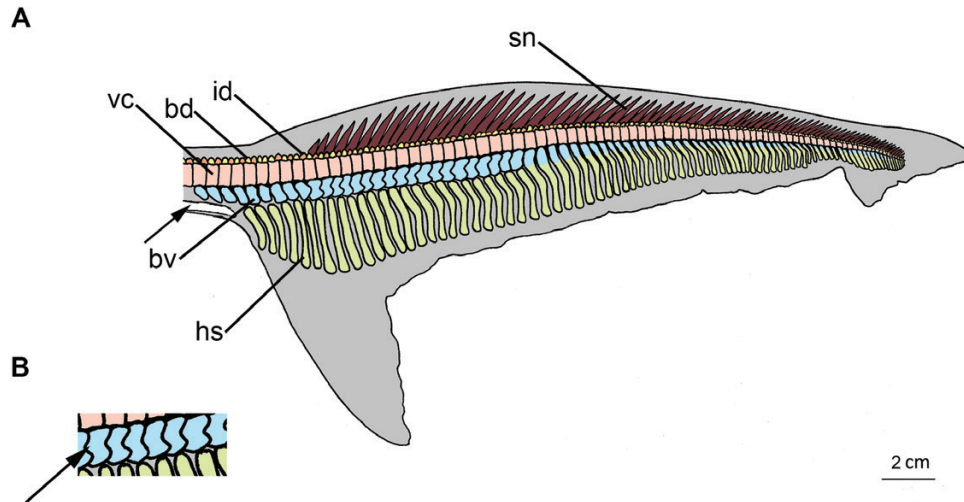
Figure 12. The caudal fin of *Sphyrna tiburo* (UERJ, uncatalogued). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).

some Palaeozoic sharks, such as *Akmonistion* (Coates & Sequeira, 2001), *Cladoselache* (Dean, 1909), *Cobelodus* (Zangerl & Case, 1976; Zangerl, 1981), *Goodrichthys* (Moy-Thomas, 1936) and *Ctenacanthus* (Schaeffer & Williams, 1977). Therefore, determining which pattern (undivided or divided caudal fin skeleton) is derived for living chondrichthyans is not straightforward.

The undivided caudal skeleton described herein for catsharks, within carcharhiniforms (scyliorhinoid caudal fin type), is also found in many other sharks and batoids. The caudal fin in squaliforms (Mivart, 1879; Shirai, 1992; Shirai & Okamura, 1992), in the angel shark *Squatina* (Vaz & Carvalho, 2013) and in

pristiophorids and batoids (Shirai, 1992) has haemal spines continuous with the basiventral cartilages.

According to Goto (2001), most orectolobiforms have an undivided caudal skeleton. However, Goto & Nishida (2001) report that in *Rhincodon*, some haemal spines are segmented. A caudal fin skeleton divided into anterior and posterior diplospondylic caudal regions, as described for species of Triakidae, Hemigaleidae, Carcharhinidae and Sphyrnidae, is also found in *Ginglymostoma* (Fig. 15) and has been reported in *Lamna* (Mivart, 1879), *Isurus* (Garman, 1913) and *A. vulpinus* (Little & Bemis, 2004). The caudal skeleton of *Heterodontus*, according to Whitehouse (1910), has anterior haemal spines detached from basiventrals

Figure 13. The caudal fin of *Sphyrna lewini* (AC. UERJ 915). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).
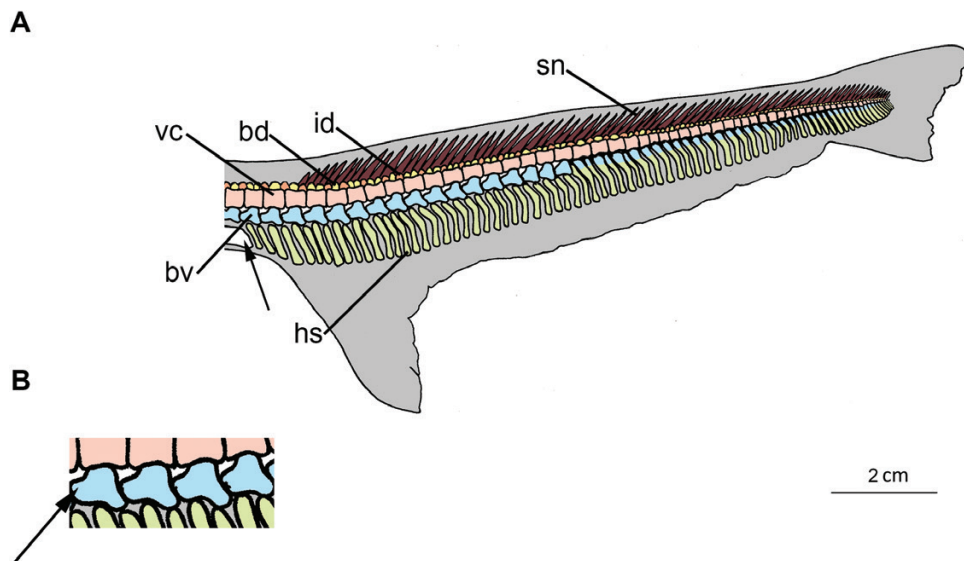
Figure 14. The caudal fin of *Eusphyra blochii* (CAS 88058). A, left side of the caudal fin skeleton. Arrow indicates the cartilaginous plate preceding the caudal fin. B, basiventral cartilage. Arrow indicates the apophyses. Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).

in *Heterodontus portusjacksoni* (as *Heterodontus philippi*), and the caudal fin of *Heterodontus francisci* illustrated by Daniel (1915: pl. 5, fig. 17, p. 487; 1934: fig. 78A, p. 72) seems to have the first haemal spine detached from the basiventral cartilage. The caudal fin of *Chlamydoselachus* (Schmalhausen, 1912) and *Heptranchias* is divided into anterior and posterior diplospondylic regions (Fig. 16). Therefore, the divided caudal fin skeleton can support the monophyly of the order Hexanchiformes, as previously suggested by de Carvalho (1996) and supported by Soares & Carvalho (2013) and by the molecular phylogeny of Naylor *et al.* (2012) and Naylor (2018) (Fig. 17).

The monophyly of sharks is not corroborated by hypotheses based on morphological data (Shirai, 1996; de Carvalho, 1996), but molecular phylogenetic hypotheses consistently recover an all-shark collective that excludes batoids (Naylor *et al.*, 2012; Naylor, 2018). The

interrelationship scheme based on morphological data suggests that the undivided caudal fin, with all haemal spines continuous with the basiventral cartilages (scyliorhinoid caudal type) evolved convergently in galeomorphs in the family Scylorhinidae (Carcharhiniforms) and in the Hemiscylliidae (Orectolobiformes) (Fig. 18). However, the phylogenetic hypothesis based on molecular data suggests that the undivided caudal fin is plesiomorphic (Fig. 17), as it is also present in squaliforms, pristiophoriforms, squatiniforms and batoids. The molecular phylogeny of elasmobranchs (Naylor *et al.*, 2012; Naylor, 2018) and the morphological phylogenetic hypotheses (Shirai, 1996; de Carvalho, 1996) corroborate the close interrelationships of squaliforms, pristiophoriforms and squatiniforms (Figs 17, 18), differing only with regard to the inclusion of batoids (included in the morphological phylogeny but excluded in the molecular tree). The caudal fin skeleton of *Echinorhinus* (Echinorhiniformes) is unknown.

In galeomorphs, the caudal fin skeleton is divided into anterior and posterior diplospondylic caudal regions and is found in the well-supported clade composed of Lamniformes and Carharhiniformes (Figs 17, 18). However, the relationships between Heterodontiformes and Orectolobiformes are still open to debate, despite having been discussed in detail, and they are suggested either to be sister groups (Compagno, 1977, 1988; Soares & Carvalho, 2013) or that heterodontiforms are basal to other galeomorphs (Shirai, 1992, 1996; de Carvalho, 1996; see summary by Soares & Carvalho, 2013). The caudal fin skeleton of Heterodontiformes, based on Whitehouse (1910) and Daniel (1915; 1934), does not present a pattern similar to orectolobiforms, in which *Ginglymostoma* resembles the carcharhinoid type (Fig. 15), whereas the caudal fin of *Hemiscyllium freycineti* shown by Goto (2001; see also Dingerkus & DeFino, 1983), despite having all haemal spines continuous with the basiventrals, presents a convex shape similar to the triakoid caudal fin type. Therefore, the caudal fin skeleton suggests a separately derived pattern for Heterodontiformes and *H. freycineti* within orectolobiforms.
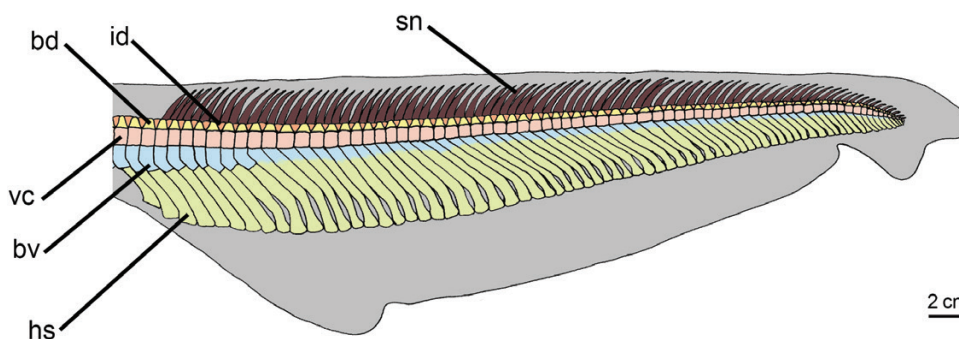
Figure 15. Left side of the caudal fin of *Ginglymostoma cirratum* (AC. UERJ 1439). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).
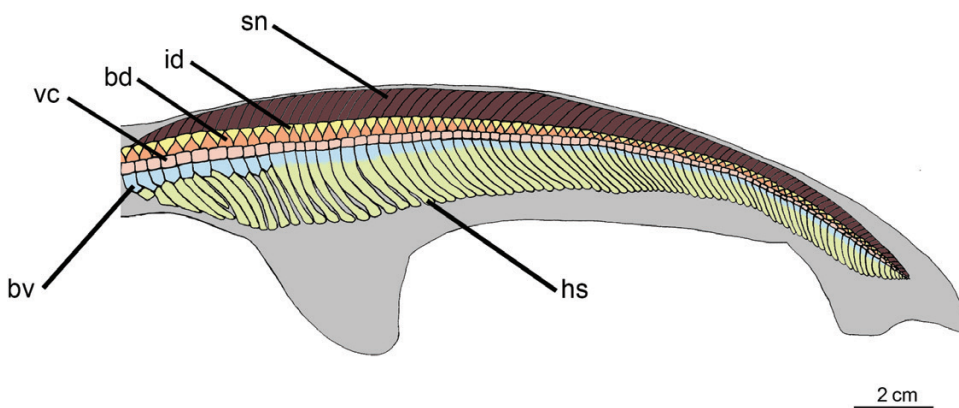

Figure 16. Left side of the caudal fin of *Heptranchias perlo* (UERJ, uncatalogued). Abbreviations: bd, basidorsal (yellow); bv, basiventral (blue); hs, haemal spine (green); id, interdorsal (orange); sn, supraneural (brown); vc, vertebral centrum (beige).
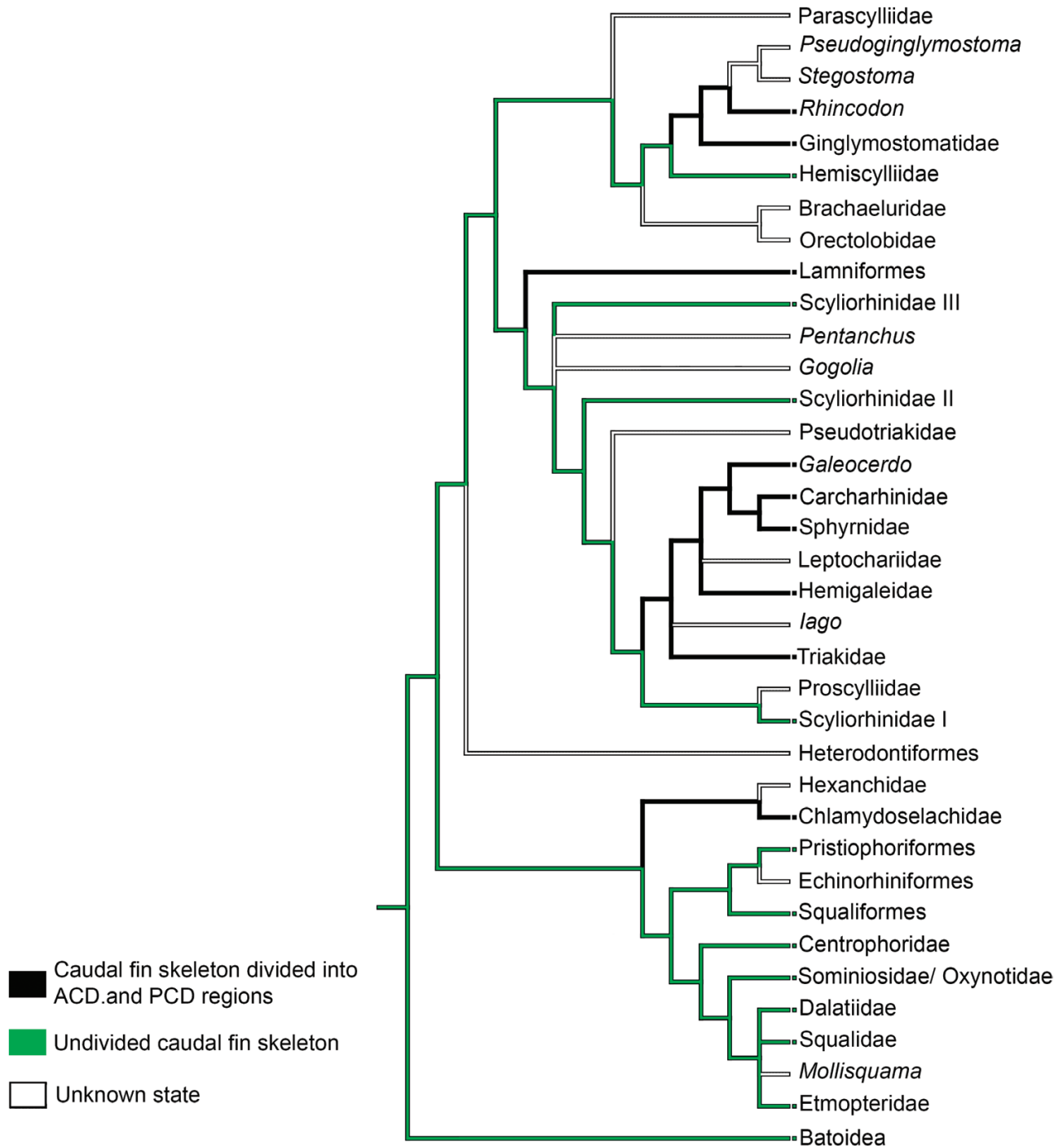
Figure 17. Molecular hypothesis of phylogenetic relationships modified from Naylor (2018), with the distribution of the undivided caudal skeleton and the caudal fin divided into anterior (ADC) and posterior (PDC) diplospondylic caudal regions.

The scyliorhinoid, triakoid, carcharhinoid and eusphyrnoid types of caudal fin skeletons suggested herein do not define monophyletic groups and are not related, for example, to the main clasper types proposed by Compagno (1988). Species of the possibly paraphyletic family Triakidae (Compagno, 1988; Naylor *et al.*, 2012) share the same pattern of caudal fin skeletons. Compagno (1988) previously suggested that catsharks are paraphyletic, and Naylor *et al.* (2012) separated the group into three paraphyletic
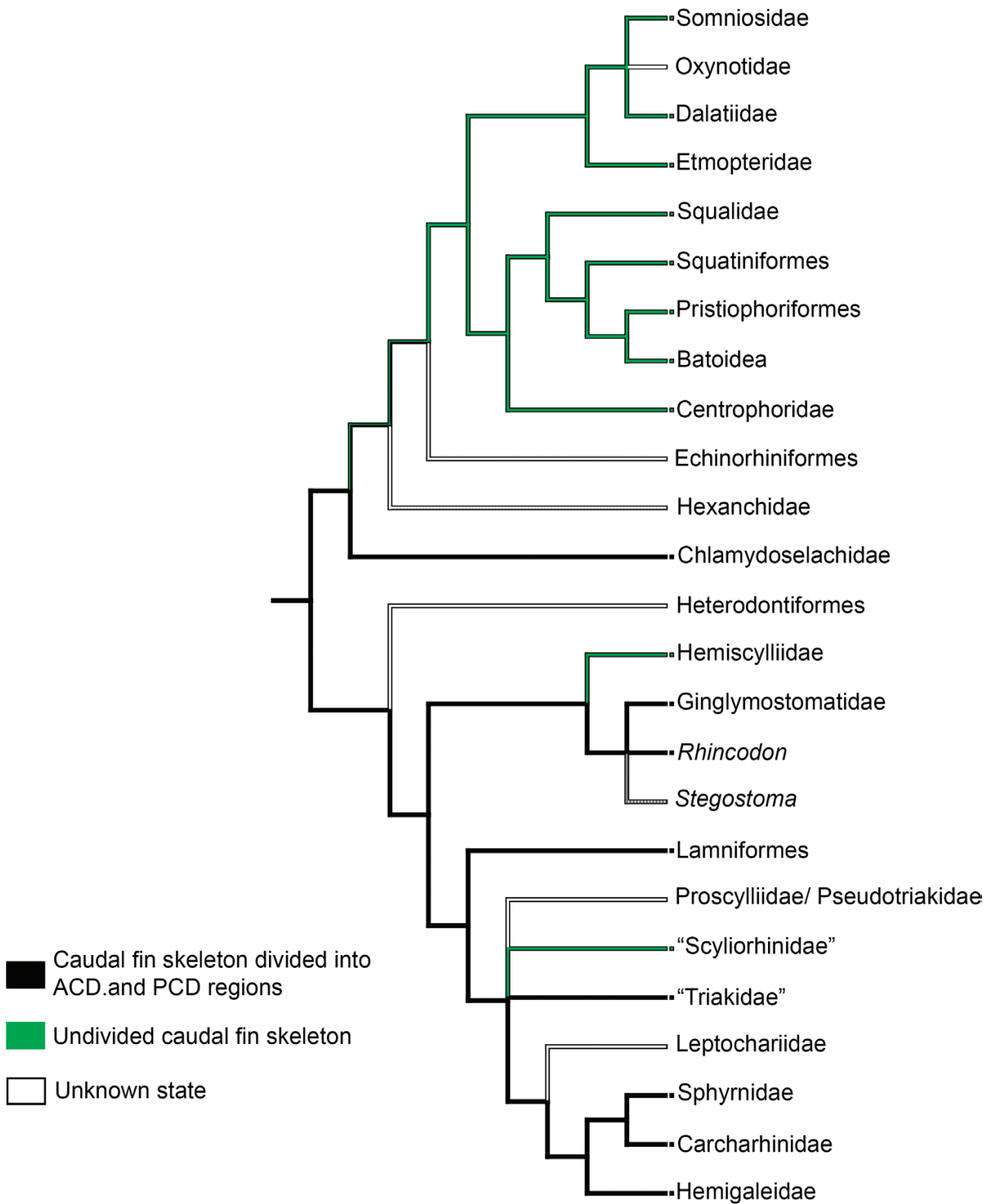
Figure 18. Morphological hypothesis of phylogenetic relationships modified from Shirai (1996), showing the distribution of the undivided caudal skeleton and the caudal fin divided into anterior (ADC) and posterior (PDC) diplospondylic caudal regions.
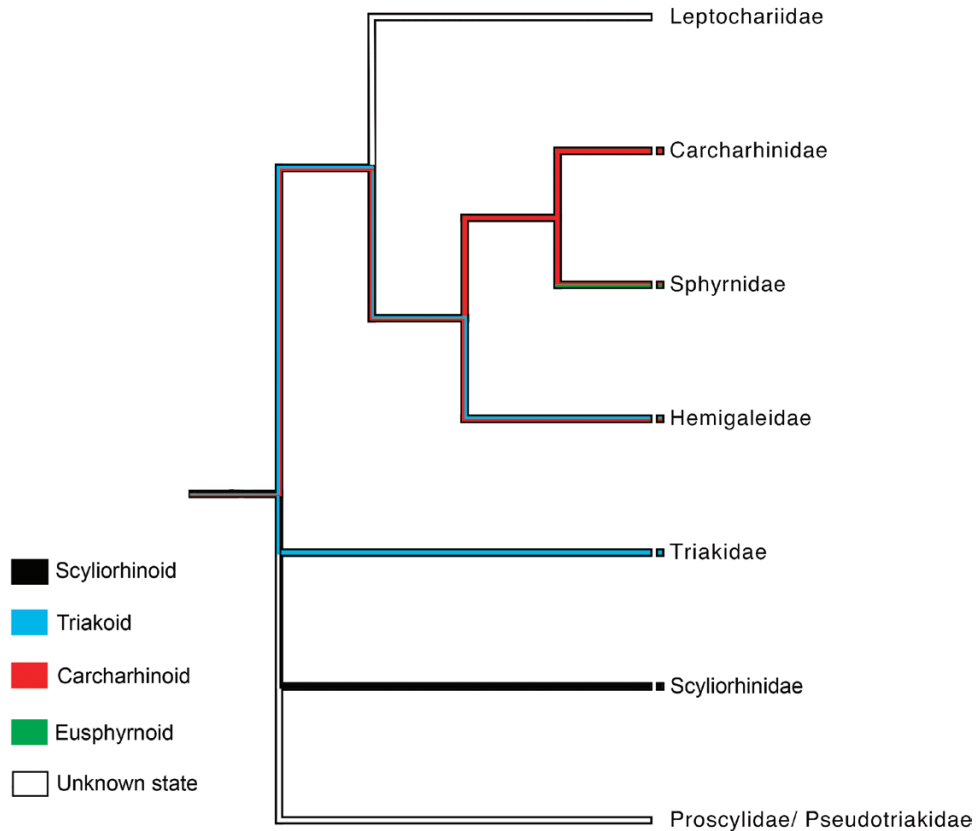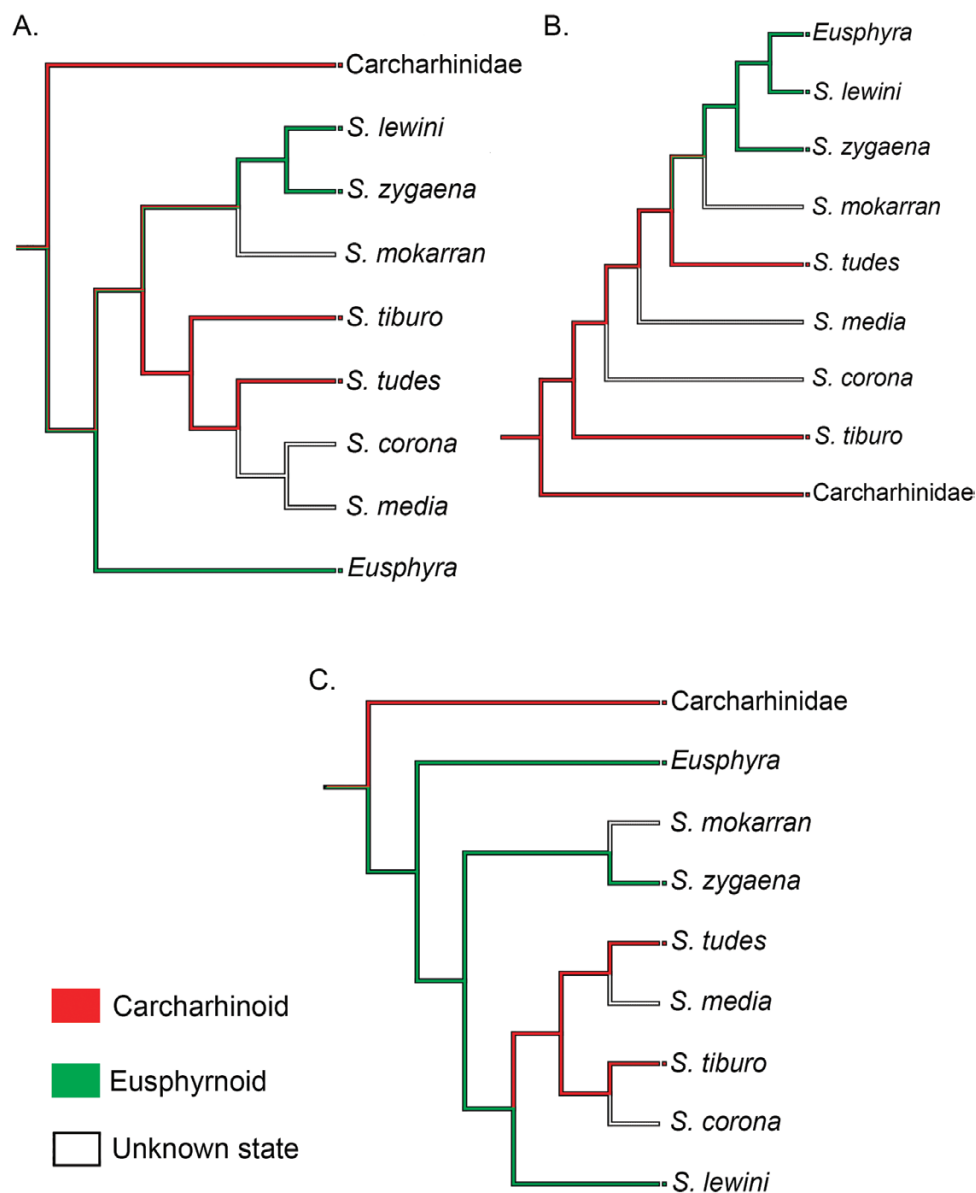
Figure 19. Interrelationships of the order Carcharhiniformes modified from Shirai (1996), with the distribution of the caudal fin skeletal pattern. Distribution of the caudal fin skeletal pattern proposed in the present paper (constructed using parsimony and unordered characters option in MESQUITE).

groups in their molecular phylogeny. However, a similar skeletal pattern (scyliorhinoid caudal fin) is found in each scyliorhinid lineage, such as in *Atelomycterus*, *Schroederichthys*, *Galeus*, *Apristurus* and *Scyliorhinus*. Furthermore, hemigaleids, despite being strongly supported as monophyletic (Compagno, 1988; Shirai, 1996; Naylor *et al.*, 2012), appear to have two separate caudal fin types (Fig. 19): one that resembles the triakoid type (*Paragaleus* and *Chaenogaleus*) and another more similar to the carcharhinoid type (*Hemigaleus* and *Hemipristis*).

The carcharhinoid caudal skeleton type present in carcharhinids, *S. tudes* and *S. tiburo* supports the close interrelationships among Carcharhinidae and Sphyrnidae (Figs 19, 20), which has been strongly corroborated in morphological and molecular phylogenetic hypotheses (Compagno, 1988; Shirai, 1992; Naylor *et al.*, 2012). Furthermore, the carcharhinoid caudal type suggests that hammerhead sharks, with a relatively smaller cephalofoil (*S. tiburo*, *S. media*, *S. corona* and *S. tudes*), are basal in Sphyrnidae (Fig. 20B). This hypothesis was previously suggested by Compagno (1988), who stated that the slight lateral expansion

of the head of *Scoliodon* is an incipient cephalofoil and that Carcharhinidae is a monophyletic group only if hammerhead sharks are included. However, Sphyrnidae is supported as a monophyletic group by Gilbert (1967) and recent molecular studies (Lim *et al.* 2010; Naylor *et al.*, 2012).

The alternative sphyrnid interrelationships proposed in the morphological phylogeny by Gilbert (1967), and later corroborated by Cavalcanti (2007), suggest that *Eusphyra* is basal within Sphyrnidae. In this scenario, the carcharhinoid caudal skeleton type independently evolved in Carcharhinidae and sphyrnids with a smaller cephalofoil (Fig. 20A). The molecular study by Lim *et al.* (2010) also supports *Eusphyra* as the most basal sphyrnid (Fig. 20C), whereas Naylor *et al.* (2012) proposed a different pattern of interrelationships, with a lineage comprising hammerhead sharks with small cephalofoils plus *S. lewini* in a polytomy with other sphyrnids. However, the eusphyrnoid caudal skeleton type is clearly the more derived condition within carchariniforms and corroborates the monophyletic group previously proposed by Compagno (1988), which included *S. zygaena*,

Figure 20. Hypotheses of interrelationships of members of the Sphyrnidae, showing the distribution of the caudal fin skeletal pattern proposed in the present paper (constructed using parsimony and unordered characters option in MESQUITE). A, phylogeny modified from Gilbert (1967) and Cavalcanti (2007). B, phylogeny modified from Compagno (1988). C, phylogeny modified from Lim *et al* (2010).

S. lewini, possibly *S. mokarran* (not available for dissection), and *Eusphyra*.

CONCLUSION

The caudal fin skeleton provides evidence that may help to elucidate relationships between shark groups. However, the complex variations in morphology among fossil sharks impedes a clearer interpretation of which pattern (undivided caudal fin skeleton or caudal fin skeleton divided into anterior and posterior diplospondylic portions) is derived for living sharks. Carcharhiniform sharks have four main caudal fin skeleton types: scyliorhinoid (Scyliorhinidae), triakoid (Triakidae, *Paragaleus* and *Chaenogaleus*), carcharhinoid (Carcharhinidae, *Hemipristis*, *Hemigaleus*, *S. tudes* and *S. tiburo*) and eusphyrnoid (*Eusphyra*, *S. lewini* and *S. zygaena*). However, the four caudal fin skeleton types do not necessarily define monophyletic groups and are found in other living elasmobranchs. The caudal skeletal pattern shared by carcharhiniform

taxa suggests close relationships among hammerhead sharks with relatively smaller cephalofoils and carcharhinids, but this shared feature might reflect a primitive condition in these taxa. The derived eusphyrnoid caudal fin type is found exclusively in a lineage that includes *S. zygaena*, *S. lewini*, probably *S. mokarran*, and *Eusphyra*.

ACKNOWLEDGEMENTS

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APPENDIX

MATERIAL EXAMINED

Asterisk indicates radiograph only.

Atelomycterus marmoratus (NMMBP 15349)*, *Schroederichthyes saurisqualus* (AC. UERJ 1285.1; AC. UERJ 1285.2), *Galeus mincaronei* (AC. UERJ 1436), *Apristurus parvipinnis* (UERJ 2056), *Scyliorhinus haeckelii* (AC. UERJ 1420; AC. UERJ 1423; UERJ 1496.2; UERJ 1690), *Triakis semifasciatus* (UERJ 1610.1; UERJ not catalogued), *Mustelus canis* (UERJ 1678; UERJ 1821), *Mustelus schmitti* (UERJ 364), *Galeorhinus galeus* (UERJ 291), *Paragaleus tengi* (neotype NMMBP 6452)*, *Hemigaleus microstoma* (NMMBP not catalogued)*, *Chaenogaleus macrostuma* (NMMBP 6414)*, *Hemipristis elongata* (MZUSP not catalogued), *Galeocerdo cuvier* (UERJ 2184), *Isogomphodon oxyrhynchus* (UERJ 2215), *Carcharhinus plumbeus* (UERJ 653), *Carcharhinus melanopterus* (UERJ 2216), *Carcharhinus brevipinna* (UERJ 2022), *Carcharhinus acronotus* (UERJ 1117), *Carcharhinus signatus* (UERJ 1680), *Carcharhinus porosus* (UERJ 1124.3; UERJ 1124.5), *Carcharhinus longimanus* (UERJ 1606), *Prionace glauca* (UERJ 1866.1; UERJ not catalogued), *Negaprion brevirostris* (MNRJ 16589), *Rhizoprionodon lalandii* (AC. UERJ 285; AC. UERJ 546), *Rhizoprionodon porosus* (AC. UERJ 332; AC. UERJ 486; AC. UERJ 487; UERJ 371), *Loxodon macrohinus* (NMMBP not catalogued)*, *Sphyrna tiburo* (UERJ not catalogued), *Sphyrna tudes* (UERJ 1121.4), *Sphyrna zygaena* (UERJ 1922; UERJ 2218), *Sphyrna lewini* (AC. UERJ 1463; UERJ 2217), *Eusphyra blochii* (CAS 88058; USNM 195846*; USNM 197512*), *Ginglymostoma cirratum* (AC. UERJ 1439), *Heptranchias perlo* (UERJ, uncatalogued).