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# Body Forms in Sharks (Chondrichthyes: Elasmobranchii), and Their Functional, Ecological, and Evolutionary Implications

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# Body Forms in Sharks (Chondrichthyes: Elasmobranchii), and Their Functional, Ecological, and Evolutionary Implications

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Partial Fulfilment of the
Requirements for the Degree of
Master of Science

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# Abstract

Sharks are among the oldest vertebrate lineages in which their success has been attributed to their diversity in body shape and locomotor design. In this study, I investigated the diversity of body forms in extant sharks using landmark-based geometric morphometric analyses on lateral view illustrations of nearly all the known (ca. 470) extant sharks in a published guidebook. I ran three different analyses: the ‘full body,' ‘precaudal body,’ and ‘caudal fin' analyses. My study suggests that there are two basic body forms in sharks. The two major body forms are characterized as a ‘shallow-bodied’ form (Group A) and ‘deep-bodied’ form (Group B). This pattern is also present in the precaudal body analysis, but the caudal fin analysis indicates that all sharks essentially have one basic caudal fin design. My geometric morphometric analyses have significant functional, ecological and evolutionary implications. First, I found that swimming modes in sharks are highly correlated with body forms. For example, Group A sharks are predominantly anguilliform swimmers, whereas Group B sharks are represented by carangiform and thunniform swimmers. Second, the majority of Group A sharks are found to be benthic whereas pelagic forms are relatively common among Group B sharks. Third, based on the known fossil record as well as previously published molecular-based phylogenetic trees, each of the two superorders of sharks, Squalomorphii and Galeomorphii, must have gone through complex evolutionary history where each superorder contains both Group A sharks and Group B sharks, possibly involving parallel evolution from one group to the other or at least one episode of evolutionary reversal. Lastly, the most ancestral shark, the clade that unites Squalomorphii and Galeomorphii, was possibly a benthic form with a Group A body form. My study demonstrates that a use of an identification guidebook can be a powerful method for the field of comparative anatomy.

# INTRODUCTION

It is a well-known concept in biology that form is tightly related to its function (Russell, 1916), and such examination is significant because it is highly informative for making inferences about evolutionary and ecological relationships (Lauder *et al*., 1995). In the classical studies of *Anolis* lizards, those with longer hindlimbs can run across broad substrates whereas those with shorter limbs can balance on narrow branches (Losos, 1990, Kolbe *et al*., 2012). Among many other examples, another excellent case is the relationship between the body form of fishes and their mode of swimming where pelagic forms of fishes commonly exhibit a laterally compressed body whereas benthic forms are dorsoventrally flattened (Alexander, 1965; Webb, 1984; Weihs, 1989; Blake, 2004). The same pattern is particularly evident in elasmobranchs, a monophyletic group of cartilaginous fishes (Chondrichthyes), consisting of over 500 species of sharks (Selachii) under two superorders, Squalomorphii and Galeomorphii, and 630 species of rays (Batoidea) (Weigmann, 2016; Fig. 1A). In sharks alone, the white shark, *Carcharodon carcharias* (Linnaeus 1758), capable of fast-swimming and attacking highly mobile pinnipeds has a streamlined body, whereas bottom-dwelling angel sharks (*Squatina* spp.) wait in the substrate to ambush their prey have a dorsoventrally flattened body (Motta & Huber, 2012).

Sharks have a long geologic history that appeared nearly 200 million years ago (Maisey *et al*., 2004; Grogan *et al*., 2012; Maisey, 2012), and they remain a major component of all marine ecosystems (Compagno, 1990). Their success is generally attributed to the vast diversity of their locomotor designs (Lauder & Di Santo, 2016). Much of the work has focused on the morphology and function of their caudal fin referred to as heterocercal tail characterized by the upward flexure of the notochordal axis (Thomson, 1976; Thomson & Simanek, 1977; Wilga &

Lauder, 2002; Maia *et al*., 2012). One of the pioneer works on classifying sharks according to different body forms is that by Thomson & Simanek (1977). They recognized four basic body forms or "groups" of sharks using simple morphometric measurements based on 56 different species (Fig. 1B). Group 1 sharks are characterized by having a deep body, large pectoral fins, a caudal peduncle with lateral keels or a caudal fluke, and a symmetrical with a high-aspect ratio. An example of Group 1 sharks is the white shark, *Carcharodon carcharias*. Group 2 sharks have a body less deep then Group 1, no caudal fluke, and a low heterocercal angle. This group includes most carcharhinid sharks such as the bull shark, *Carcharhinus leucas* (Müller & Henle 1839). Group 3 sharks have a very large head and blunt snout, more anteriorly positioned pelvic fins, more posteriorly placed first dorsal fins, and a low heterocercal angle with a large subterminal lobe and small or no hypochordal lobe, and catsharks (Scyliorhinidae) represent this group. The dogfish sharks (Squaliformes) represent Group 4 sharks characterized by a caudal fin with a higher aspect angle similar to that of Group 2 but lacking an anal fin.

Since Thomson & Simanek's (1977) work, additional studies have explored the relationship between the body form and locomotion in sharks. For example, Scacco *et al.* (2010) examined the body morphometrics and swimming diversity of Mediterranean demersal sharks that revealed a change in body morphology as a function on swimming capabilities. Irschick & Hammerschlag (2014) showed four different species of sharks with differing ecology and life history exhibit changes in the caudal fin through ontogeny (see also Reiss & Bonnan, 2010). Subsequently, Iosilevskii & Papastamatiou (2016) compared the body morphology of sharks with their buoyancy and energetics, and showed that larger sharks increase buoyancy to compensate for longer pectoral fins. More recently, Irschick *et al*. (2017) examined eight shark species to determine if ecology influenced body form. Despite all these studies, the four body groups proposed by Thomson & Simanek (1977) have been assumed to capture the body form diversity in sharks (e.g., Maia *et al.*, 2012; Shadwick & Goldbogen, 2012; Irschick & Hammerschlag, 2014; Lauder & Di Santo, 2016; Irschick *et al.*, 2017) even though their study was based on only about one-tenth (56 different species) of all known shark species using simple morphometrics.

The goal of this present study is to revisit Thomson & Simanek's (1977) study by quantitatively examine the body form diversity in sharks. I examine nearly all the known (ca. 470) extant shark species included in the most recent comprehensive field guide of sharks, *Sharks of the World: A Fully Illustrated Guide* by Ebert *et al.* (2013), using landmark-based geometric morphometrics (Rohlf & Marcus, 1993; Mitteroecker & Gunz, 2009). Based on the results of my body shape analyses, I evaluate the variation of body forms in sharks, examine how my data correspond with Thomson & Simanek's (1977) four basic body forms in sharks (Fig. 1B), and discuss the functional, ecological, and evolutionary implications of the newly observed body form pattterms.

## MATERIALS AND METHODS

### PRIMARY SAMPLES

Thomson & Simanek (1977) used illustrations of sharks from Bigelow & Schroeder's (1948) *The Fishes of the Western North Atlantic* (Volume 1), that was arguably the most comprehensive literature with illustrations of diverse sharks available to them then. I used Thomson & Simanek's (1977) strategy by basing my study on the most recent comprehensive guidebook of sharks, *Sharks of the World: A Fully Illustrated Guide* by Ebert *et al*. (2013) that was built on work by Bigelow & Schroeder (1948) and many other subsequent landmark literatures on sharks (e.g., Compagno, 1984, 2002; Compagno *et al.*, 2005). Ebert *et al*.'s (2013) book includes about 470 species of extant sharks that were known to science at the time when the book went into press. Although approximately 80 new species have been discovered since then (Weigmann, 2016; White *et al*., 2019), I did not include them in order to keep the quality of illustrations used to be consistent. For example, Ebert *et al*.'s (2013) illustrations include lateral drawings with a scale bar drawn by a single illustrator with a uniform method, including the left pectoral fin and pelvic fin that are consistently depicted to be ventrally directed (see review by Jawad, 2013; note that, unless otherwise indicated, one exception is Squatiniformes where only one lateral image is provided for the entire shark order). The exclusion of those recently described taxa were considered not to affect the overall result of my study, because they have phylogenetically close relatives with nearly identical body forms represented in Ebert *et al*.'s (2013) book. Appendix 1 shows all the species examined in this study, along with their 'species codes' used for the morphometric analyses (see below) as well as known maximum total length (TL) for each species and the page number in Ebert *et al*.'s (2013)'s book where each illustration can be found.

## SECONDARY SAMPLES

As a 'fully illustrated' guidebook, the premise of Ebert *et al*.'s (2013) illustrations is that they are depicted as accurately as possible to allow identification of sharks. Nevertheless, I examined the caudal fin shape in one preserved, non-embryonic specimen of a representative species in each shark family to confirm, as a pilot study, the overall accuracy of Ebert *et al*.'s (2013) illustrations. Examined specimens belong to the following institutions: Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, USA; California Academy of Sciences (CAS), San Francisco, California, USA; Field Museum of Natural History (FMNH), Chicago, Illinois, USA;

Florida Museum of Natural History, University of Florida (UF), Gainesville, USA; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA; Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington, New Zealand; National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C., USA; Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA; Oregon State University Ichthyology Collection (OS), Corvallis, Oregon, USA; Scripps Institution of Oceanography (SIO), University of California, San Diego, California, USA; South African Museum (SAM), Cape Town, South African; South Australian Museum, Adelaide (SAMA), Australia; University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan, USA. Appendix 2 lists specific taxa and specimens examined. I chose to focus specifically on comparing the caudal fins because 1) the precaudal body in preserved specimens is often dissected or fixed in a distorted posture (Glenn & Mathias, 1987), and 2) because the caudal fin is a planar structure in which its shape can be traced easily and accurately.

## MORPHOMETRIC ANALYSES

To explore the body form diversity in sharks quantitatively, I conducted three separate landmark-based geometric morphometric analyses using MorphoJ 1.07a (Klingenberg, 2011). The first analysis, herein referred to as the ‘full body analysis,’ examined the entire body of the shark (i.e., precaudal body + caudal fin) in lateral view and used a total of 13 homologous landmarks as well as 100 semilandmarks (Fig. 2A). The second analysis, referred to as the ‘precaudal body analysis,’ focused on the shape of only the precaudal portion of the shark body of the shark in lateral view by excluding the caudal fin data from the total landmark data (i.e., 11 homologous landmarks and 60 semilandmarks: Fig. 2B). The third analysis, the ‘caudal fin analysis,’ focused only on the caudal fin shape in lateral view by excluding the precaudal body data from the total landmark data (i.e., four homologous landmarks and 40 semilandmarks: Fig. 2C). In this study, the second dorsal fin and anal fin were not taken into consideration because Echinorhiniformes and Squaliformes, respectively, lack them (see Ebert *et al*., 2013).

I followed Zelditch *et al.*'s (2012) methods, procedures, and protocols for morphometric analyses. First, all images of the sharks were scanned directly from Ebert *et al*.'s (2013) book. Computer software programs tpsUtil64 and tpsDig232 (Rohlf, 2015) were then used to create an electronic storage folder to upload and organize the image files and to digitize landmarks (Fig. 2). Instead of sequentially sampling from the first image in the book to the last image in the book, I made an effort to sample images of sharks from across different orders randomly throughout my digitization process. Whereas homologous landmarks could be decisively located (Fig. 3), semilandmarks were plotted along homologous curves to capture additional morphological information from each sample. These curves included dorsal and ventral curves of the precaudal body as well as the curves of each lobe from the caudal fin (Fig. 3). Each curve was digitized using the trace function in tpsdig232 and semilandmarks were appended to landmarks using tpsUtil64. The actual size of sharks was accounted by the accompanied scale bar in each scanned image using the measure tool also in tpsDig232. Next, another computer software, MorphoJ 1.07a (Klingenberg, 2011), was used to perform a Procrustes fit to generate a covariance matrix. A Procrustes fit eliminates differences in location, scale, and orientation of each sample, so that all samples are superimposed in shape measurement. The covariance matrix was then used to conduct each principal component analysis (PCA) as well as a shape change analysis.

## ANALYSIS OF COVARIANCE

The effect of size on shape is investigated routinely using geometric morphometrics (Klingenberg, 2016). Therefore, I examined if sharks differ in shape not only due to size but also if taxonomic classification plays a role in shape determination. I used an Analysis of Covariance (ANCOVA) to determine if taxonomic order (‘factor’) and shark size (‘covariate’) had an effect on overall shape in sharks (‘response variable’). In this study, I chose to use the results of the precaudal body analysis, because many comparative papers on shark morphology (e.g., Irschick & Hammerschlag, 2014; Fu *et al*., 2016; Irschick *et al*., 2017) relied on the use of the precaudal length (PCL). Furthermore, certain taxa (e.g., *Alopias* and *Stegostoma*) have caudal fins nearly the length of the body, possibly causing statistical outliers. Using my PCA data from precaudal body analysis, I obtained the size correction of each shark sample ('log centroid size') and mean overall shape of each sample (RegressionScore1 or 'shape score') from MorphoJ 1.07a. These data were organized based on taxonomic orders of sharks and were saved in a comma-separated value (CSV) file format for my ANCOVA using R version 3.5.2 (R Core Team, 2016).

## LIMITATIONS OF THIS STUDY

There are two major limitations to this study that should be noted. First, this study examines the body forms of sharks only in lateral two-dimensional view and excludes other physical characteristics that may be potentially critical for understanding the full range of body form diversity in sharks, such as the head shape and body shape in dorsal view or their three-dimensionality. However, whereas Thomson & Simanek (1977) did discuss some observations regarding the head shape, it should be noted that their characterization of each of their four body forms (Fig. 1B) involved only the features observed from the lateral view with a potential exception of "blunt snout" for Group 3 sharks (see Introduction). Because the aim of this study is to revisit Thomson & Simanek's (1977) study, I therefore chose to focus also on the lateral aspect of sharks. Second, the lack of the second dorsal fin and anal fin in Echinorhiniformes and Squaliformes, respectively, did not allow me to consider those fins because the geometric morphometric software, tpsDig232, did not allow any missing data, meaning that all selected homologous landmarks must be represented across all examined samples. In addition, Thomson & Simanek's (1977) characterization of the four body forms included the knowledge about the presence or absence of lateral fluke at the caudal peduncle, but like with the second dorsal and anal fins, my geometric morphometrics cannot take this piece of anatomical information into consideration. Because my geometric morphometric study cannot take the three-dimensionality and certain aforementioned anatomical characteristics into account, conclusions drawn from this study, that constitutes the most comprehensive study of the body forms in sharks since Thomson & Simanek's (1977) work, should still be considered working hypotheses.

## RESULTS

### PILOT STUDY

Before conducting the three analyses (see above), I ran a pilot study to confirm whether or not shark illustrations from Ebert *et al.*'s (2013) book reasonably reflect the morphology of actual sharks. I applied the same landmark scheme used for the caudal fin analysis (Fig. 2C) to the caudal fins of my 'secondary samples' (see above) and compared those with Ebert *et al.*'s (2013) illustrations. Appendix 2 lists all specimens used along with their species codes, and Figure 3 shows the results of my pilot study of one representative species from each family of sharks. A corollary of this pilot study is that the majority of the plots of Ebert *et al.*'s (2013) illustrations and those of my tracings of actual shark samples of respective species occur in close proximity in the morphospace. Although a minor spread between the two plots of each species is present that can be explained by intraspecific variation, the close proximity of the two plots, some of which even practically overlap one another, implies that the book illustrations represent the actual shark samples well. Furthermore, the fact that the book illustration and actual shark sample of each species occupy one specific region of the morphospace indicates that each species possesses a distinct shape relative to other shark species. Therefore, the outline of each shark species from Ebert *et al.*'s (2013) work is considered to capture adequately the shape of each species sufficient for the purpose of our study.

## FULL BODY ANALYSIS

Figure 4A shows the color-coding scheme of each shark order used for plots of my full body analysis depicted in Figure 4B (for taxonomic identity of each plot, see Appendix 3). The first five principal components explain 84.89% of the total variation observed in shark body shape. The first principal component (PC1) explains 34.32% of the variation that is largely affected by the position of the first dorsal fin. Sharks with the first dorsal fin positioned more posteriorly on the precaudal body have lower PC1 values compared to those with a more anteriorly located first dorsal fin. The second principal component (PC2) explains 23.75% of the variation that is greatly affected by the aspect ratio of the caudal fin. Higher PC2 values are the result of low aspect ratio with a larger dorsal lobe and small to absent lower lobe, whereas lower PC2 values indicate a high aspect ratio caudal fin. The third principal component (PC3) explains 16.15% of the variation that is mainly affected by the location of the pelvic fins. Sharks with pelvic fins more posteriorly placed score higher compared to sharks with more anteriorly placed pelvic fins. The fourth principal component (PC4) explains 7.29% of the variation. It is affected by the overall length of the pectoral fin, where sharks with shorter pectoral fins score higher PC4 values than those with longer pectoral fins. The fifth principal component (PC5) explains 3.38% of the total variation that is largely affected by the depth of the lower lobe of the caudal fin, where sharks with a deeper lower lobe scores lower than sharks with a narrower lower lobe.

My full body analysis plotting the relationship between PC1 and PC2 (Fig. 4B) reveals that there are two major divisions in shark body shape. The same pattern is also observed even when changing the *y*-axis in the scatter plot diagram to PC3, PC4, or PC5 (Appendices 4–6). Therefore, I consider PC1 and PC2 alone adequately capture the overall body form patterns in sharks where the discussion hereafter focuses specifically on PC1 and PC2. In general, members of each shark order cluster together to occupy one specific region of the morphospace with the exception of Carcharhiniformes and Lamniformes. Hexanchiformes, Pristiophoriformes, Squatiniformes, Orectolobiformes (except Stegostomatidae: see below), and the catshark species (Scyliorhinidae) of Carcharhiniformes, occupy the top left side of the overall plot distribution due to the posterior position of their first dorsal fin within the precaudal body. Echinorhiniformes, shows a split distribution with one species located in the left major cluster whereas the other is located between the two major clusters. Squaliformes, Heterodontiformes, Lamniformes (except Alopiidae: see below), and houndshark and requiem shark species (Triakidae and Carcharhinidae) of Carcharhiniformes occupy the top right side of the overall plot distribution. Relative to other shark orders, Lamniformes shows the greatest distribution especially because the thresher sharks, *Alopias* spp. (Alopiidae), fall outside the larger plot distribution together with one orectolobiform, the zebra shark or *Stegostoma faciatum* (Hermann

1783) (Stegostomatidae), because of their exceptionally elongated caudal fin (i.e., three dark green and one light blue plots in the lower left corner of Fig. 4B).

## PRECAUDAL BODY ANALYSIS

The first five principle components explain 91.63% of the total variation of the precaudal body shape in sharks. Similar to the full body analysis, PC1 explains 47.84% of the variation, stemming largely from the position of the first dorsal fin. Sharks with a more posteriorly located first dorsal fin have lower PC1 scores, whereas those with higher PC1 scores have a more anteriorly located first dorsal fin. PC2 explains 25.49% of the total variation in precaudal body shape in sharks, and it is mainly linked to the position of the pectoral and pelvic fins. Higher PC2 values are associated with pectoral and pelvic fins that are positioned closely to one another; in contrast, lower PC2 values are associated with widely separated pectoral and pelvic fins. PC3 explains 9.53% of the total variation primarily from the dorsal ventral length of the pectoral fin, where sharks with shorter pectoral fins score higher compared to sharks with longer pectoral fins. PC4 explains 5.40% of the total variation and is affected by the curvature of the pectoral fins. Sharks with shorter but highly curved pectoral fins score higher compared to sharks with longer more pointed pectoral fins. PC5 explains 3.37% of the total variation that stems from the dorsal ventral depth of the posterior half of the precaudal body. Sharks with a narrower posterior half of the precaudal body score higher compared to sharks with a deeper posterior half of the precaudal body.

Figure 4C depicts the result of my precaudal body analysis showing the relationship between PC1 and PC2 (see Fig. 4A for color-coding scheme; for taxonomic identity of each plot, see Appendix 7) that exhibits a similar distribution pattern of plots to the full body analysis (Fig.

4B). Overall, members of each shark order clusters tightly together to occupy one specific region with the exception of a major division in Carcharhiniformes. Plots of Hexanchiformes, Squatiniformes, Orectolobiformes, and scyliorhinid (catsharks) Carcharhiniformes are clustered together on the left side of the diagram, whereas the right side of the diagram are occupied by plots of Squaliformes, Heterodontiformes, Lamniformes, and the houndsharks (Triakidae) and requiem sharks (Carcharhinidae) of the Carcharhiniformes. Unlike the full body analysis, however, plots of Pristiophoriformes are conspicuously distributed between the two aforementioned major clusters of plots, and the two known species of Echinorhiniformes are uniquely located on the bottom left region the diagram.

## CAUDAL FIN ANALYSIS

The first five principle components explain 90.81% of the total variation observed in the caudal fin shape of sharks. PC1 explains 51.18% of the variation and is associated with the aspect ratio of the caudal fin. Sharks with higher PC1 scores have a caudal fin with a high aspect ratio, whereas those with low aspect ratios have lower scores. PC2 explains 24.12% of the total variation, and it is associated with the overall depth of the upper lobe of the caudal fin. Sharks with a larger, more pronounced upper lobe have higher PC2 scores compared to those with a narrower upper lobe. PC3 explains 8.39% of the total variation and is associated with the depth of the tip of both the upper and lower lobes. Sharks with deeper fin tips score higher compared to sharks with narrower tips. PC4 explains 3.76% of the variation, and it is mainly associated with the angle of the ventral lobe at its origin where sharks with a larger angle score higher compared to those with a lower angle. PC5 explains 3.37% of the total variation caudal fins, and it mainly focused on the depth of both the upper and lower lobes where sharks with narrow upper lobes but deeper lower lobes score higher than sharks with deeper upper lobes but narrower lower lobes.

Figure 4D shows the result of my caudal fin analysis that plots PC1 against PC2 (see Fig. 4A for color-coding scheme; for taxonomic identity of each plot, see Appendix 8). The plots (Fig. 4D) display wide distribution without any major division unlike the full body and precaudal body analyses (Fig. 4B, C). Nevertheless, members of each shark order tend to cluster close together, filling its own space in the morphospace with the arguable exception of Lamniformes. For example, Echinorhiniformes, Pristiophoriformes, and the majority of Orectolobiformes and Carcharhiniformes are found towards the left half of the total range of plot distribution, whereas Hexanchiformes, Squaliformes-Echinorhiniformes, and Heterodontiformes are distributed, respectively, at the bottom center, center, and top center of the total plot distribution range. Squatiniformes uniquely occurs in the upper right corner of the morphospace, Lamniformes and the remaining species of Carcharhiniformes and Orectolobiformes are located on the right half of the total plot distribution range, although Lamniformes occur in three distinct clusters: 1) a cluster of three outliers at the bottom center represented by Alopiidae, 2) a cluster of six plots to the far right side of the scatter plot diagram consisting of Cetorhinidae (basking shark) and Lamnidae (white, mako, salmon, and porbeagle sharks), and 3) a cluster near the center of the diagram represented by the remaining lamniform taxa (Mitsukurinidae. Odontaspididae, Pseudocarchariidae, and Megachasmidae). One outlier of Orectolobiformes that occurs together with the Cetorhinidae-Lamnidae cluster is the whale shark, *Rhincodon typus* Smith 1829 (Rhincodontidae).

## EFFECT OF SIZE ON SHAPE BY SHARK ORDER

Figure 5 shows the results of my ANCOVA to examine the effect of size on shape by each shark order. A confidence ellipse is included for each shark order to show the spread of its splits in the scatter plot diagram. Figure 5A shows the location of taxonomic orders in the scatter plot diagram of mean overall shape against size. Among all shark orders, Carcharhiniformes shows the largest overall shape variation when measured against size with the slope of the confidence ellipse (Fig. 5A). The remaining graphs (Figure 5B–F) depict how size effects of shark order in relation to the first five principle components (PC1–PC5) in which they explain most (84.89%) of the total shape variation observed in sharks. Similar to mean overall shape against size (Fig. 5A), PC1 against size shows that Carcharhiniformes is most affected by size as compared to the other shark orders (Fig. 5B). My analyses of size against PC2 (Fig. 5C) and PC3 (Fig. 5D) show that most shark orders have shape differences due to size although the differences in the case of PC3 are not as large as that of PC2. In my analyses of size against PC4 (Fig. 5E) and PC5 (Fig. 5F), only Pristiophoriformes shows rather large shape differences by size. Whereas such differences may observed in isolated morphological features, overall, when all sharks are combined and examined together as a whole (Fig. 5A), my analysis indicates that size does have an effect on overall body shape (ANOVA: $df = 1, 452$; $F = 243.54$; $p<0.001$). Additionally, my analysis shows that each taxonomic order also differ in mean shape (ANOVA: $df = 1, 452$; $F = 2.2$; $p<0.05$).

## DISCUSSION

### BODY SHAPE VARIATION IN SHARKS

Thomson & Simanek (1977) examined 56 species of sharks represented by a wide taxonomic range, where the four body form groups (Fig. 1B) have continued to be the basis of subsequent studies (e.g., Irschick & Hammerschlag, 2014; Irschick *et al.*, 2017) and reviews on shark morphology and body mechanics (e.g., Maia *et al*., 2012; Shadwick & Goldbogen, 2012; Lauder & Di Santo, 2016). However, my landmark-based geometric morphometric analyses clearly show that there are two broad categories of body forms, rather than four, among extant sharks (Fig. 4B). The major source of the division comes from the morphology of the precaudal portion of the body (Fig. 4C) and not from the shape of the caudal fins (Fig. 4D). One of the two major groups, that is located on the left side of the scatter plot diagram (Fig. 4B), consists of elongated ('shallow-bodied') fusiform carcharhiniforms and hexanchiforms as well as dorsoventrally flattened ('shallow-bodied') orectolobiforms, pristiophoriforms, and squatiniforms. For the purpose of this study, I refer this group to 'Group A' sharks. The other major group located on the right side of the scatter plot diagram (Fig. 4B) consists of stout ('deep-bodied') fusiform sharks, including the remaining carcharhiniforms, heterodontiforms, lamniforms, and the vast majority of squaliforms. This assemblage of sharks is referred herein to 'Group B' sharks. The four specific outliers, *Stegostoma faciatum* and the three species of *Alopias*, seen in the bottom left corner of the scatter plot diagram (Fig. 4B) are characterized by an exceptionally elongate caudal fin that is as long as the precaudal body. However, my precaudal body analysis (Fig. 4C) does not find those four species to be distinctively different. Therefore, I regard *S. faciatum* to be an extreme form of Group A, and *Alopias* spp. an extension of Group B (Fig. 4B). In addition, it is noteworthy that the two echinorhiniform species and a few species of Squaliformes (cookiecutter and pygmy sharks: *Isistius brasiliensis* (Quoy & Gaimard, 1824), *I. labialis* Meng *et al.*, 1985, *I. plutodos* Garrick & Springer, 1964 and *Euprotomicrus bispinatus* (Quoy & Gaimard, 1824)) occur in the gap between Groups A and B with their tendency towards Group A. However, because they do not form any distinct clusters, they do not merit a separate group assignment. Based on these interpretations, Table 1 lists shark taxa belonging to each of the two groups. Although Group A (245 species) and Group B (259 species) have similar total numbers of species, Group A (44 genera) has a noticeably smaller generic diversity than Group B (60 genera).

Thomson & Simanek (1977) noted that the position of the first dorsal fin and the aspect ratio of the heterocercal caudal fin represent the two most important factors that determine the body form in sharks and formed the basis of differentiating their four body form groups (Fig. 1B). Based on my full body analysis (Fig. 4B), I found their proposition to be true. For example, most of the variation from PC1 was the result of the position of the first dorsal fin. A more posteriorly located first dorsal fin would result in a negative value placing sharks on the left side of the scatter plot diagram, whereas a more anteriorly placed first dorsal fin would result in a positive value placing sharks on the right side of the diagram. Likewise, much of the variation in PC2 was due to differences in the aspect ratio of the caudal fin. Sharks with a more upright caudal fin would lead to a negative value placing them in the bottom region of the diagram, whereas those with a low aspect ratio would place them in the top region of the diagram. It is worth noting that I found no additional body shape divisions in sharks in the full body analysis when using PC3, PC4, or PC5, in place of PC2, although there was some segregation by taxonomic order (see Appendices 4–6) suggesting some morphological differences are present but confined to each order.

My precaudal body analysis did not account for the caudal fin data that would correspond to PC2 in the full body analysis. Yet, the scatter plot diagram resulted in two major divisions (Fig. 4C) that are essentially identical to Group A and Group B found in the full body analysis (Fig. 4B). This finding strongly suggests that the precaudal body shape has a much stronger influence over the overall body forms than to the caudal fin shape in sharks. The plot distributions of orectolobiforms and elongated carcharhiniforms overlap nearly completely as in the full body analysis (Fig. 4B, C), but hexanchiforms and echinorhiniforms as well as dorsoventrally flattened pristiophoriforms and squatiniforms are noticeably diverged from the main cluster of Group A. Sharks of Group B in the full body analysis are also represented in the major cluster on the right side of the diagram (i.e., squaliforms, heterodontiforms, lamniforms. and the stout carcharhiniforms); however, the plots are likewise distributed more widely in the precaudal fin analysis (Fig. 4C) than the full body analysis (Fig. 4B).

Thomson & Simanek (1977) noticed that the positions of the dorsal, pectoral, and pelvic fins to be key features that influence the body forms in sharks where the positions of the latter two types of fins were the basis for the recognition of their Groups 3 and 4 sharks (Fig. 1B). My study shows that the variable causing the most variation in the precaudal body shape is the position of the first dorsal fin (PC1), followed by the position of the pectoral and pelvic fins (PC2). A large separation between the pectoral fin to the pelvic fin resulted in a lower score placing such sharks in the lower half of the scatter plot diagram, whereas the pectoral and pelvic fins that were placed closely to each other resulted in a higher score.

The caudal fin of sharks is typically regarded to show a wide range of variation (e.g., Thomson, 1976; Thomson & Simanek, 1977; Scacco *et al.*, 2010). However, unlike the full body and precaudal body analyses, my caudal fin analysis shows no major division of plots. Instead, although each order tends to occupy its own region in the morphospace, plots overall occur as one large cluster, suggesting that different forms of caudal fin recognized (e.g., Thomson & Simanek, 1977, fig. 6) are essentially variation of one basic design. A few notable extremes of the continuum are Squatiniformes with a significantly large ventral lobe compared to most sharks, Cetorhinidae, Lamnidae, and Rhincodontidae with a nearly symmetrical, lunate caudal fin, and Alopiidae with an exceptionally elongated whip-like dorsal lobe.

There are two major distinct body forms, Group A and Group B (Fig. 4B), recognized, but it is worth noting that Group A comprises two seemingly different forms, sharks with elongated fusiform body and dorsoventrally flattened forms. Whereas my examination that focused on the body form only in lateral profile may have a risk of over-generalizing the body forms (see ‘Limitations of This Study’ above), both body forms can nevertheless be characterized as ‘shallow-bodied’ sharks, that rather sharply contrasts Group A sharks with a deep-bodied fusiform precaudal design.

At first glance, the recognition of only two major body forms (Fig. 4B) would appear also not to support Thomson & Simanek's (1977) four basic body forms in sharks (Fig. 1B). However, it is noteworthy that Thomson & Simanek's (1977) four body form groups are not randomly distributed. Figure 6 is essentially the same scatter plot diagram as the full body analysis shown in Figure 4B but plots only species of the genera included in Thomson & Simanek's (1977) study with each of the four body form groups identified (Fig. 1B) in addition to pristiophoriform and squatiniform sharks that have a dorsoventrally flattened body. Sharks of

Thomson & Simanek's (1977) Groups 1, 2, and 4 as well as some Group 3 represent my Group B sharks, whereas the remaining sharks of Group 3 represent my Group A sharks. Furthermore, within my Group B cluster, sharks of Group 3 tend to occupy the upper region, followed downward within the cluster by sharks of Group 4, Group 1, and Group 2. Sharks of Group 3 are also represented in my Group A, some of which are suggestive of possessing a body depth as low as pristiophoriform and squatiniform sharks. This fact, combined with Thomson & Simanek's (1977) four body form groups occupying different regions of the morphospace within my Group B, indicates that there may be arguably as many as six subcategories of body forms in sharks if pristiophoriform and squatiniform sharks are considered to be a separate category by having a flat ventral body surface. However, the merit of decisively defining the six subcategories is uncertain because the separations among the subcategories in each of the two major clusters are not as sharp as the separation between Group A and Group B.

My morphometric study suggests that there are two major body forms in sharks (Fig. 4B). However, there are also some indications based on my ANCOVA that the overall body shape variation may be in part affected by the body size and taxonomic order (Fig. 5A). A similar observation was also noted by Irschick *et al*. (2017) even among the eight species of sharks they examined in their morphological study. In addition, my ANCOVA appears to suggest that there are also body shape differences based on taxonomic orders, although this is not necessarily surprising because some shark orders (e.g., Squaliformes, Orectolobiformes, and Lamniformes) have a wide range of interspecific size variation, whereas other orders are represented by species of similar sizes (e.g., Pristiophoriformes and Heterodontiformes) (see Ebert *et al*., 2013). Nevertheless, the division of the two major body form groups identified in my study (Fig. 4B) is quite sharp raising the possibility that the size and taxonomic effects on body shape can be regarded as less important when discussing the functional, ecological, and evolutionary implications of the two body forms below.

## FUNCTIONAL IMPLICATIONS

The study of the relationship between body form and swimming mechanism in fishes has a long history and is a central concept in understanding fish ecology and evolution (Breder, 1926; Lindsey, 1978; Webb, 1984; Blake, 2004). Swimming is defined as movement through water by propulsion of the body or body parts (Gray, 1933; see also Lindsey, 1978), and the two major modes of swimming in fishes are oscillatory and undulatory motions (Webb, 1984). The oscillatory motion is described as a propulsive structure swiveling on its base to generate thrust (e.g., Batoidea or rays), whereas the undulatory motion uses thrust to swim by bending the body in a backward-moving propulsive wave that extends into the caudal region (Sfakiotakis *et al*., 1999). The undulatory motion can be further divided into anguilliform, subcarangiform, carangiform, and thunniform modes (Breder, 1926; Lighthill, 1975; Webb, 1984; Sfatiokakis *et al*., 1999). Sharks use three of these four modes: anguilliform, carangiform, and thunniform (Maia *et al.*, 2012; Lauder & Di Santo, 2016). Some species of sharks have been heavily studied in regards to swimming mode whereas many others remain uninvestigated (Lingham-Soliar, 2005; Maia *et al*., 2012; Shadwick & Goldbogen, 2012; Maia & Wilga, 2016). Nevertheless, Maia *et al*. (2012) assigned one of the three swimming modes to each of many shark taxa consisting of a wide range of lineages, and they are summarized in Table 1. One striking observation that can be gleaned from the distribution of the three swimming modes in Table 1 is that Group A almost entirely consists of anguilliform sharks whereas Group B consists of carangiform and thunniform sharks.

Table 1 strongly suggests that, in sharks, swimming modes are highly correlated with body forms. Anguilliform is described as ‘eel-like’ swimming in which the entire trunk and caudal fin undulate with several waves transmitted through the body axis, whereas carangiform shows limited lateral movement that is mostly confined to the posterior half of the body (Maia *et al.*, 2012). Thunniform has the least lateral movement of the body in which the movement is restricted to the caudal fin from the caudal peduncle (Maia *et al.*, 2012). My study demonstrates that the shallower-bodied forms (Group A sharks) swim with more undulatory lateral movements throughout the body axis compared to the deeper-bodied sharks (Group B sharks with a more stout girth) with restricted lateral movement confined largely to the posterior portion of the body. Similar trends are also observed in many other fish taxa (see Blake, 2004).

## ECOLOGICAL IMPLICATIONS

Sharks exhibit a great diversity in their habitat and depth distribution in the marine ecosystem (Compagno, 1990). For example, Dulvy *et al.* (2014) attempted to assign sharks to one of five possible habitats, including (1) coastal and continental shelf, (2) pelagic, (3) meso- and bathypelagic, (4) deepwater, and (5) freshwater. However, because habitat data of shark species are not reported in a consistent manner, decisively assigning a specific Dulvy *et al.*'s (2014) habitat category to every known shark species is not possible at the present time. However, I attempted to divide the habitats of shark genera into two broad categories, benthic and pelagic, based on the habitat information provided by Ebert *et al.* (2013). If the preferred habitat of a shark taxon was described using one or more of the following expressions, it was categorized as 'benthic': ‘benthic,’ ‘on muddy bottom,’ ‘along continental shelves,’ ‘on sediment,’ ‘bottom on insular continental shelves,’ or ‘near continental shelves.’ The following expressions were categorized as 'pelagic': ‘pelagic,’ ‘epipelagic,’ ‘bathypelagic,’ ‘open ocean,’ or ‘oceanic.’ My dichotomous scheme (benthic vs. pelagic) used in this study is appreciably coarse, where non-obligatory benthic sharks, such as demersal forms (e.g., *Carcharias, Dalatias, Odontaspis, Rhizoprionodon*, etc.) are even classified as ‘benthic.’ However, this decision is deliberate in order to tease out the ‘true pelagic forms’ conservatively by broadening the range of the benthic regime, because my goal is to examine the differences in the proportion between benthic and pelagic sharks in each body form group (Group A vs. Group B). Table 1 summarizes the categorizations denoted by genera in bold or with an asterisk.

Table 1 clearly shows that Group A is dominated by benthic sharks, whereas pelagic forms are more common in Group B relative to Group A. Only three of the 44 Group A genera are pelagic, and only seven species among the 245 species (i.e. only 2.86%) in Group A are pelagic. On the other hand, 21 of the 60 Group B genera are pelagic, where 66 species among the 259 species (25.48%) are pelagic in Group B. If the sharks that are 'occasionally pelagic' (taxa with asterisk) are included, the total number of pelagic species in Group A remains small (4.49%), whereas that in Group B nearly doubles (47.10%). The fact that even the conservative criterion for 'pelagic' I used shows such a large difference between the two groups clearly indicates that, whereas benthic lifestyles can be achieved with both body forms (Groups A and B), the body form of Group B has greater potential to be able to exploit pelagic, or more open-water, habitats through evolution by means of carangiform and thunniform swimming modes (see above). The predominantly benthic lifestyle of Group A sharks may be constrained by the anguilliform swimming mode (see above). The anguilliform swimming is said to be energetically more costly compared to carangiform and thunniform swimming (Webb, 1988), requiring them to rest on the seafloor more frequently—hence benthic.

## EVOLUTIONARY IMPLICATIONS

Sharks represent some of the oldest, yet one of the most diverse groups of vertebrates (Grogan *et al.*, 2012). In both the fossil record (e.g., Maisey, 2012) and molecular studies (e.g., Naylor *et al.*, 2012), modern sharks are classified into two superorders, Squalomorphii and Galeomorphii (Fig. 1A). Whereas many phylogenetic studies on extant elasmobranchs exist (Kitamura, 1996; Heinicke *et al*., 2009; Maisey *et al*., 2004; Human *et al*., 2006; Vélez-Zuazo & Agnarsson, 2011; Pavan-Kumar *et al*., 2013; Amaral *et al*., 2018), Naylor *et al*.'s (2012) work remains to be the most extensive molecular-based (mitochondrial NADH 2 sequence) elasmobranch phylogeny based on 595 extant species. Below, I use Naylor *et al*.'s (2012) phylogenetic tree (Fig. 1A) to discuss the patterns and pathways of the body form evolution in sharks, and add further comments on the evolutionary implications. It should be noted that morphology-based phylogenetic studies of elasmobranchs (e.g., de Carvalho, 1996; Shirai, 1996) are deliberately avoided for discussion. This is because any discussion on the body forms using such trees would be circular arguments as characters to build those trees include variables related to body parts that constitute the body form in the first place.

My full body geometric morphometric analysis shows that phylogenetically the most basal as well as the two most derived squalomorph sharks—Hexanchiformes, Pristiophoriformes, and Squatiniformes (Fig. 7A)—fall in Group A (Fig. 4B). Other squalomorphs, notably squaliforms are found in Group B, whereas the two species of Echinorhiniformes arguably occur between the two major groups. These order-level taxonomic distributions suggest that shallow-bodied forms (Group A) are plesiomorphic within Squalomorphii, that Squaliformes marks the evolution of deep-bodied forms (Group B), that Echinorhiniformes represents somewhat intermediate between Group A and Group B, and that the ultimate step in the body form evolution of Squalomorphii is marked by the dorsoventral flattening in Pristiophoriformes and

Squatiniformes (Figs. 4A, B, 7A). On the other hand, phylogenetically the most basal order within Galeomorphii, Heterodontiformes, as well as a large number of the most derived galeomorphs, Lamniformes and non-scyliorhinid species of Carcharhiniformes, are found in Group B (Figs. 4A, B, 7A). The order that is arguably phylogenetically intermediate within Galeomorphii, orectolobiforms, and the basal group of Carcharhiniformes, scyliorhinid carcharhiniforms (see Naylor *et al*., 2012), belong to Group A (Fig. 7A).

If Naylor *et al*.'s (2012) phylogenetic tree, that has an identical order-level topology as da Cunha *et al*.’s (2017; except exclusion of Echinorhiniformes) tree, is used at face value, possible evolutionary patterns of body forms in Squalomorphii and Galeomorphii can be summarized as exactly opposite to one another where there are at least two possible scenarios (Fig. 7B). One scenario is to assume that Squalomorphii is fundamentally an assemblage of Group A sharks, but certain members, Squaliformes and Echinorhiniformes, independently evolved to become Group B sharks. Galeomorphii may be considered essentially as an assemblage of Group B shark, but eventually gave rise to two separate lineages of Group A sharks, Orectolobiformes and scyliorhinid Carcharhiniformes. In other words, the evolutionary shift in body forms in this first scenario is considered ‘unidirectional’ parallel evolution (Fig. 7B, top). The second scenario can be characterized as ‘bidirectional’ convergent evolution or evolutionary reversal (Fig. 7B, bottom). In this scenario, where the most basal squalomorph (Hexanchiformes) and galeomorph (Heterodontiformes) are nested within Group A and Group B, respectively, the next phylogenetically successive squalomorphs (Squaliformes and Echinorhiniformes) and galeomorphs (Orectolobiformes and scyliorhinid Carcharhiniformes) evolved to become, or at least showed a tendency towards becoming, Group B and Group A, respectively. The most derived squalomorphs (Pristiophoriformes and Squatiniformes) and galeomorph (Lamniformes and non-scyliorhinid Carcharhiniformes) then evolved to become Group A and Group B sharks, respectively. Furthermore, it is entirely possible that one of the two superorders could have undergone ‘unidirectional’ evolution and the other ‘bidirectional.’

The possible scenarios shown in Figure 7 rely on the tree topology of each superorder attained by Naylor *et al*. (2012) that must be viewed with caution. Whereas some molecular-based phylogenetic analyses are regarded as not robust because of a small number of taxa examined (e.g., Kitamura, 1996; Human *et al*., 2006; Pavan-Kumar *et al*., 2013), practically all other molecular-based studies with a wide range of elasmobranch taxa yielded an identical tree topology for Galeomorphii as Naylor *et al.*’s (2012) tree (Fig. 1A) (Heinicke *et al*., 2009; Maisey *et al*., 2004; Amaral *et al*., 2018). Therefore, the two possible evolutionary pathways for Galeomorphii depicted in Figure 7 are equally plausible (but see below for further discussion). In practically all molecular-based analyses with a large number of taxa examined, Hexanchiformes is the basal-most Squalomorphii, but the exact phylogenetic interrelationship among the rest of the squalomorph orders remains to be tenuous. For example, Maisey *et al*. (2004, fig. 5A) and Heinicke *et al*. (2009, fig. 2) found the following topological arrangement: [Hexanchiformes + [Pristiophoriformes + [Squaliformes + [Echinorhiniformes + Squatiniformes]]]]. On the other hand, Amaral *et al.’s* (2018, fig. 5) study that did not include Echinorhiniformes yielded [Hexanchiformes + [[Pristiophoriformes + Squaliformes] + Squatiniformes]]. Vélez-Zuazo & Agnarsson (2011, fig. 4) attained [Hexanchiformes + [Squaliformes + [[Pristiophoriformes + Echinorhiniformes] + Squatiniformes]]], but we consider their work to be questionable because some taxa with overwhelming support for their monoplyly are shown to be non-monophyletic (e.g., Squaliformes, specifically Etmopteridae and *Squatina*, and Orectolobiformes). Nevertheless, whereas it is reasonable to assert that Hexanchiformes as a pioneer squalomorph taxon that belongs to Group A, the conflicting order-level tree topologies for the remaining squalomorphs make the evolutionary pathway suggested for Squalomorphii in Figure 7 less convincing. Regardless, in sharks as a whole, the body form evolution was clearly complex where each superorder (Squalomorphii and Galeomorphii) exploited both body form morphospaces through its phylogeny. The complex evolution of body forms in sharks is evident even if one maps Thomson & Simanek's (1977) four body form groups (Fig. 1B) on the same phylogenetic tree, where the mapping (Fig. 7C) indicates that Group 1, 2, and 3 each evolved twice within the clade that consists of Orectolobiformes, Lamniformes, and Carcharhiniformes.

The earliest squalomorph as well as the earliest galeomorph are represented in the Early Jurassic record by Hexanchiformes and Heterodontiformes, respectively (Maisey, 2012), that is congruent with their basal-most position in the respective superorder suggested by molecular-based phylogenetic studies (Heinicke *et al*., 2009; Maisey *et al*., 2004; Naylor *et al*., 2012; Amaral *et al.*, 2018; Fig. 1A). The fossil record indicates that, besides Hexanchiformes and Heterodontiformes, the major lineages of elasmobranchs had already become established by the Late Jurassic, at least including Squaliformes, Squatiniformes, Orectolobiformes, Lamniformes, and Carcharhiniformes (e.g., Kriwet & Klug, 2004; Thies & Leidner, 2011; Cappetta, 2012; Maisey, 2012). Although taxonomically not diverse, each of these shark orders has at least one representative taxon known by complete, articulated skeletal remains, some of which even preserve their body outline (Kriwet & Klug, 2004; Thies & Leidner, 2011). Although those fossil skeletons are two-dimensionally preserved taphonomically, many of the fossil taxa are reminiscent to their modern relatives in their respective order, suggesting that the body form diversity within each order has been relatively stable through geologic time. However, exceptions do exist. For example, a putative Late Jurassic lamniform, *Palaeocarcharias stromeri* de Beaumont, 1960, is interpreted to have had a relatively dorsoventrally flattened body suited for benthic lifestyle (Duffin, 1988; Cappetta, 2012), meaning that it likely represents a Group A shark unlike any other lamniforms examined in my study. In addition, the vast majority of fossil sharks are known only from their teeth (Cappetta, 2012; Maisey, 2012) where their body forms can only be speculated. In addition, there are even many extinct clades not represented in the modern shark lineages, including an extinct shark order Synechodontiformes (e.g., Kriwet & Klug, 2004; Thies & Leidner, 2011; Cappetta, 2012). The fact that exceptions and extinct forms exist strongly suggests that the actual evolutionary pathways in each superorder must have been even more complex than either scenario depicted in Figure 7.

The clade that unites Squalomorphii and Galeomorphii is the basal-most Selachii (Fig. 1A), but whether the earliest shark was a Group A shark or a Group B shark is uncertain. However, the fact that the earliest batoids (skates and rays) are also known from Early Jurassic rocks (Cappetta, 2012; Maisey, 2012) and that Batoidea is sister to Selachii (Fig. 1A) suggests that the earliest shark could have had a shallow body depth. If so, it is reasonable to postulate a hypothesis that the earliest shark was possibly a Group A shark.

## CONCLUSIONS

Sharks have a long geologic history (Grogan *et al*., 2012; Maisey, 2012) in which their success has been attributed to their diversity in body shape and locomotor design (Lauder & Di Santo, 2016). Traditionally, sharks were classified into four groups according to their basic body forms (Thomson & Simanek, 1977), but the proposition was based only on 56 species using simple morphometric analysis. In my study, I examined the body forms of nearly all the known (ca.

470) extant shark species illustrated in the shark field guide, *Sharks of the World: A Fully Illustrated Guide* by Ebert *et al*. (2013). I used landmark-based geometric morphometrics, and I ran three different analyses: the ‘full body,’ ‘precaudal body,’ and ‘caudal fin' analyses.

Although there are some indications that the body size and taxonomic order may have some effects on the overall body shape variation, the results of my full body analysis strongly suggest that there are two major body forms in sharks, rather than four. The two major body form divisions are characterized as a ‘shallow-bodied’ form (Group A) and ‘deep-bodied’ form (Group B). This pattern is also present in the precaudal body analysis, because there were also two major divisions. In contrast, the caudal fin analysis indicated no major plot divisions, implying that all sharks share essentially one basic caudal fin design. However, it is noteworthy that sharks of Thomson & Simanek's (1977) Groups 1, 2, and 4 as well as some Group 3 are found to occupy different regions within the Group B morphospace, whereas the remaining sharks of Group 3 represent my Group A sharks. If distinctively dorsoventrally flattened pristiophoriform and squatiniform sharks are considered to be an additional category, this observation would mean that there may be arguably as many as six subcategories of body forms in sharks. However, decisively separating among the six subcategories is not possible from my data, because their morphospaces in part overlap one another within each of my two major groups.

Based on my geometric morphometric analyses, particularly the results from the full body analysis that shows two major body forms in sharks, I made inferences about the functional, ecological and evolutionary implications. First, I found that swimming modes in sharks are highly correlated with body forms. For example, Group A sharks are predominantly anguilliform swimmers whereas Group B sharks are represented by carangiform and thunniform swimmers. Second, the majority of Group A sharks are found to be benthic, whereas pelagic forms are relatively common among Group B sharks. Third, based on the known fossil record as well as previously published molecular-based phylogenetic trees, each of the two superorders of sharks, Squalomorphii and Galeomorphii, must have gone through complex evolutionary history. This proposition is because each superorder contains both Group A and Group B sharks, possibly involving parallel evolution from one group to the other or at least one episode of evolutionary reversal. Lastly, the most ancestral shark, the clade that unites Squalomorphii and Galeomorphii, was possibly a benthic form with a Group A body form.

This study represents the most comprehensive investigation of the body forms in sharks since Thomson & Simanek's (1977) work. However, it is important to emphasize that conclusions drawn from my data must be viewed as working hypotheses because of the limitations that were imposed to my geometric morphometric analyses where the three-dimensionality as well as certain anatomical parts (the second dorsal and anal fins as well as the caudal fluke) could not be captured in my data (see Materials and Methods). It may be potentially fruitful to investigate the overall head and body shapes not only based on a two-dimensional geometric morphometrics on their dorsoventral aspect (that would also capture the caudal fluke), but also using three-dimensional geometric morphometrics. Such analyses may allow one to tease out any additional morphological differences or even potentially different groupings of body forms in sharks in which my study could not elucidate.

By building on Thomson & Simanek's (1977) conceptual framework, the results of this study provides a fresh look at the body form diversity in sharks. To elucidate further the functional, ecological, and evolutionary implications of the two identified major body forms in sharks, it may be worth to collect the first occurrence data of each major lineage of sharks in the geologic record. Such data may help to examine whether or not a certain 'cross-over' event from one body form group to the other body form group would correspond to any major geologic event or environmental shift. A morphometric investigation of the body form of extinct sharks, including completely extinct lineages where their skeletons and body outlines are known (e.g., Synechodontiformes) may also shed additional insights into the evolution of the body form diversity patterns.

Thomson & Simanek (1977) used a relatively comprehensive guidebook of sharks available to them at that time (i.e., Bigelow & Schroeder, 1948). I applied the same strategy by using a quite comprehensive guidebook of extant sharks (i.e., Ebert *et al*., 2013) and a more rigorous technique, landmark-based geometric morphometrics. My study demonstrates that such a use of an identification guidebook, especially if illustrations are given in a uniform manner, can be a powerful tool for the field of comparative anatomy to investigate a wide morphological spectrum of a given set of organisms.

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**Table 1.** Genera of Group A and B sharks (see Fig. 4B) and their taxonomic order (CAR, Carcharhiniformes; ECH, Echinorhiniformes; HET, Heterodontiformes; HEX, Hexanchiformes; LAM, Lamniformes; ORE, Orectolobiformes; PRI, Pristiophoriformes; SQL, Squaliformes; SQT, Squatiniformes), families, and total numbers of species in parentheses. Superscripts indicate swimming modes assigned by Maia *et al*. (2012) (1, anguilliform; 2, carangiform; 3, thunniform: see text). Genera in bold are taxa identified as 'pelagic,' and genera with asterisk (*) represent benthic taxa that are occasionally pelagic (see text). In this table, all known extant species of Squatiniformes (*Squatina*) are counted.

| Group A (44 genera; 245 species) | Group B (60 genera; 259 species) |
|---|---|
| *Apristurus* (CAR: Scyliorhinidae; 35)$^1$ | *Aculeola* (SQL: Etompteridae; 1)$^2$ |
| *Asymbolus* (CAR: Scyliorhinidae; 9)$^1$ | ***Carcharhinus*** (CAR: Carcharhinidae; 32)$^2$ |
| *Atelomycterus* (CAR: Scyliorhinidae; 5)$^1$ | *Carcharias* (LAM: Odontaspididae; 1)$^2$ |
| *Aulohalaelurus* (CAR: Scyliorhinidae; 2)$^1$ | ***Carcharodon*** (LAM: Lamnidae; 1)$^3$ |
| *Brachaelurus* (ORE: Brachaeularidae; 2)$^1$ | **Centrophorus* (SQL: Centrophoridae; 13)$^2$ |
| *Bythaelurus* (CAR: Scyliorhinidae; 8)$^1$ | *Centroselachus* (SQL: Somniosidae; 1)$^2$ |
| *Cephaloscyllium* (CAR: Scyliorhinidae; 21)$^1$ | *Centroscyllium* (SQL: Etompteridae; 7)$^2$ |
| *Cephalurus* (CAR: Scyliorhinidae; 1)$^1$ | *Centroscymnus* (SQL: Somniosidae; 2)$^2$ |
| *Chiloscyllium* (ORE: Hemiscylliidae; 7)$^1$ | ***Cetorhinus*** (LAM: Cetorhinidae; 1) |
| **Chlamydoselachus* (HEX: Chlamydosechalid.; 2)$^1$ | *Chaenogaleus* (CAR: Hemigaleidae; 1) |
| *Cirrhoscyllium* (ORE: Parascylliidae; 3)$^1$ | *Cirrhagaleus* (SQL: Squalidae; 3)$^2$ |
| ***Ctenacis*** (CAR: Proscylliidae; 1)$^1$ | *Dalatias* (SQL: Dalatiidae; 1)$^2$ |
| **Echinorhinus* (ECH: Echinorhinidae; 2) | *Deania* (SQL: Centrophoridae; 4)$^2$ |
| *Eridacnis* (CAR: Proscylliidae; 3)$^1$ | **Etmopterus* (SQL: Etompteridae; 37)$^2$ |
| ***Eucrossorhinus*** (ORE: Orectolobidae; 1)$^1$ | **Euprotomicroides* (SQL: Dalatiidae; 1)$^2$ |
| *Figaro* (CAR: Scyliorhinidae; 2)$^1$ | ***Euprotomicrus*** (SQL: Dalatiidae; 1)$^2$ |
| *Galeus* (CAR: Scyliorhinidae; 17)$^1$ | ***Eusphyra*** (CAR: Sphyrnidae; 1)$^2$ |
| *Ginglymostoma* (ORE: Ginglymostomatidae; 1)$^1$ | *Furgaleus* (CAR: Triakidae; 1) |
| *Gollum* (CAR: Pseudotriakidae; 3)$^1$ | ***Galeocerdo*** (CAR: Carcharhinidae; 1)$^2$ |
| *Halaelurus* (CAR: Scyliorhinidae; 7)$^1$ | *Galeorhinus* (CAR: Triakidae; 1) |
| *Haploblepharus* (CAR: Scyliorhinidae; 9)$^1$ | ***Glyphis*** (CAR: Carcharhinidae; 5)$^2$ |
| *Hemiscyllium* (ORE: Hemiscylliidae; 8)$^1$ | *Gogolia* (CAR: Triakidae; 1) |
| *Heptranchias* (HEX: Hexanchidae; 1)$^1$ | *Hemigaleus* (CAR: Hemigaleidae; 2) |
| *Hexanchus* (HEX: Hexanchidae; 2)$^1$ | ***Hemipristis*** (CAR: Hemigaleidae; 1) |
| *Holohalaelurus* (CAR: Scyliorhinidae; 5)$^1$ | *Hemitriakis* (CAR: Triakidae; 7) |
| ***Isistius*** (SQL: Dalatiidae; 3)$^2$ | *Heterodontus* (HET: Heterodontidae; 9) |
| *Nebrius* (ORE: Ginglymostomatidae; 1)$^1$ | ***Heteroscymonoides*** (SQL: Dalatiidae; 1) |
| *Notorynchus* (HEX: Hexanchidae; 1)$^1$ | ***Hypogaleus*** (CAR: Triakidae; 1) |
| *Orectolobus* (ORE: Orectolobidae; 10)$^1$ | *Iago* (CAR: Triakidae; 3) |
| *Parascyllium* (ORE: Parascylliidae; 5)$^1$ | ***Isogomphodon*** (CAR: Carcharhinidae; 1)$^2$ |
| *Parmaturus* (CAR: Scyliorhinidae; 9)$^1$ | ***Isurus*** (LAM: Lamnidae; 2)$^3$ |
| *Pilotrema* (PRI: Pristiophoridae; 1) | *Lamiopsis* (CAR: Carcharhinidae; 1)$^2$ |
| *Planonasus* (CAR: Pseudotriakidae; 1)$^1$ | *Lamiospsis* (CAR: Carcharhinidae; 1)$^2$ |
| *Poroderma* (CAR: Scyliorhinidae; 2)$^1$ | ***Lamna*** (LAM: Lamnidae; 2)$^3$ |

*Pristiophorus* (PRI: Pristiophoridae; 7)
*Proscyllium* (CAR: Proscylliidae; 2)[1]
*Pseudoginglymostoma* (ORE: Ginglymostomat.;1)[1]
*Pseudotriakis* (CAR: Pseudotrakidae; 1)[1]
*Schroederichthys* (CAR: Scyliorhinidae; 5)[1]
*Scyliorhinus* (CAR: Scyliorhinidae; 15)[1]
***Squaliolus*** (SQL: Dalatiidae; 2)
*Squatina* (SQT: Squatinidae; 20)
*Stegostoma* (ORE: Stegostomatidae; 1)
*Sutorectus* (ORE: Orectolobidae; 1)[1]
*Leptocharias* (CAR: Leptochariidae; 1)
***Megachasma*** (LAM: Megachasmidae; 1)
***Mitsukurina*** (LAM: Mitsukurinidae; 1)
*Mollisquama* (SQL: Dalatiidae; 1)[2]
*Mustelus* (CAR: Triakidae; 27)
*Nasolamia* (CAR: Carcharhinidae; 1)[2]
*Negaprion* (CAR: Carcharhinidae; 2)[2]
*Odontaspis* (LAM: Odontaspididae; 2)
*Oxynotus* (SQL: Oxynotidae; 5)[2]
*Paragaleus* (CAR: Hemigaleidae; 4)
***Prionace*** (CAR: Carcharhinidae; 1)[2]
*Proscymnodon* (SQL: Somniosidae; 2)[2]
***Pseudocarcharias*** (LAM:Pseudocarchar.; 1)
***Rhincodon*** (ORE: Rhincodontidae; 1)
*Rhizoprionodon* (CAR: Carcharhinidae; 7)[2]
*Scoliodon* (CAR: Carcharhinidae; 2)[2]
***Scylliogaleus*** (CAR: Triakidae; 1)
*Scymnodon* (SQL: Somniosidae; 1)[2]
***Scymnodalatias*** (SQL: Somniosidae; 4)[2]
*Somniosus* (SQL: Somniosidae; 5)[2]
***Sphyrna*** (CAR: Sphyrnidae; 7)[2]
*Squalus* (SQL: Squalidae; 25)[2]
**Triakis* (CAR: Triakidae; 5)
*Trianodon* (CAR: Carcharhinidae; 1)[2]
*Trigonognathus* (SQL: Etompteridae; 1)[2]
*Zameus* (SQL: Somniosidae; 2)[2]

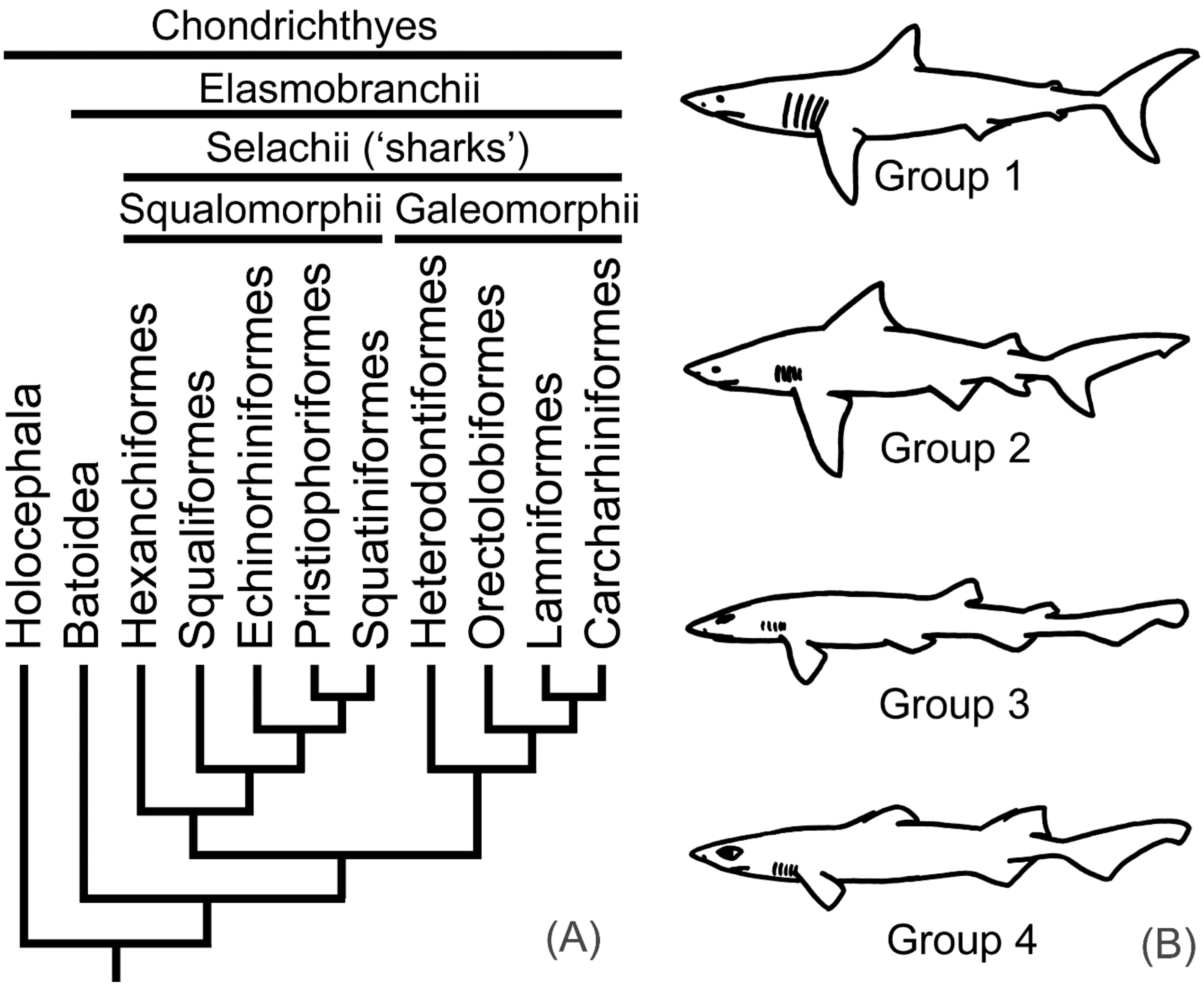

**Figure 1.** A, Molecular-based phylogeny of Chondrichthyes showing systematic position and interrelationships of shark orders (after Naylor *et al*., 2012). B, Thomson & Simanek's (1977) four groups of shark body forms (representative genera: *Carcharodon*, *Cetorhinus*, *Isurus*, *Lamna* and *Rhincodon* for Group 1; representative genera: *Alopias*, *Aprionodon*, *Carcharias*, *Carcharhinus*, *Galeocerdo*, *Hypoprion*, *Negaprion*, *Paragaleus*, *Prionace*, *Scoliodon* and *Sphyrna* for Group 2; representative genera: *Aspristurus*, *Galeus*, *Ginglymostoma*, *Mustelus*, *Pseudotriakis*, *Scyliorhinus* and *Triakis* for Group 3; representative genera: *Centroscyllium*, *Centroscymnus*, *Dalatias*, *Echinorhinus*, *Etmopterus*, *Isistius*, *Somniosus* and *Squalus* for Group 4).

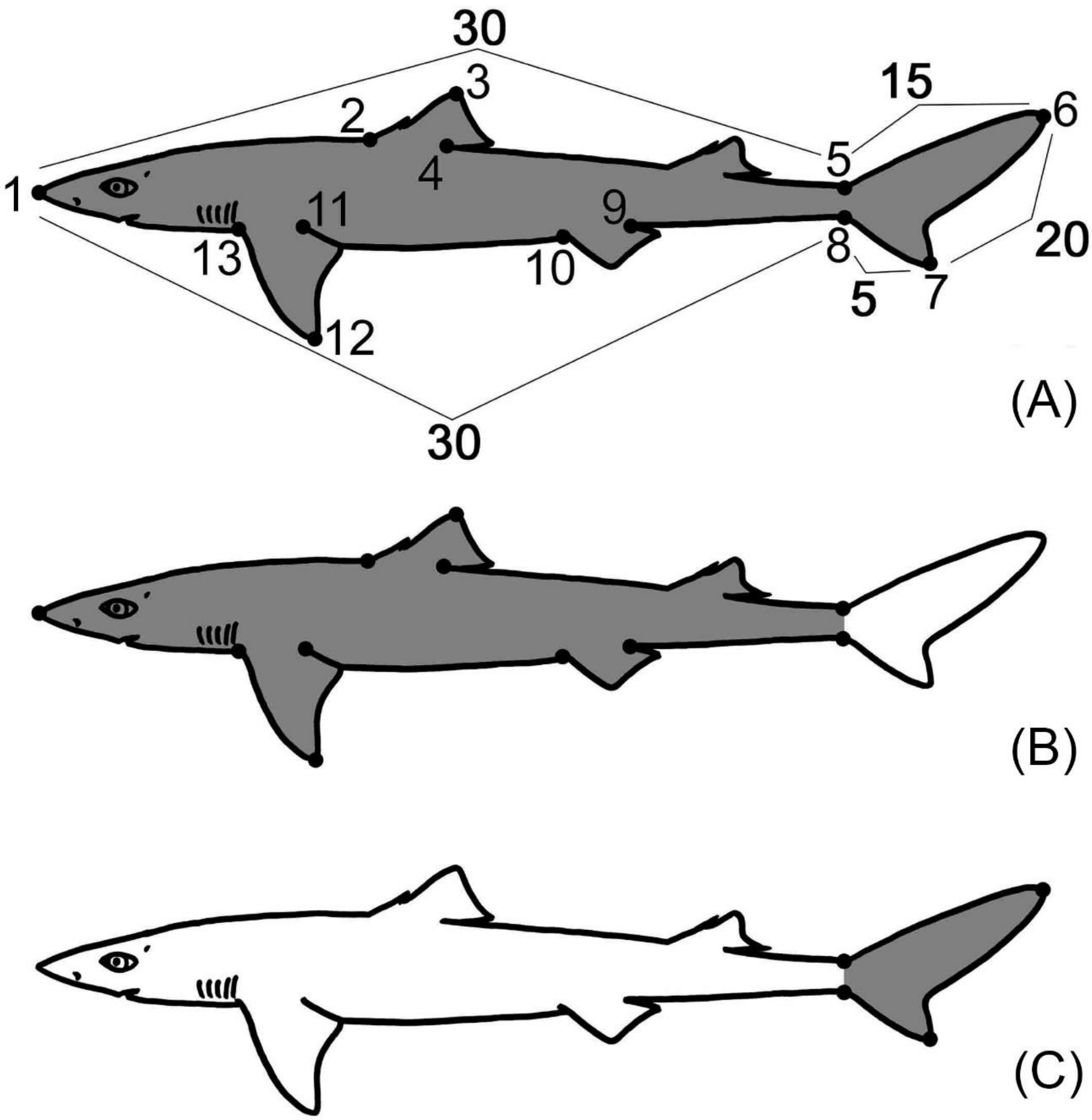

**Figure 2.** Homologous landmarks (circles) and non-homologous semi-landmarks (each bracket with total plot number within the range in bold: see text) used for morphometric analyses in this study (drawing of *Squalus acanthias* as an example: after Ebert *et al*., 2013, p. 83; not to scale). A, 'Full body analysis' showing 13 homologous landmarks (1, tip of the snout; 2, dorsal fin origin; 3, dorsal fin apex; 4, dorsal fin insertion; 5, caudal fin upper origin; 6, posterior tip of dorsal lobe; 7, ventral tip of ventral lobe; 8, lower origin of caudal fin; 9, pelvic fin insertion; 10, pelvic fin origin; 11, pectoral fin insertion; 12, pectoral fin apex; 13, pectoral fin origin). B, 'Precaudal body analysis' showing 11 of 13 homologous landmarks along with total of 60 (= 30 + 30) non-homologous semi-landmarks (see Fig. 2A) used. C, 'Caudal fin analysis' showing four of 13 homologous landmarks along with total of 40 (= 15 + 20 + 5) non-homologous semi-landmarks (see Fig. 2A) used.

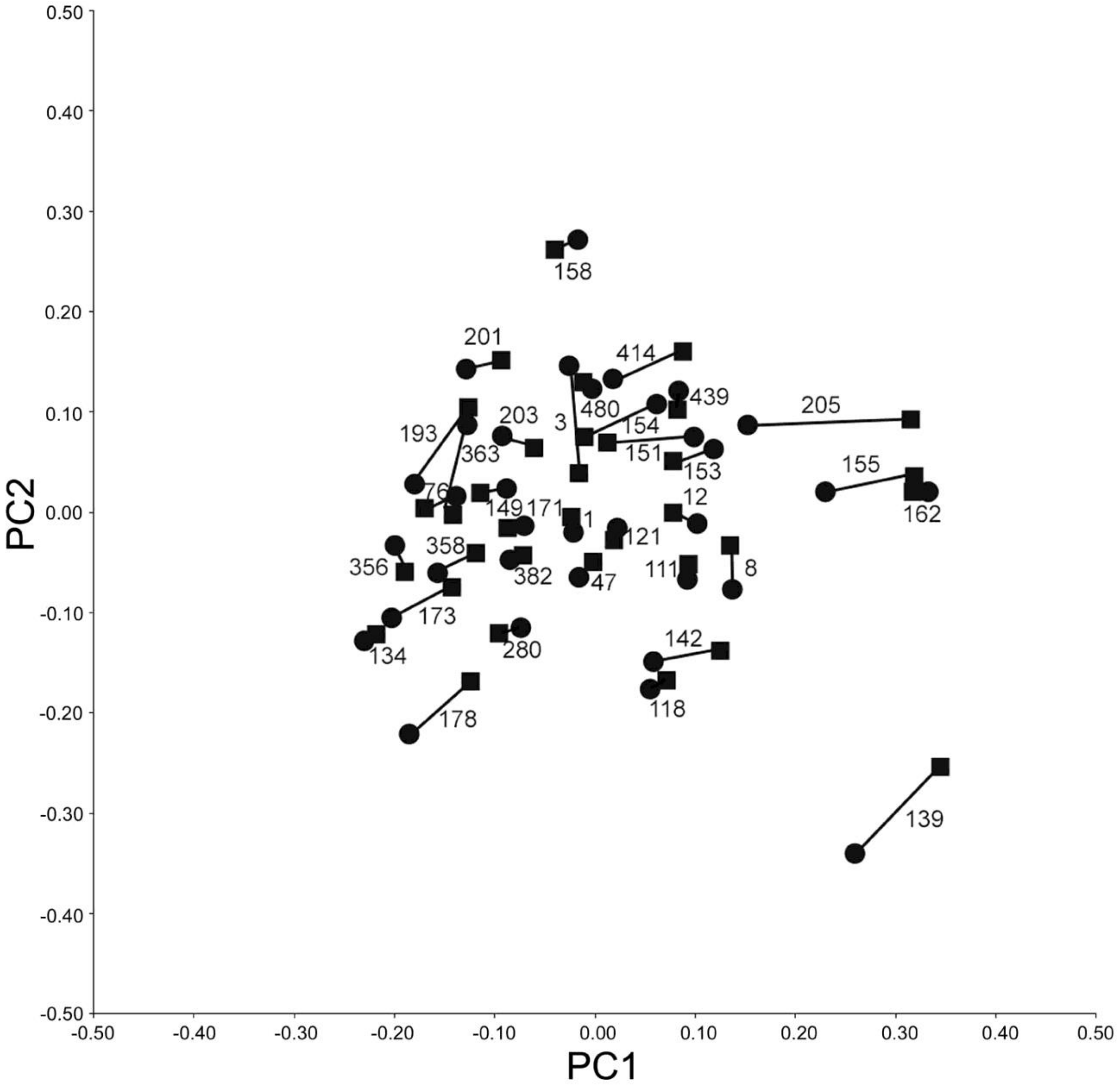

**Figure 3.** Pilot study of caudal fin shapes in one representative shark species of each shark family (see text), demonstrating similarity between Ebert *et al*.'s (2013) book illustrations (squares) and caudal fins directly traced from museum specimens (circles; see Appendix 2). Number indicates species code (see Appendix 1) with line connecting Ebert *et al*.'s (2013) illustration and museum specimen for each examined species.

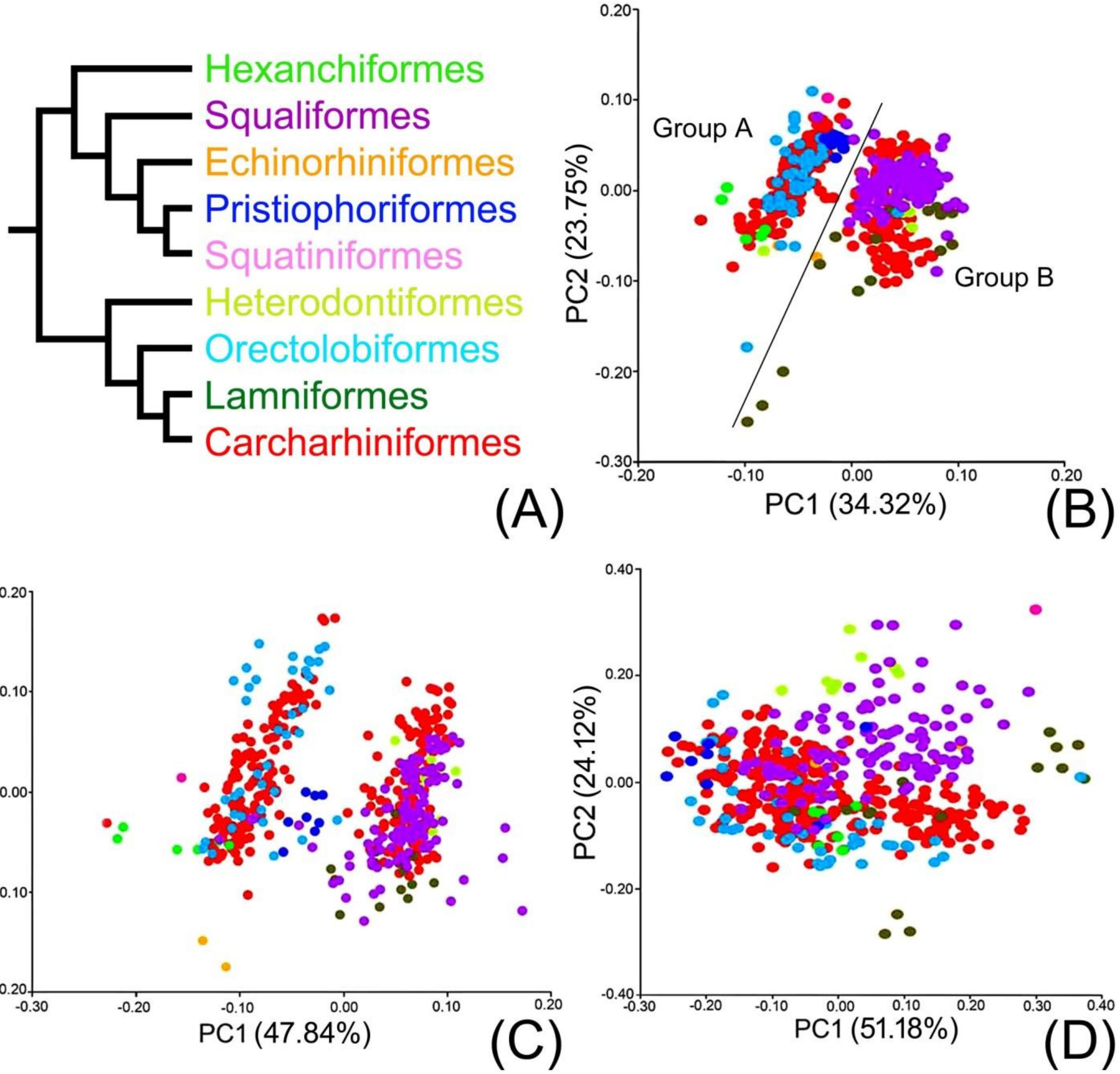

**Figure 4.** A, Phylogenetic tree of shark orders (after Naylor *et al*., 2012) showing color-coding scheme of taxonomic orders used for plots in Fig. 4B–D. B, Scatter plot diagram of full body analysis showing division (line) between Group A and Group B discussed in this paper. C, Scatter plot diagram of precaudal body analysis. D, Scatter plot diagram of caudal fin analysis. Percentage in parentheses in each axis denotes percent variation explained by that principle component.

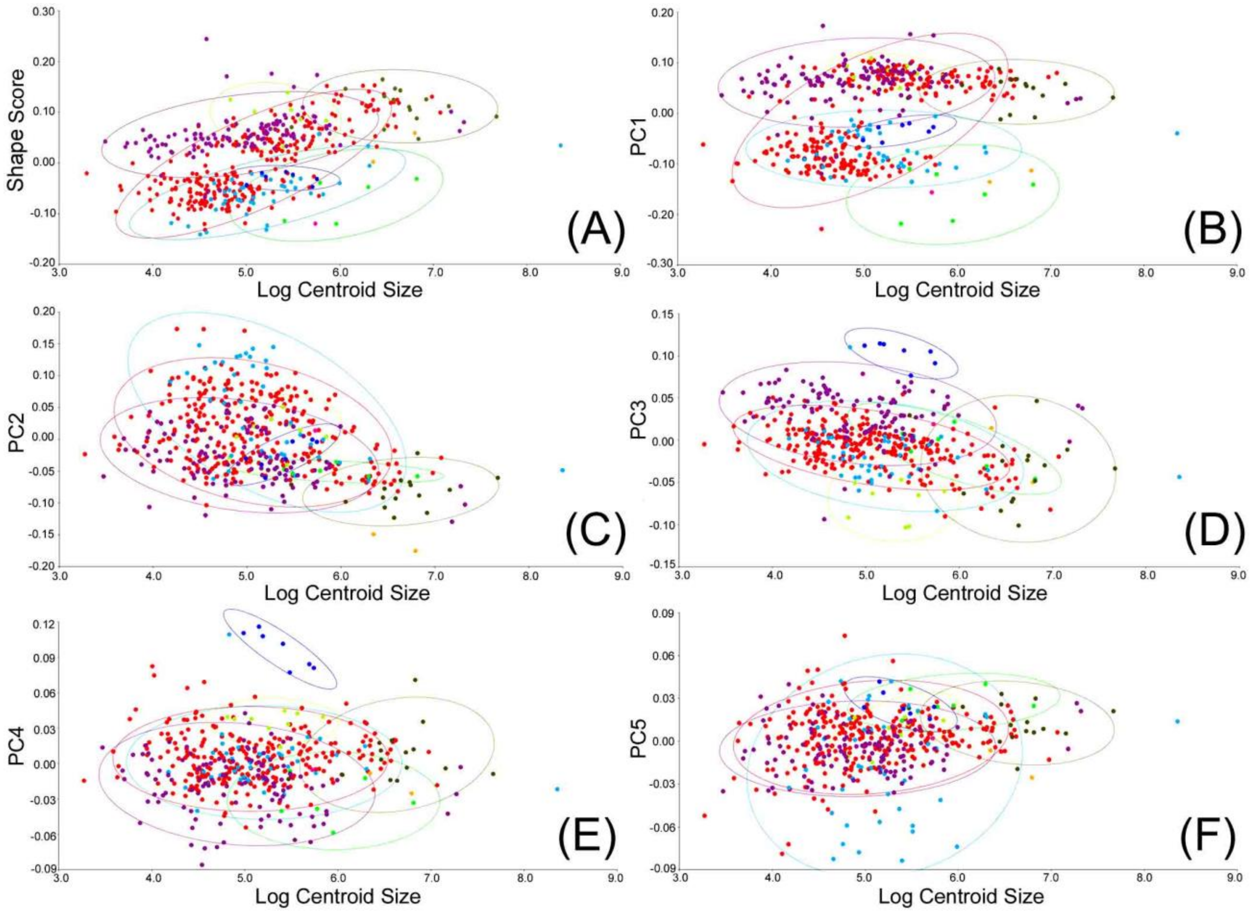

**Figure 5.** Scatter plot diagrams between log centroid size (*x*) and shape score (*y*) of precaudal body for 471 species of sharks examined (see Fig. 4A for color codes). A, Log centroid size and mean shape score. B, Log centroid size and PC1 scores. C, Log centroid size and PC2 scores. D, Log centroid size and PC3 scores. E, Log centroid size and PC4 scores. F, Log centroid size and PC5 scores. Each oval indicates confidence ellipse for each order to show the spread of its plots.

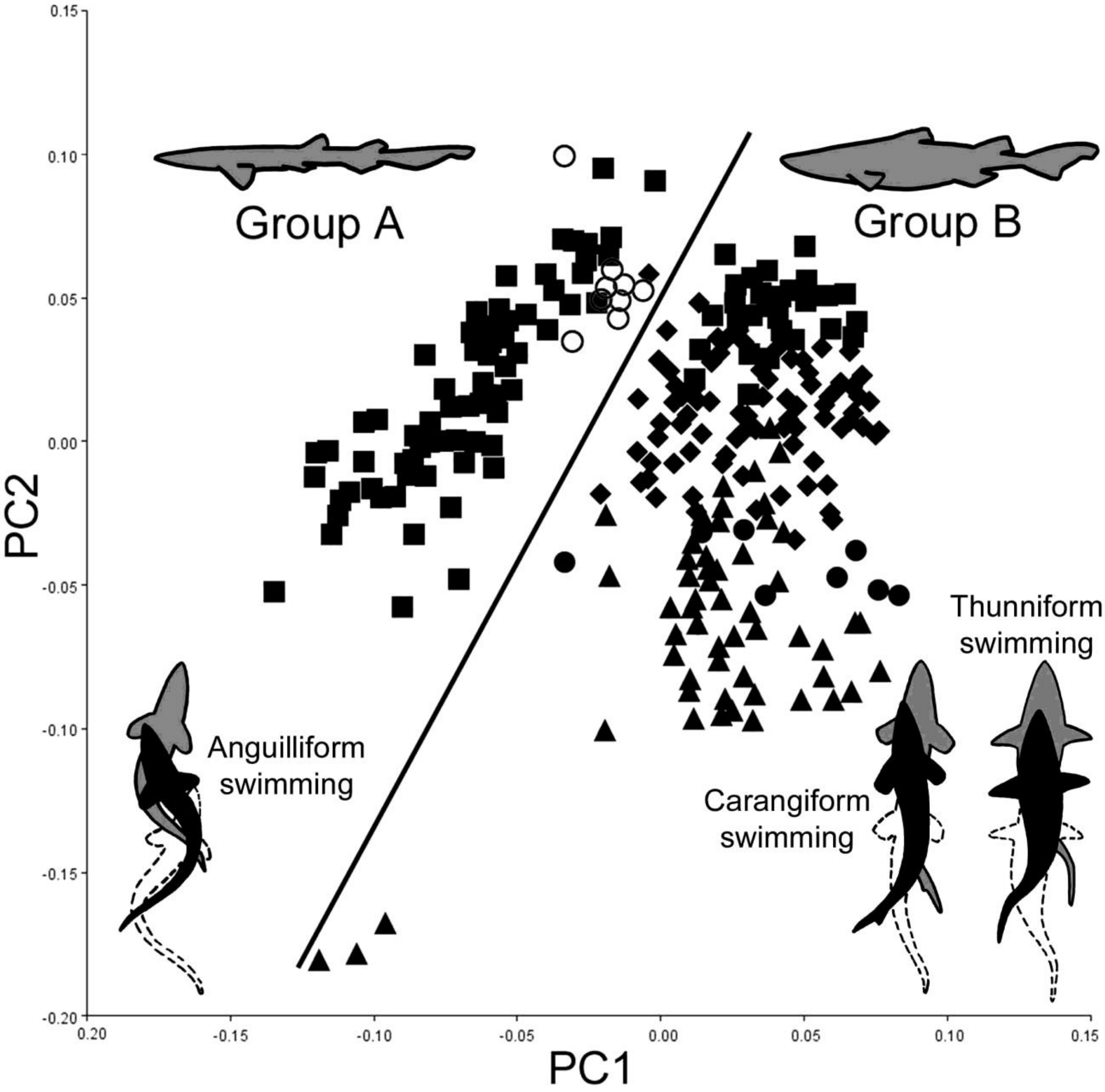

**Figure 6.** Scatter plot diagram showing division (line) between Group A and Group B of full body analysis (cf. Fig. 4B) where plots consist only of pristiophoriform and squatiniform taxa (open circles) and species of genera examined by Thomson & Simanek (1977) (solid circles, Group 1 sharks; triangles, Group 2 sharks; squares, Group 3 sharks; diamonds, Group 4 sharks). Top two silhouette images of sharks in lateral view represent respective generalized body form of taxa located at approximate center of each of the two main clusters of plots in Figure 4B (example of species used for each silhouette: Groups A, *Bythaelurus hispidius*; Group B, *Centroscyllium kamoharai*). Bottom three silhouette images of sharks in dorsal view illustrate three swimming modes and their distribution by body form group (see text; modified after CC Lindsey's illustration reproduced by Sfakiotakis *et al*., 1999, fig. 7).

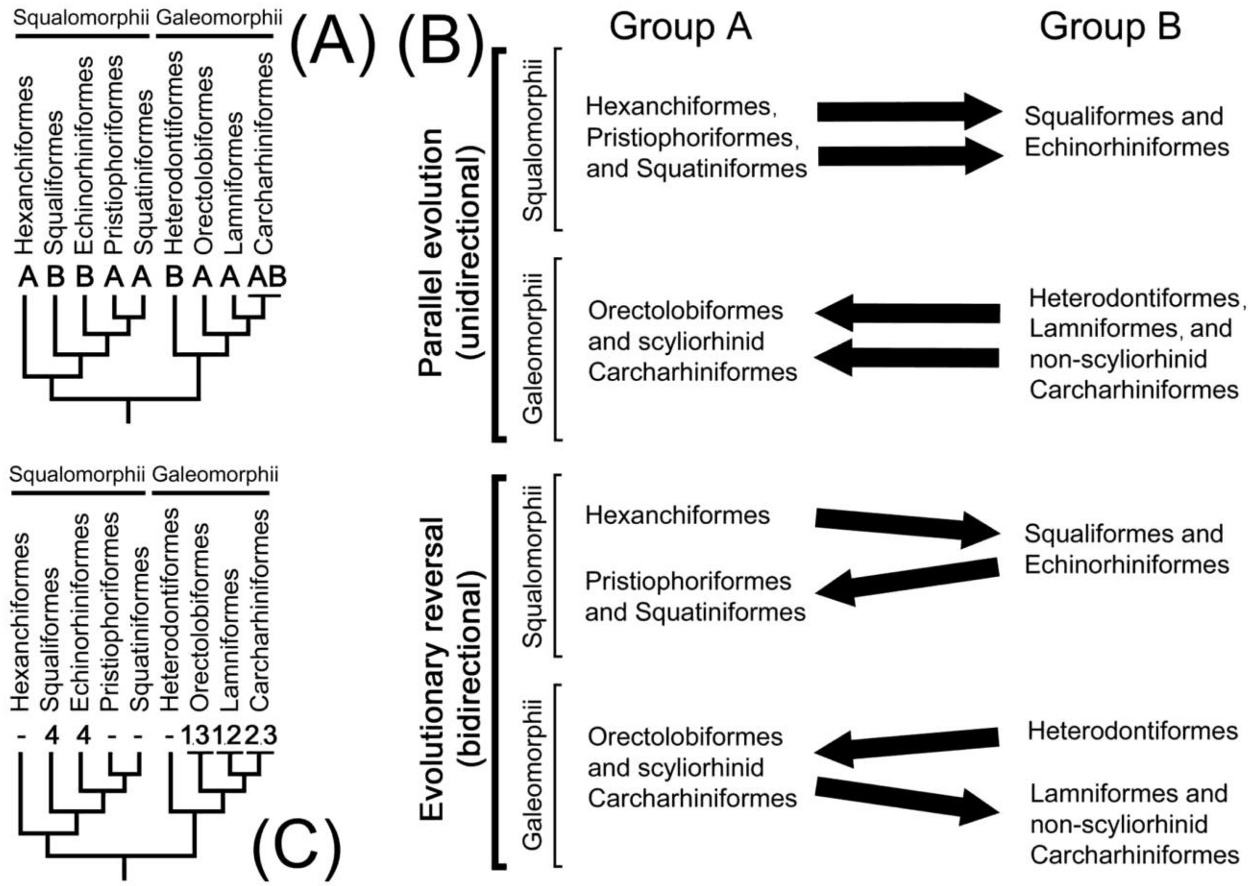

**Figure 7.** Possible evolutionary scenarios of body forms in sharks. A, Distribution of Group A and Group B body forms by shark orders mapped onto Naylor *et al*.'s (2012; see also Fig. 1A) phylogenetic tree. B, Two alternative conceptual evolutionary pathways between Group A and Group B body forms (Figs. 4B, 6) in each of the two superorders, Squalomorphii and Galeomorphii. C, Distribution of Thomson & Simanek's (1977) Groups 1, 2, 3, and 4 body forms (Figs. 1B, 6) by shark orders mapped onto Naylor *et al*.'s (2012; see also Fig. 1A) phylogenetic tree (dashes indicate taxa that were not included in Thomson & Simanek's study).

**Appendix 1.** List of all extant species of sharks examined in this study showing the species code, common name, maximum total length (maxTL; in cm), and page number where each illustration used for geometric morphometric analyses is located in Ebert *et al*.'s (2013) book. Asterisk (*) indicates genus in which all of its members (20 species) are examined as one taxon because only one representative lateral view was presented for the entire genus in Ebert *et al*.'s (2013) book.

| Code | Scientific name | Common name | maxTL | Page |
|---|---|---|---|---|
| HEXANCHIFORMES | | | | |
| Chlamydoselachidae | | | | |
| 1 | *Chlamydoselachus africana* | South African frilled shark | 117 | 66 |
| 2 | *Chlamydoselachus anguineus* | Frilled shark | 196 | 67 |
| Hexanchidae | | | | |
| 3 | *Heptranchias perlo* | Sharpnose sevengill shark | 139 | 68 |
| 4 | *Hexanchus nakamurai* | Bigeye sixgill shark | 180 | 68 |
| 5 | *Hexanchus griseus* | Bluntnose sixgill shark | 550 | 69 |
| 6 | *Notorynhchus cepedianus* | Broadnose sevengill shark | 296 | 70 |
| ECHINORHINIFORMES | | | | |
| Echinorhinidae | | | | |
| 7 | *Echinorhinus brucus* | Bramble shark | 310 | 72 |
| 8 | *Echinorhinus cookei* | Prickly shark | 450 | 72 |
| SQUALIFORMES | | | | |
| Squalidae | | | | |
| 9 | *Cirrhagaleus asper* | Roughskin spurdog | 118 | 81 |
| 10 | *Cirrhagaleus australis* | Southern Mandarin dogfish | 123 | 81 |
| 11 | *Cirrhgaleus barbifer* | Mandarin dogfish | 122 | 82 |
| 12 | *Squalus acanthias* | Piked dogfish | 200 | 83 |
| 13 | *Squalus albifrons* | Eastern highfin spurdog | 86 | 84 |
| 14 | *Squalus altipinnis* | Western highfin spurdog | 59 | 84 |
| 15 | *Squalus blainville* | Longnose spurdog | 89 | 85 |
| 16 | *Squalus brevirostris* | Japanese shortnose spurdog | 59 | 85 |
| 17 | *Squalus bucephalus* | Bighead spurdog | 90 | 86 |
| 18 | *Squalus chloroculus* | Greeneye spurdog | 99 | 86 |
| 19 | *Squalus crassispinus* | Fastspine spurdog | 58 | 87 |
| 20 | *Squalus cubensis* | Cuban dogfish | 110 | 87 |
| 21 | *Squalus edmundsi* | Edmund's spurdog | 87 | 88 |
| 22 | *Squalus formosus* | Taiwan spurdog | 81 | 88 |
| 23 | *Squalus graham* | Eastern longnose spurdog | 73 | 89 |
| 24 | *Squalus griffin* | New Zealand dogfish | 110 | 89 |
| 25 | *Squalus hemipinnis* | Indonesian shortsnout dogfish | 74 | 90 |
| 26 | *Squalus japonicus* | Japanese spurdog | 95 | 90 |
| 27 | *Squalus lalannei* | Seychelles spurdog | 79 | 91 |
| 28 | *Squalus megalops* | Shortnose spurdog | 77 | 91 |
| 29 | *Squalus melanurus* | Blacktail spurdog | 75 | 92 |
| 30 | *Squalus mitsukurii* | Shortspine spurdog | 125 | 92 |

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|---|---|---|---|---|
| 31 | *Squalus montalbani* | Philippines spurdog | 101 | 93 |
| 32 | *Squalus nasutus* | Western longnose spurdog | 77 | 93 |
| 33 | *Squalus notocaudatus* | Bartail spurdog | 62 | 94 |
| 34 | *Squalus rancureli* | Cyrano spurdog | 77 | 94 |
| 35 | *Squalus raolensis* | Kermadec spiny dogfish | 73 | 95 |
| 36 | *Squalus suckleyi* | North Pacific spiny dogfish | 150 | 95 |
| Centrophoridae | | | | |
| 37 | *Centrophorus acus* | Needle dogfish | 161 | 101 |
| 38 | *Centrophorus altromarginatus* | Dwarf gulper shark | 94 | 101 |
| 39 | *Centrophorus granulosus* | Gulper shark | 110 | 102 |
| 40 | *Centrophorus harrisoni* | Longnose gulper shark | 114 | 102 |
| 41 | *Centrophorus isodon* | Blackfin gulper shark | 108 | 103 |
| 42 | *Centrophorus lusitanicus* | Lowfin gulper shark | 100 | 103 |
| 43 | *Centrophorus mouccenisis* | Smallfin gulper shark | 100 | 104 |
| 44 | *Centrophorus niakung* | Taiwan gulper shark | 170 | 104 |
| 45 | *Centrophorus seychellorum* | Seychelles gulper shark | 80 | 105 |
| 46 | *Centrophorus squamosus* | Leafscale gulper shark | 164 | 105 |
| 47 | *Centrophorus tessellatus* | Mosaic gulper shark | 89 | 106 |
| 48 | *Centrophorus westraliensis* | Western gulper shark | 91 | 106 |
| 49 | *Centrophorus zeehaani* | Southern dogfish | 108 | 107 |
| 50 | *Deania calcea* | Birdbeak dogfish | 122 | 108 |
| 51 | *Deania hystricosa* | Rough longnose dogfish | 111 | 108 |
| 52 | *Deania profundorum* | Arrowhead dogfish | 97 | 109 |
| 53 | *Deania quadrispinosa* | Longsnout dogfish | 114 | 109 |
| Etompteridae | | | | |
| 54 | *Aculeola nigra* | Hooktooth dogfish | 121 | 121 |
| 55 | *Centroscyllium excelsum* | Highfin dogfish | 64 | 121 |
| 56 | *Centroscyllium fabricii* | Black dogfish | 107 | 122 |
| 57 | *Centroscyllium granulatum* | Granular dogfish | 28 | 122 |
| 58 | *Centroscyllium kamoharai* | Bareskin dogfish | 63 | 123 |
| 59 | *Centroscyllium nigrum* | Combtooth dogfish | 52 | 123 |
| 60 | *Centroscyllium ornatum* | Ornate dogfish | 30 | 124 |
| 61 | *Centroscyllium ritteri* | Whitefin dogfish | 43 | 124 |
| 62 | *Etmopterus baxteri* | Giant lanternshark | 86 | 125 |
| 63 | *Etmopterus bigelowi* | Blurred smooth lanternshark | 72 | 125 |
| 64 | *Etmopterus brachyurus* | Shorttail lanternshark | 42 | 126 |
| 65 | *Etmopterus bullisi* | Lined lanternshark | 27 | 126 |
| 66 | *Etmopterus burgessi* | Broadsnout lanternshark | 41 | 127 |
| 67 | *Etmopterus carteri* | Cylindrical lanternshark | 21 | 127 |
| 68 | *Etmopterus caudistigmus* | Tailspot lanternshark | 34 | 128 |
| 69 | *Etmopterus compagnoi* | Brown lanternshark | 67 | 128 |
| 70 | *Etmopterus decacuspidatus* | Combtooth lanternshark | 29 | 129 |
| 71 | *Etmopterus dianthus* | Pink lanternshark | 41 | 129 |
| 72 | *Etmopterus dislineatus* | Lined lanternshark | 45 | 130 |
| 73 | *Etmopterus evansi* | Blackmouth lanternshark | 32 | 130 |
| 74 | *Etmopterus fusus* | Pygmy lanternshark | 30 | 131 |

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|---|---|---|---|---|
| 75 | *Etmopterus gracilispnis* | Broadband lanternshark | 33 | 131 |
| 75 | *Etmopterus granulosus* | Southern lanternshark | 85 | 132 |
| 76 | *Etmopterus hillianus* | Caribbean lanternshark | 28 | 132 |
| 77 | *Etmopterus joungi* | Shortfin smooth lanternshark | 46 | 133 |
| 78 | *Etmopterus litvinovi* | Smalleye lanternshark | 61 | 133 |
| 79 | *Etmopterus lucifer* | Blackbelly lanternshark | 47 | 134 |
| 80 | *Etmopterus molleri* | Slendertail lanternshark | 46 | 134 |
| 81 | *Etmopterus perryi* | Dwarf lanternshark | 21 | 135 |
| 82 | *Etmopterus polli* | African lanternshark | 24 | 135 |
| 83 | *Etmopterus princeps* | Great lanternshark | 89 | 136 |
| 84 | *Etmopterus pseudosqualiolus* | False lanternshark | 45 | 136 |
| 85 | *Etmopterus pusillus* | Smooth lanternshark | 50 | 137 |
| 86 | *Etmopterus pycnolepis* | Denescale lanternshark | 45 | 137 |
| 87 | *Etmopterus robinsi* | West Indian lanternshark | 34 | 138 |
| 88 | *Etmopterus schultzi* | Fringefin lanternshark | 30 | 138 |
| 89 | *Etmopterus sculptus* | Sculptured lanternshark | 53 | 139 |
| 90 | *Etmopterus sentosus* | Thorny lanternshark | 27 | 139 |
| 91 | *Etmopterus sheikoi* | Rasptooth dogfish | 43 | 140 |
| 92 | *Etmopterus spinax* | Velvet belly | 41 | 140 |
| 93 | *Etmopterus splendidus* | Splendid lanternshark | 26 | 141 |
| 94 | *Etmopterus unicolor* | Brown lanternshark | 79 | 141 |
| 95 | *Etmopterus viator* | Traveller lanternshark | 58 | 142 |
| 96 | *Etmopterus villosus* | Hawaiian lanternshark | 17 | 142 |
| 97 | *Etmopterus virens* | Green lanternshark | 26 | 143 |
| 98 | *Trigonognathus kabeyai* | Viper dogfish | 54 | 143 |
| Somniosidae |  |  |  |  |
| 99 | *Centroscymnus coelolepis* | Portuguese dogfish | 122 | 151 |
| 100 | *Centroscymnus owstoni* | Roughskin dogfish | 120 | 151 |
| 101 | *Centroselachus crepidater* | Longnose velvet dogfish | 105 | 152 |
| 102 | *Proscymnodon macracanthus* | Largespine velvet dogfish | 68 | 152 |
| 103 | *Proscymnodon plunketi* | Plunket’s shark | 170 | 153 |
| 104 | *Scymnodalatias albicauda* | Whitetail dogfish | 110 | 153 |
| 105 | *Scymnodalatias garricki* | Azores dogfish | 40 | 154 |
| 106 | *Scymnodalatias oligodon* | Sparsetooth dogfish | 26 | 154 |
| 107 | *Scymnodalatias sherwoodi* | Sherwood dogfish | 85 | 155 |
| 108 | *Scymnodon ringens* | Knifetooth dogfish | 110 | 155 |
| 109 | *Somniosus antarcticus* | Southern sleeper Shark | 600 | 156 |
| 110 | *Somniosus longus* | Frog shark | 140 | 156 |
| 111 | *Somniosus microcephalus* | Greenland shark | 730 | 157 |
| 112 | *Somniosus pacificus* | Pacific sleeper shark | 700 | 158 |
| 113 | *Somniosus rostratus* | Little sleeper shark | 143 | 158 |
| 114 | *Zameus ichiharai* | Japanese velvet dogfish | 146 | 159 |
| 115 | *Zameus squamulosus* | Velvet dogfish | 84 | 159 |
| Oxynotidae |  |  |  |  |
| 116 | *Oxynotus bruniensis* | Prickly dogfish | 91 | 162 |
| 117 | *Oxynotus carribaeus* | Caribbean roughshark | 49 | 163 |

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|---|---|---|---|---|
| 118 | *Oxynotus centrina* | Angular roughshark | 150 | 163 |
| 119 | *Oxynotus japonicus* | Japanese roughshark | 54 | 164 |
| 120 | *Oxynotus paradoxus* | Sailfin roughshark | 118 | 164 |
| Dalatiidae | | | | |
| 121 | *Dalatias licha* | Kitefin shark | 182 | 168 |
| 122 | *Euprotomicroides zantedeschia* | Taillight shark | 41 | 168 |
| 123 | *Euprotomicrus bispinatus* | Pygmy shark | 27 | 169 |
| 124 | *Heteroscymnoides marleyi* | Longnose pygmy shark | 37 | 169 |
| 125 | *Isistius brasiliensis* | Cookiecutter shark | 50 | 170 |
| 126 | *Isistius labialis* | South China cookiecutter shark | 44 | 171 |
| 127 | *Isistius plutodus* | Largetooth cookiecutter shark | 42 | 171 |
| 128 | *Mollisquama parini* | Pocket shark | 40 | 172 |
| 129 | *Squaliolus aliae* | Smalleye pygmy shark | 22 | 172 |
| 130 | *Squaliolus laticaudus* | Spined pygmy shark | 28 | 173 |
| PRISTIOPHORIFORMES | | | | |
| Pristiophoridae | | | | |
| 131 | *Pilotrema warreni* | Sixgill sawshark | 136 | 179 |
| 132 | *Pristiophorus cirratus* | Longnose sawshark | 149 | 179 |
| 133 | *Pristiophorus delicatus* | Tropical sawshark | 85 | 180 |
| 134 | *Pristiophorus japonicus* | Japanese sawshark | 153 | 180 |
| 135 | *Pristiophorus nancyae* | African dwarf sawshark | 62 | 181 |
| 136 | *Pristiophorus nudipinnis* | Shortnose sawshark | 124 | 181 |
| 137 | *Pristiophorus schroederi* | Bahamas sawshark | 81 | 182 |
| 138 | *Pristiophorus* sp. C | Philippine sawshark | 73 | 182 |
| SQUATINIFORMES | | | | |
| Squatinidae | | | | |
| 139 | Squatina spp.* | ‘Angel sharks’ | 244 | 183 |
| HETERODONTIFORMES | | | | |
| Heterodontidae | | | | |
| 140 | *Heterodontus francisci* | Horn shark | 122 | 203 |
| 141 | *Heterodontus galeatus* | Crested bullhead shark | 130 | 208 |
| 142 | *Heterodontus japonicus* | Japanese bullhead shark | 120 | 208 |
| 143 | *Heterodontus mexicanus* | Mexican hornshark | 70 | 209 |
| 144 | *Heterodontus omanensis* | Oman bullhead shark | 61 | 209 |
| 145 | *Heterodontus portusjacksoni* | Port Jackson shark | 237 | 210 |
| 146 | *Heterodontus quoyi* | Galapagos bullhead shark | 105 | 211 |
| 147 | *Heterodontus ramalheira* | Whitespotted bullhead shark | 83 | 212 |
| 148 | *Heterodontus zebra* | Zebra bullhead shark | 122 | 212 |
| LAMNIFORMES | | | | |
| Mitsukurinidae | | | | |
| 149 | *Mitsukurina owstoni* | Goblin shark | 550 | 216 |
| Odontaspididae | | | | |
| 150 | *Carcharias taurus* | Sandtiger shark | 430 | 217 |
| 151 | *Odontaspis ferox* | Smalltooth sandtiger | 450 | 218 |
| 152 | *Odontaspis noronhai* | Bigeye sandtiger | 427 | 218 |
| Pseudocarchariidae | | | | |

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|---|---|---|---|---|
| 153 | *Pseudocarcharias kamoharai* | Crocodile shark | 122 | 219 |
| Megachasmidae |  |  |  |  |
| 154 | *Megachasma pelagios* | Megamouth shark | >550 | 219 |
| Cetorhinidae |  |  |  |  |
| 155 | *Cetorhinus maximus* | Basking shark | >1,000 | 222 |
| Alopiidae |  |  |  |  |
| 156 | *Alopias vulpinus* | Thresher shark | 635 | 223 |
| 157 | *Alopias pelagicus* | Pelagic thresher | 365 | 226 |
| 158 | *Alopias superciliosus* | Bigeye thresher | 480 | 226 |
| Lamnidae |  |  |  |  |
| 159 | *Carcharodon carcharias* | White shark | 600 | 227 |
| 160 | *Isurus oxyrinchus* | Shortfin mako | 400 | 230 |
| 161 | *Isurus paucus* | Longfin mako | 430 | 231 |
| 162 | *Lamna ditropis* | Salmon shark | 305 | 231 |
| 163 | *Isurus nasus* | Porbeagle shark | 355 | 232 |
| ORECTOLOBIFORMES |  |  |  |  |
| Parascylliidae |  |  |  |  |
| 164 | *Cirrhoscyllium expolitum* | Barbelthroat carpetshark | 33.5 | 236 |
| 165 | *Cirrhoscyllium formosanum* | Taiwan saddled carpetshark | 39 | 236 |
| 166 | *Cirrhoscyllium japonicum* | Saddled carpetshark | 49 | 237 |
| 167 | *Parascyllium collare* | Collared carpetshark | 87 | 237 |
| 168 | *Parascyllium elongatum* | Elongate carpet shark | 42 | 238 |
| 169 | *Parascyllium ferrugineum* | Rusty carpetshark | 80 | 238 |
| 170 | *Parascyllium sparsimaculatum* | Sparsely spotted carpetshark | 79 | 239 |
| 171 | *Parascyllium variolatum* | Necklace carpetshark | 90 | 239 |
| Brachaeularidae |  |  |  |  |
| 172 | *Brachaelurus colcloughi* | Bluegrey carpetshark | 75 | 240 |
| 173 | *Brachaelurus waddi* | Blind shark | 120 | 241 |
| Orectolobidae |  |  |  |  |
| 174 | *Eucrossorhinus dasypogon* | Tasselled wobbegong | 125 | 248 |
| 175 | *Orectolobus floridus* | Florida banded wobbegong | 75 | 248 |
| 176 | *Orectolobus halei* | Gulf wobbegong | 206 | 249 |
| 177 | *Orectolobus hutchinsi* | Western wobbegong | 149 | 249 |
| 178 | *Orectolobus japonicus* | Japanese wobbegong | 118 | 250 |
| 179 | *Orectolobus leptolineatus* | False cobbler wobbegong | 120 | 250 |
| 180 | *Orectolobus maculatus* | Spotted wobbegong | 170 | 251 |
| 181 | *Orectolobus ornatus* | Ornate wobbegong | 110 | 251 |
| 182 | *Orectolobus parvimaculatus* | Dwarf spotted wobbegong | 94 | 252 |
| 183 | *Orectolobus reticalatus* | Network wobbegong | 52 | 252 |
| 184 | *Orectolobus wardi* | Northern wobbegong | 100 | 253 |
| 185 | *Sutorectus tenataculatus* | Cobbler wobbegong | 92 | 253 |
| Hemiscylliidae |  |  |  |  |
| 186 | *Chiloscyllium arabicum* | Arabian carpetshark | 70 | 258 |
| 187 | *Chiloscyllium burmensis* | Burmese bambooshark | 57 | 259 |
| 188 | *Chiloscyllium griseum* | Grey bambooshark | 77 | 259 |
| 189 | *Chiloscyllium hasselti* | Indonesian bambooshark | 61 | 260 |

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|---|---|---|---|---|
| 190 | *Chiloscyllium indicum* | Slender bambooshark | 65 | 260 |
| 191 | *Chiloscyllium plagiosum* | Whitespotted bambooshark | 95 | 261 |
| 192 | *Chiloscyllium punctatum* | Brownbanded bambooshark | 132 | 261 |
| 193 | *Hemiscyllium freycineti* | Indonesian speckled carpetshark | 72 | 262 |
| 194 | *Hemiscyllium galei* | Gale's epaulette shark | 57 | 262 |
| 195 | *Hemiscyllium hallstromi* | Paupian epaulette carpetshark | 77 | 263 |
| 196 | *Hemiscyllium henryi* | Henry's epaulette shark | 70 | 263 |
| 197 | *Hemiscyllium michaeli* | Michael's epaulette shark | 82 | 264 |
| 198 | *Hemiscyllium ocellatum* | Epaulette carpetshark | 107 | 264 |
| 199 | *Hemiscyllium strahani* | Hooded carpetshark | 80 | 265 |
| 200 | *Hemiscyllium trispeculare* | Speckled carpetshark | 79 | 265 |
| Stegostomatidae |  |  |  |  |
| 201 | *Stegostoma fasciatum* | Zebra shark | 235 | 268 |
| Ginglymostomatidae |  |  |  |  |
| 202 | *Pseudoginglymostoma brevicaudatum* | Shorttail nurse shark | 75 | 269 |
| 203 | *Ginglymostoma cirratum* | Nurse shark | 300 | 270 |
| 204 | *Nebrius ferrungineus* | Tawny nurse shark | 320 | 271 |
| Rhincodontidae |  |  |  |  |
| 205 | *Rhincodon typus* | Whale shark | 2,100 | 272 |
| CARCHARHINIFORMES |  |  |  |  |
| Scyliorhinidae |  |  |  |  |
| 206 | *Apristurus albisoma* | White-bodied catshark | 60 | 284 |
| 207 | *Apristurus ampliceps* | Roughskin catshark | 87 | 284 |
| 208 | *Apristurus aphyodes* | White ghost catshark | 54 | 285 |
| 209 | *Apristurus australis* | Pinocchio catshark | 62 | 285 |
| 210 | *Apristurus brunneus* | Brown catshark | 69 | 286 |
| 211 | *Apristurus bucephalus* | Bighead catshark | 68 | 286 |
| 212 | *Apristurus canutus* | Hoary catshark | 46 | 287 |
| 213 | *Apristurus exsanguis* | Flaccid catshark | 91 | 287 |
| 214 | *Apristurus fedorovi* | Stout catshark | 68 | 288 |
| 215 | *Apristurus gibbosus* | Humpback catshark | 51 | 288 |
| 216 | *Apristurus herklotsi* | Longfin catshark | 49 | 289 |
| 217 | *Apristurus indicus* | Smallbelly catshark | 34 | 289 |
| 218 | *Apristurus internatus* | Shortnose demon catshark | 42 | 290 |
| 219 | *Apristurus investigatoris* | Broadnose catshark | 26 | 291 |
| 220 | *Apristurus japonicus* | Japanese catshark | 71 | 291 |
| 221 | *Apristurus kampae* | Longnose catshark | 65 | 291 |
| 222 | *Apristurus laurussonii* | Iceland catshark | 72 | 292 |
| 223 | *Apristurus longicephalus* | Longhead catshark | 59 | 292 |
| 224 | *Apristurus macrorhynchus* | Flathead catshark | 66 | 293 |
| 225 | *Apristurus macrostomus* | Broadmouth catshark | 38 | 293 |
| 226 | *Apristurus manis* | Ghost catshark | 88 | 294 |
| 227 | *Apristurus melanoasper* | Fleshynose catshark | 79 | 294 |
| 228 | *Apristurus microps* | Smalleye catshark | 61 | 295 |
| 229 | *Apristurus micropterygeus* | Smalldorsal catshark | 37 | 295 |
| 230 | *Apristurus nasutus* | Largenose catshark | 59 | 296 |

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|---|---|---|---|---|
| 231 | *Apristurus parvipinnis* | Smallfin catshark | 52 | 296 |
| 232 | *Apristurus pinguis* | Bulldog catshark | 65 | 297 |
| 233 | *Apristurus platyrhynchus* | Spatulasnout catshark | 71 | 297 |
| 234 | *Apristurus profundorum* | Deepwater catshark | 76 | 298 |
| 235 | *Apristurus riveri* | Broadgill catshark | 48 | 298 |
| 236 | *Apristurus saldanha* | Saldanha catshark | 89 | 299 |
| 237 | *Apristurus sibogae* | Pale catshark | 21 | 299 |
| 238 | *Apristurus sinensis* | South China catshark | 82 | 300 |
| 239 | *Apristurus spongiceps* | Spongehead catshark | 51 | 300 |
| 240 | *Apristurus stenseni* | Panama ghost catshark | 46 | 301 |
| 241 | *Asymbolus analis* | Grey harspotted catshark | 61 | 301 |
| 242 | *Asymbolus funebris* | Blotched catshark | 44 | 306 |
| 243 | *Asymbolus galacticus* | Starry catshark | 48 | 306 |
| 244 | *Asymbolus occiduus* | Western spotted catshark | 60 | 307 |
| 245 | *Asymbolus pallidus* | Pale spotted catshark | 47 | 307 |
| 246 | *Asymbolus parvus* | Dwarf catshark | 40 | 308 |
| 247 | *Asymbolus rubiginosus* | Orange spotted catshark | 53 | 308 |
| 248 | *Asymbolus submaculatus* | Variegated catshark | 44 | 309 |
| 249 | *Asymbolus vincenti* | Gulf catshark | 61 | 309 |
| 250 | *Atelomycterus basiliensis* | Bali catshark | 47 | 310 |
| 251 | *Atelomycterus fasciatus* | Banded sand catshark | 45 | 310 |
| 252 | *Atelomycterus macleaya* | Australian marbled catshark | 60 | 311 |
| 253 | *Atelomycterus marmoratus* | Coral catshark | 70 | 311 |
| 254 | *Atelomycterus marnkalha* | Whitespotted sand catshark | 49 | 312 |
| 255 | *Aulohalaelurus kanakorum* | New Caledonia catshark | 79 | 313 |
| 256 | *Aulohalaelurus labiosus* | Blackspotted catshark | 67 | 313 |
| 257 | *Bythaelurus canescens* | Dusky catshark | 70 | 316 |
| 258 | *Bythaelurus clevai* | Broadhead catshark | 42 | 316 |
| 259 | *Bythaelurus dawsoni* | New Zealand catshark | 42 | 317 |
| 260 | *Bythaelurus giddingsi* | Jaguar catshark | 45 | 317 |
| 261 | *Bythaelurus hispidus* | Bristly catshark | 29 | 318 |
| 262 | *Bythaelurus immaculatus* | Spotless catshark | 76 | 318 |
| 263 | *Bythaelurus incanus* | Dusky catshark | 45 | 319 |
| 264 | *Bythaelurus lutarius* | Mud catshark | 39 | 319 |
| 265 | *Cephaloscyllium albipinnum* | Whitefin swellshark | 110 | 324 |
| 266 | *Cephaloscyllium cooki* | Cook’s swellshark | 30 | 324 |
| 267 | *Cephaloscyllium fasciatum* | Reticulated swellshark | 42 | 325 |
| 268 | *Cephaloscyllium hiscosellum* | Australian reticulated swellshark | 52 | 325 |
| 269 | *Cephaloscyllium isabellum* | Draughtsboard shark | 150 | 326 |
| 270 | *Cephaloscyllium laticeps* | Australian swellshark | 150 | 326 |
| 271 | *Cephaloscyllium maculatum* | Spotted swellshark | 19 | 327 |
| 272 | *Cephaloscyllium pardelotum* | Leopard-spottd swellshark | 20 | 327 |
| 273 | *Cephaloscyllium pictum* | Painted swellshark | 72 | 328 |
| 274 | *Cephaloscyllium sarawakensis* | Sarawak swellshark | 37 | 328 |
| 275 | *Cephaloscyllium signourum* | Flagtail swellshark | 74 | 329 |
| 276 | *Cephaloscyllium silasi* | Indian swellshark | 36 | 329 |

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|---|---|---|---|---|
| 277 | *Cephaloscyllium speccum* | Speckled swellshark | 69 | 330 |
| 278 | *Cephaloscyllium stevensi* | Steven’s swellshark | 66 | 330 |
| 279 | *Cephaloscyllium sufflans* | Balloon shark | 110 | 331 |
| 280 | *Cephaloscyllium umbratile* | Japanese swellshark | 120 | 331 |
| 281 | *Cephaloscyllium variegatum* | Saddled swellshark | 74 | 332 |
| 282 | *Cephaloscyllium ventriosum* | Swellshark | 100 | 332 |
| 283 | *Cephaloscyllium zebrum* | Narrowbar swellshark | 45 | 333 |
| 284 | *Cephalurus cephalus* | Lollipop catshark | 30 | 333 |
| 285 | *Figaro boardmani* | Australian sawtail catshark | 61 | 338 |
| 286 | *Figaro striatus* | Northern sawtail catshark | 42 | 338 |
| 287 | *Galeus antillensis* | Antilles catshark | 46 | 339 |
| 288 | *Galeus area* | Roughtail catshark | 33 | 339 |
| 289 | *Galeus atlanticus* | Atlantic sawtail catshark | 46 | 340 |
| 290 | *Galeus cadenati* | Longfin sawtail catshark | 35 | 340 |
| 291 | *Galeus eastmani* | Gecko catshark | 50 | 341 |
| 292 | *Galeus gracilis* | Slender sawtail catshark | 34 | 341 |
| 293 | *Galeus longirostris* | Longnose sawtail catshark | 80 | 342 |
| 294 | *Galeus melastomus* | Blackmouth catshark | 90 | 342 |
| 295 | *Galeus mincaronei* | Southern sawtail catshark | 43 | 343 |
| 296 | *Galeus murinus* | Mouse catshark | 63 | 343 |
| 297 | *Galeus nipponensis* | Broadfin sawtail catshark | 66 | 344 |
| 298 | *Galeus piperatus* | Peppered catshark | 30 | 344 |
| 299 | *Galeus polli* | African sawtail catshark | 43 | 345 |
| 300 | *Galeus priapus* | Phallic catshark | 46 | 345 |
| 301 | *Galeus sauteri* | Blacktip sawtail catshark | 45 | 346 |
| 302 | *Galeus schultzi* | Dwarf sawtail shark | 30 | 346 |
| 303 | *Galeus springeri* | Springer’s sawtail shark | 44 | 347 |
| 304 | *Halaelurus boesmani* | Speckled catshark | 48 | 350 |
| 305 | *Halaelurus buergeri* | Blackspotted catshark | 49 | 350 |
| 306 | *Halaelurus lineatus* | Lined catshark | 56 | 351 |
| 307 | *Halaelurus maculosus* | Indonesian speckled catshark | 53 | 351 |
| 308 | *Halaelurus natalensis* | Tiger catshark | 50 | 352 |
| 309 | *Halaelurus quagga* | Quagga catshark | 35 | 352 |
| 310 | *Halaelurus sellus* | Rusty catshark | 42 | 353 |
| 311 | *Haploblepharus edwardsii* | Puffader shyshark | 60 | 354 |
| 312 | *Haploblepharus fuscus* | Brown shyshark | 69 | 354 |
| 313 | *Haploblepharus kistnasamyi* | Natal shyshark | 50 | 355 |
| 314 | *Haploblepharus pictus* | Dark shyshark | 60 | 355 |
| 315 | *Holohalaelurus favus* | Honeycomb izak catshark | 52 | 358 |
| 316 | *Holohalaelurus grennian* | Grinning izak | 27 | 358 |
| 317 | *Holohalaelurus melanostigma* | Crying izak catshark | 38 | 359 |
| 318 | *Holohalaelurus punctatus* | African spotted catshark | 34 | 359 |
| 319 | *Holohalaelurus regani* | Izak catshark | 69 | 360 |
| 320 | *Parmaturus albimarginatus* | Whitetip catshark | 58 | 361 |
| 321 | *Parmaturus albipenis* | White-clasper catshark | 42 | 361 |
| 322 | *Parmaturus bigus* | Beige catshark | 71 | 364 |

| | | | | |
|---|---|---|---|---|
| 323 | *Parmaturus compechiensis* | Campeche catshark | 16 | 364 |
| 324 | *Parmaturus lanatus* | Velvet catshark | 36 | 365 |
| 325 | *Parmaturus macmillani* | New Zealand filetail | 53 | 365 |
| 326 | *Parmaturus melanobranchius* | Blackgill catshark | 85 | 366 |
| 327 | *Parmaturus pilosus* | Salamander catshark | 64 | 366 |
| 328 | *Parmaturus xaniurus* | Filetail catshark | 61 | 367 |
| 329 | *Pentanchus profundicolus* | Onefin catshark | 51 | 367 |
| 330 | *Poroderma africanum* | Pyjama shark | 97 | 370 |
| 331 | *Poroderma pantherium* | Leopard catshark | 77 | 370 |
| 332 | *Schroederichthys bivius* | Narrowmouth catshark | 82 | 371 |
| 333 | *Schroederichthys chilensis* | Redspotted catshark | 70 | 371 |
| 334 | *Schroederichthys maculatus* | Narrowtail catshark | 35 | 376 |
| 335 | *Schroederichthys saurisquaus* | Lizard catshark | 70 | 376 |
| 336 | *Schroederichthys tenuis* | Slender catshark | 47 | 377 |
| 337 | *Scyliorhinus besnardi* | Polkadot catshark | 47 | 377 |
| 338 | *Scyliorhinus boa* | Boa catshark | 54 | 378 |
| 339 | *Scyliorhinus canicular* | Smallspotted catshark | 100 | 378 |
| 340 | *Scyliorhinus capensis* | Yellowspotted catshark | 122 | 379 |
| 341 | *Scyliorhinus cervigoni* | West African catshark | 76 | 379 |
| 342 | *Scyliorhinus comoroensis* | Comoro catshark | 46 | 380 |
| 343 | *Scyliorhinus garmani* | Brownspotted catshark | 36 | 380 |
| 344 | *Scyliorhinus haeckelii* | Freckled catshark | 50 | 381 |
| 345 | *Scyliorhinus hesperius* | Whitesaddled catshark | 47 | 381 |
| 346 | *Scyliorhinus meadi* | Blotched catshark | 49 | 382 |
| 347 | *Scyliorhinus rotifer* | Chain catshark | 59 | 382 |
| 348 | *Scyliorhinus stellaris* | Nursehound | 162 | 383 |
| 349 | *Scyliorhinus tokubee* | Izu catshark | 41 | 383 |
| 350 | *Scyliorhinus torazame* | Cloudy catshark | 48 | 384 |
| 351 | *Scyliorhinus torrei* | Dwarf catshark | 32 | 384 |
| Proscylliidae | | | | |
| 352 | *Ctenacis fehlmanni* | Harlequin catshark | 46 | 385 |
| 353 | *Eridacnis barbouri* | Cuban ribbontail catshark | 34 | 388 |
| 354 | *Eridacnis radcliffei* | Pygmy ribbontail catshark | 24 | 388 |
| 355 | *Eridacnis sinuans* | African ribbontail catshark | 37 | 389 |
| 356 | *Proscyllium habereri* | Graceful catshark | 65 | 389 |
| 357 | *Proscyllium magnificum* | Magnificent catshark | 49 | 390 |
| Pseudotriakidae | | | | |
| 358 | *Gollum attenuates* | Slender smoothhound | 110 | 391 |
| 359 | *Gollum suluensis* | Sulu gollumshark | 65 | 391 |
| 360 | *Gollum* sp. B | Whitemarked gollumshark | 60 | 392 |
| 361 | *Pseudotriakis microdon* | False catshark | 295 | 392 |
| 362 | *Planonasus parini* | Pygmy false catshark | 56 | 393 |
| Leptochariidae | | | | |
| 363 | *Leptocharias smithii* | Barbeled houndshark | 82 | 393 |
| Triakidae | | | | |
| 364 | *Furgaleus macki* | Whiskery shark | 160 | 407 |

|  |  |  |  |  |
|---|---|---|---|---|
| 365 | *Gogolia filewoodi* | Sailback houndshark | 74 | 407 |
| 366 | *Galeorhinus galeus* | Tope | 195 | 408 |
| 367 | *Hemitriakis abdita* | Deepwater sicklefin houndshark | 80 | 409 |
| 368 | *Hemitriakis complicofasciata* | Striped topeshark | 93 | 409 |
| 369 | *Hemitriakis falcata* | Sicklefin houndshark | 77 | 410 |
| 370 | *Hemitriakis indroyonoi* | Indonesian houndshark | 120 | 410 |
| 371 | *Hemitriakis japonica* | Japanese topeshark | 120 | 411 |
| 373 | *Hemitriakis leucoperiptera* | Whitefin topeshark | 96 | 411 |
| 374 | *Hypogaleus hyugaensis* | Blacktip topeshark | 130 | 412 |
| 375 | *Iago garricki* | Longnose houndshark | 75 | 412 |
| 376 | *Iago mangalorensis* | Mangalore houndshark | 41 | 413 |
| 377 | *Iago omanensis* | Bigeye houndshark | 58 | 413 |
| 378 | *Mustelus albipinnis* | White-margin fin houndshark | 118 | 414 |
| 379 | *Mustelus antarcticus* | Gummy shark | 185 | 414 |
| 380 | *Mustelus asterias* | Starry smoothhound | 140 | 415 |
| 381 | *Mustelus californicus* | Grey smoothhound | 125 | 415 |
| 382 | *Mustelus canis* | Dusky smoothhound | 150 | 416 |
| 383 | *Mustelus dorsalis* | Sharptooth smoothhound | 64 | 416 |
| 384 | *Mustelus fasciatus* | Striped smoothhound | 155 | 417 |
| 385 | *Mustelus griseus* | Spotless smoothhound | 101 | 417 |
| 386 | *Mustelus henlei* | Brown smoothound | 100 | 418 |
| 387 | *Mustelus higmani* | Smalleye smoothhound | 64 | 418 |
| 388 | *Mustelus lenticulatus* | Rig | 151 | 419 |
| 389 | *Mustelus lunulatus* | Sicklefin smoothhound | 175 | 419 |
| 390 | *Mustelus manazo* | Starspotted smoothhound | 112 | 420 |
| 391 | *Mustelus mento* | Speckled smoothhound | 130 | 420 |
| 392 | *Mustelus minicanis* | Venezuelan dwarf smoothhound | 57 | 421 |
| 393 | *Mustelus mosis* | Arabian smoothhound | 150 | 421 |
| 394 | *Mustelus mustelus* | Smoothhound | 164 | 422 |
| 395 | *Mustelus norrisi* | Narrowfin smoothhound | 98 | 422 |
| 396 | *Mustelus palumbes* | Whitespot smoothhound | 113 | 423 |
| 397 | *Mustelus punctulatus* | Blackspot smoothhound | 95 | 423 |
| 398 | *Mustelus ravidus* | Australian grey smoothhound | 101 | 424 |
| 399 | *Mustelus schmitti* | Narrownose smoothhound | 109 | 424 |
| 400 | *Mustelus sinusmexicanus* | Gulf of Mexico smoothhound | 140 | 425 |
| 401 | *Mustelus stevensi* | Whitespotted gummy shark | 103 | 425 |
| 402 | *Mustelus walker* | Eastern spotted gummy shark | 112 | 426 |
| 403 | *Mustelus whitneyi* | Humpback smoothhound | 87 | 426 |
| 404 | *Mustelus widodoi* | Whitefin smoothhound | 110 | 427 |
| 405 | *Scylliogaleus quecketti* | Flapnose houndshark | 102 | 427 |
| 406 | *Triakis acutipinna* | Sharpfin houndshark | 102 | 428 |
| 407 | *Triakis maculata* | Spotted houndshark | 240 | 428 |
| 408 | *Triakis megalopterus* | Spotted gully shark | 208 | 429 |
| 409 | *Triakis scyllium* | Banded houndshark | 150 | 429 |
| 410 | *Triakis semifasciata* | Leopard shark | 210 | 430 |

Hemigaleidae

| | | | | |
|---|---|---|---|---|
| 411 | *Chaenogaleus macrostoma* | Hooktooth shark | 100 | 431 |
| 412 | *Hemigaleus australiensis* | Australian weasel shark | 110 | 434 |
| 413 | *Hemigaleus microstoma* | Sicklefin weasel shark | 94 | 434 |
| 414 | *Hemipristis elongatus* | Snaggletooth shark | 240 | 435 |
| 415 | *Paragaleus leucolomatus* | Whitetip weasel shark | 96 | 435 |
| 416 | *Paragaleus pectoralis* | Atlantic weasel shark | 138 | 436 |
| 417 | *Paragaleus randalli* | Slender weasel shark | 81 | 436 |
| 418 | *Paragaleus tengi* | Straighttooth weasel shark | 88 | 437 |
| Carcharhinidae | | | | |
| 419 | *Carcharhinus acronotus* | Blacknose shark | 137 | 456 |
| 420 | *Carcharhinus altimus* | Bignose shark | 300 | 456 |
| 421 | *Carcharhinus albimarginatus* | Silvertip shark | 300 | 457 |
| 422 | *Carcharhinus amblyrhynchos* | Grey reef shark | 255 | 458 |
| 423 | *Carcharhinus amblyrhynchoides* | Graceful shark | 178 | 459 |
| 424 | *Carcharhinus amboinensis* | Pigeye shark | 280 | 459 |
| 425 | *Carcharhinus borneensis* | Borneo shark | 70 | 460 |
| 426 | *Carcharhinus cautus* | Nervous shark | 150 | 460 |
| 427 | *Carcharhinus coatesi* | Coates’s shark | 88 | 461 |
| 428 | *Carcharhinus brachyurus* | Bronze whaler | 294 | 461 |
| 429 | *Carcharhinus brevipinna* | Spinner shark | 278 | 462 |
| 430 | *Carcharhinus dussumieri* | Whitecheek shark | 100 | 463 |
| 431 | *Carcharhinus fitzroyensis* | Creek whaler | 135 | 463 |
| 432 | *Carcharhinus falciformis* | Silky shark | 330 | 464 |
| 433 | *Carcharhinus galapensis* | Galapagos shark | 370 | 465 |
| 434 | *Carcharhinus hemiodon* | Pondicherry shark | 102 | 466 |
| 435 | *Carcharhinus isodon* | Finetooth shark | 200 | 466 |
| 436 | *Carcharhinus leiodon* | Smoothtooth blacktip | 142 | 467 |
| 437 | *Carcharhinus macloti* | Hardnose shark | 110 | 467 |
| 438 | *Carcharhinus leucas* | Bull shark | 340 | 468 |
| 439 | *Carcharhinus limbatus* | Blacktip shark | 255 | 469 |
| 440 | *Carcharhinus longimanus* | Oceanic whitetip shark | 395 | 470 |
| 441 | *Carcharhinus melanopterus* | Blacktip reef shark | 200 | 471 |
| 442 | *Carcharhinus porosus* | Smalltail shark | 150 | 471 |
| 443 | *Carcharhinus obscurus* | Dusky shark | 400 | 472 |
| 444 | *Carcharhinus plumbeus* | Sandbar shark | 300 | 473 |
| 445 | *Carcharhinus perezi* | Caribbean reef shark | 295 | 474 |
| 446 | *Carcharhinus sealei* | Blackspot shark | 95 | 474 |
| 447 | *Carcharhinus signatus* | Night shark | 280 | 475 |
| 448 | *Carcharhinus sorrah* | Spottail shark | 160 | 475 |
| 449 | *Carcharhinus tilsoni* | Australian blacktip shark | 200 | 476 |
| 450 | *Carcharhinus tjutjot* | Indonesian whaler shark | 94 | 476 |
| 451 | *Galeocerdo cuvier* | Tiger shark | 740 | 477 |
| 452 | *Glyphis fowlerae* | Borneo river shark | 200 | 478 |
| 453 | *Glyphis gangeticus* | Ganges shark | 204 | 479 |
| 454 | *Glyphis garricki* | New Guinea river shark | 300 | 479 |
| 455 | *Glyphis glyphis* | Speartooth shark | 300 | 482 |

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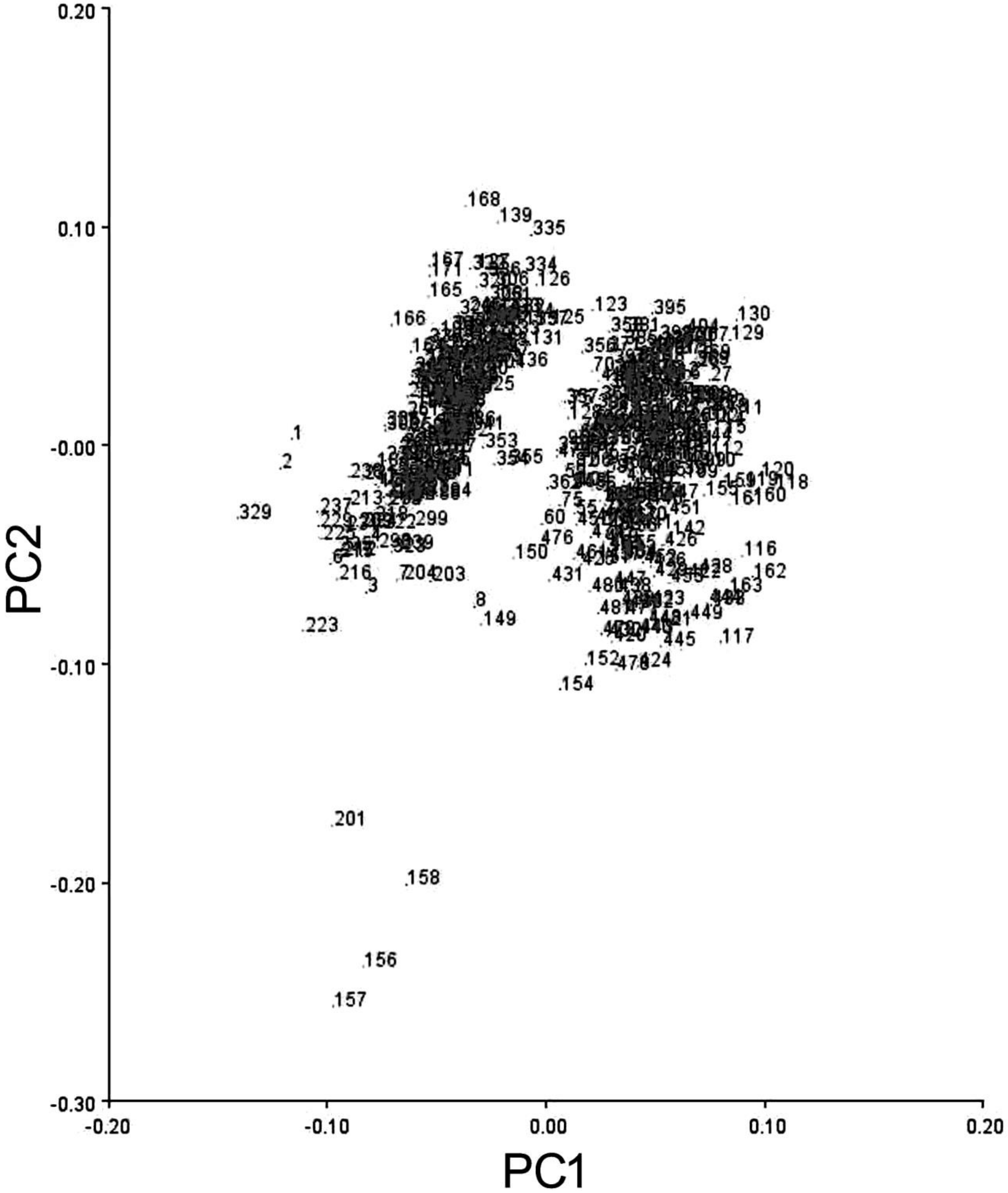
|---|---|---|---|---|
| 456 | *Glyphis siamensis* | Irrawaddy river shark | 300 | 482 |
| 457 | *Isogomphodon oxyrhynchus* | Daggernose shark | 244 | 483 |
| 458 | *Lamiopsis temmincki* | Broadfin shark | 168 | 483 |
| 459 | *Lamiospsis tephrodes* | Borneo broadfin shark | 145 | 492 |
| 460 | *Loxodon macroorhinus* | Sliteye shark | 99 | 492 |
| 461 | *Nasolamia velox* | Whitenose shark | 150 | 493 |
| 462 | *Negaprion acutidens* | Sharptooth lemon shark | 310 | 493 |
| 463 | *Negaprion brevirostris* | Lemon shark | 340 | 494 |
| 464 | *Prionace glauca* | Blue shark | 380 | 495 |
| 465 | *Rhizoprionodon acutus* | Milk shark | 178 | 496 |
| 466 | *Rhizoprionodon lalandei* | Brazilian sharpnose shark | 77 | 496 |
| 467 | *Rhizoprionodon longurio* | Pacific sharpnose shark | 154 | 497 |
| 468 | *Rhizoprionodon oligolinx* | Grey sharpnose shark | 70 | 497 |
| 469 | *Rhizoprionodon porosus* | Caribbean sharpnose shark | 110 | 498 |
| 470 | *Rhizoprionodon taylori* | Australian sharpnose shark | 67 | 498 |
| 471 | *Rhizoprionodon terraenovae* | Atlantic sharpnose shark | 110 | 499 |
| 472 | *Scoliodon laticaudus* | Spadenose shark | 74 | 499 |
| 473 | *Scoliodon macrorhynchos* | Pacific spadenose shark | 71 | 500 |
| 474 | *Trianodon obesus* | Whitetip reef shark | 213 | 500 |
| Sphyrnidae |  |  |  |  |
| 475 | *Eusphyra blochii* | Winghead shark | 186 | 501 |
| 476 | *Sphyrna corona* | Scalloped bonnethead | 92 | 506 |
| 477 | *Sphyrna media* | Scoophead shark | 150 | 506 |
| 478 | *Sphyrna lewini* | Scalloped hammerhead | 420 | 507 |
| 479 | *Sphyrna mokarran* | Great hammerhead | 610 | 508 |
| 480 | *Sphyrna tiburo* | Bonnethead shark | 150 | 508 |
| 481 | *Sphyrna tudes* | Smalleye hammerhead | 150 | 509 |
| 482 | *Sphyrna zygaena* | Smooth hammerhead | 400 | 509 |

**Appendix 2.** List of museum specimens by family used for pilot study (see Materials and Methods) along with the representative species examined (see Appendix 1 for species code) as well as its total length (TL; in cm), sex, and locality data.

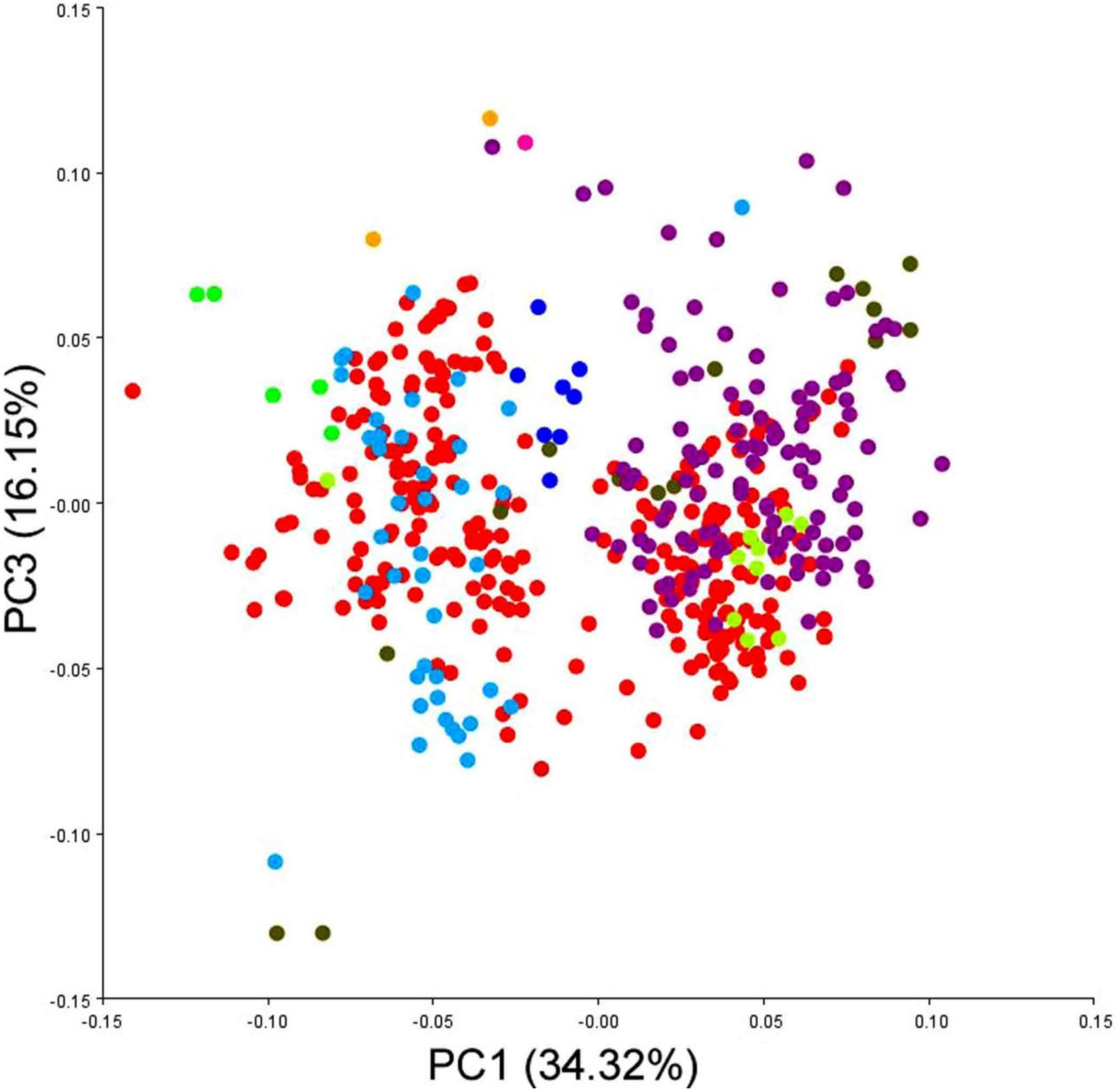
| Order and family | Code | Specimen | TL | Sex | Locality |
|---|---|---|---|---|---|
| HEXANCHIFORMES | | | | | |
| Chlamydoselachidae | 1 | SAM 31028 | 117 | F | Namibia |
| Hexanchidae | 3 | FMNH 76185 | 45 | F | Japan |
| ECHINORHINIFORMES | | | | | |
| Echinorhinidae | 8 | LACM 33827.031 | 66 | ? | North Pacific Ocean |
| SQUALIFORMES | | | | | |
| Squalidae | 12 | FMNH 31201 | 65 | M | Battle Harbor |
| Centrophoridae | 47 | FMNH 74190 | 40 | M | Japan |
| Etompteridae | 76 | FMNH 65547 | 20 | M | Caribbean Sea |
| Somniosidae | 111 | MCZ 39609 | 127 | M | North Atlantic |
| Oxynotidae | 118 | UF 41669 | 25 | F | Namibia |
| Dalatiidae | 121 | MCZ S-1116 | 115 | M | Japan |
| PRISTIOPHORIFORMES | | | | | |
| Pristiophoridae | 134 | FMNH 76686 | 67 | F | Japan |
| SQUATINIFORMES | | | | | |
| Squatinidae | 139 | UMMZ 179075 | 39 | F | Japan |
| HETERODONTIFORMES | | | | | |
| Heterodontidae | 142 | UMMZ 179075 | 39 | F | Japan |
| LAMNIFORMES | | | | | |
| Mitsukurinidae | 149 | SIO 07-46 | 115 | M | Japan |
| Odontaspididae | 151 | BPBM 9334 | 190 | F | Hawaii, USA |
| Pseudocarchariidae | 153 | FMNH 117474 | 101 | M | Hawaii, USA |
| Megachasmidae | 154 | SIO 07-53 | 215 | F | Mexico |
| Cetorhinidae | 155 | MCZ 54413 | 385 | F | Massachusetts, USA |
| Alopiidae | 158 | UF 160188 | 187 | M | Florida, USA |
| Lamnidae | 162 | USNM 201731 | 79 | F | "Pacific" |
| ORECTOLOBIFORMES | | | | | |
| Parascylliidae | 171 | SAMA F3563 | 46 | ? | South Australia |
| Brachaeularidae | 173 | USNM 197619 | ? | ? | Pacific |
| Orectolobidae | 178 | UMMZ 179035 | 86 | F | Japan |
| Hemiscylliidae | 193 | FMNH 21875 | 39 | M | Indo-Pacific |
| Stegostomatidae | 201 | UMMZ 218253 | 115 | F | Thailand |
| Ginglymostomatidae | 203 | FMNH 8180 | 38 | F | Falkland Islands |
| Rhincodontidae | 205 | OS 18090 | ? | ? | ? |
| CARCHARHINIFORMES | | | | | |
| Scyliorhinidae | 280 | FMNH 74116 | 29 | M | Japan |
| Proscylliidae | 356 | CAS 28577 | 60 | F | Taiwan |
| Pseudotriakidae | 358 | NMNZ P.001509 | 93 | ? | New Zealand |
| Leptochariidae | 363 | FMNH 118126 | 25 | M | South Atlantic |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Triakidae | 382 | UMMZ 86204 | 70 | F | Long Island, USA |
| Hemigaleidae | 414 | LACM 37712.001 | 76 | F | Indian Ocean |
| Carcharhinidae | 439 | FMNH 121470 | 102 | F | Alabama, USA |
| Sphyrnidae | 480 | FMNH 62438 | 49 | M | Panama Bay |

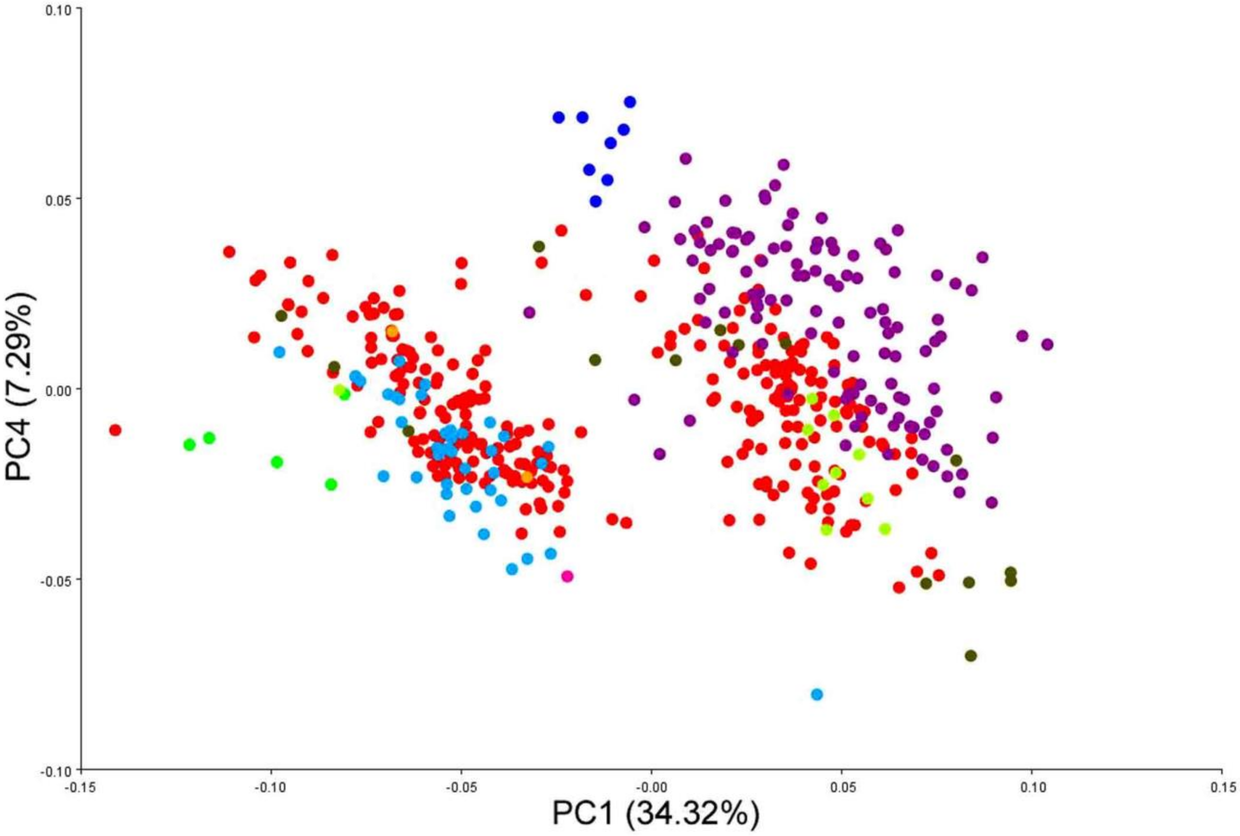
**Appendix 3.** Geometric morphometric plots (small dots) of full body analysis with species codes (see Appendix 1; cf. Fig. 4B). Overlapping numbers are appreciably difficult or impossible to read, but this illustration is intended to at least show codes of species present at extremities or representing outliers.



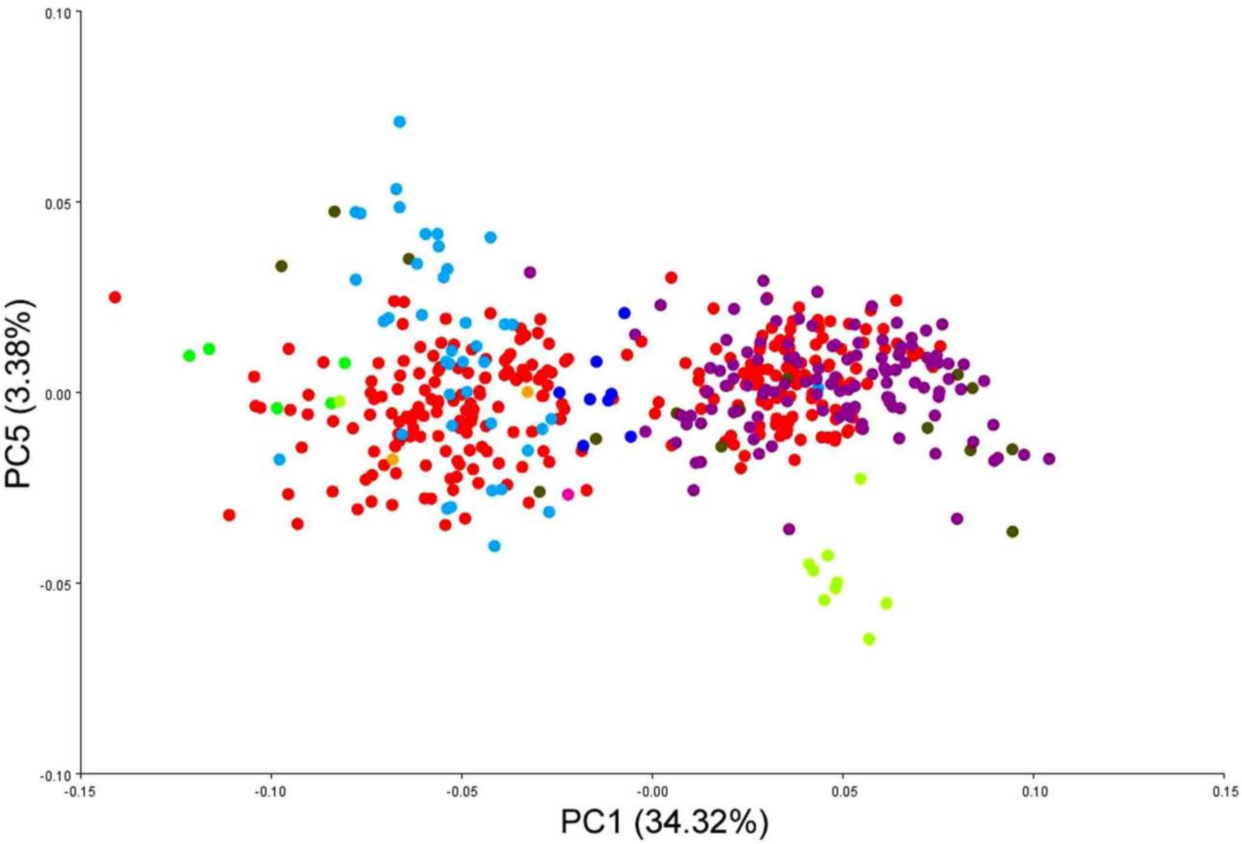
**Appendix 4.** Geometric morphometric plots of full body analysis with principle components 1 and 3. Percentage in parentheses in each axis denotes percent variation explained by that principle component.



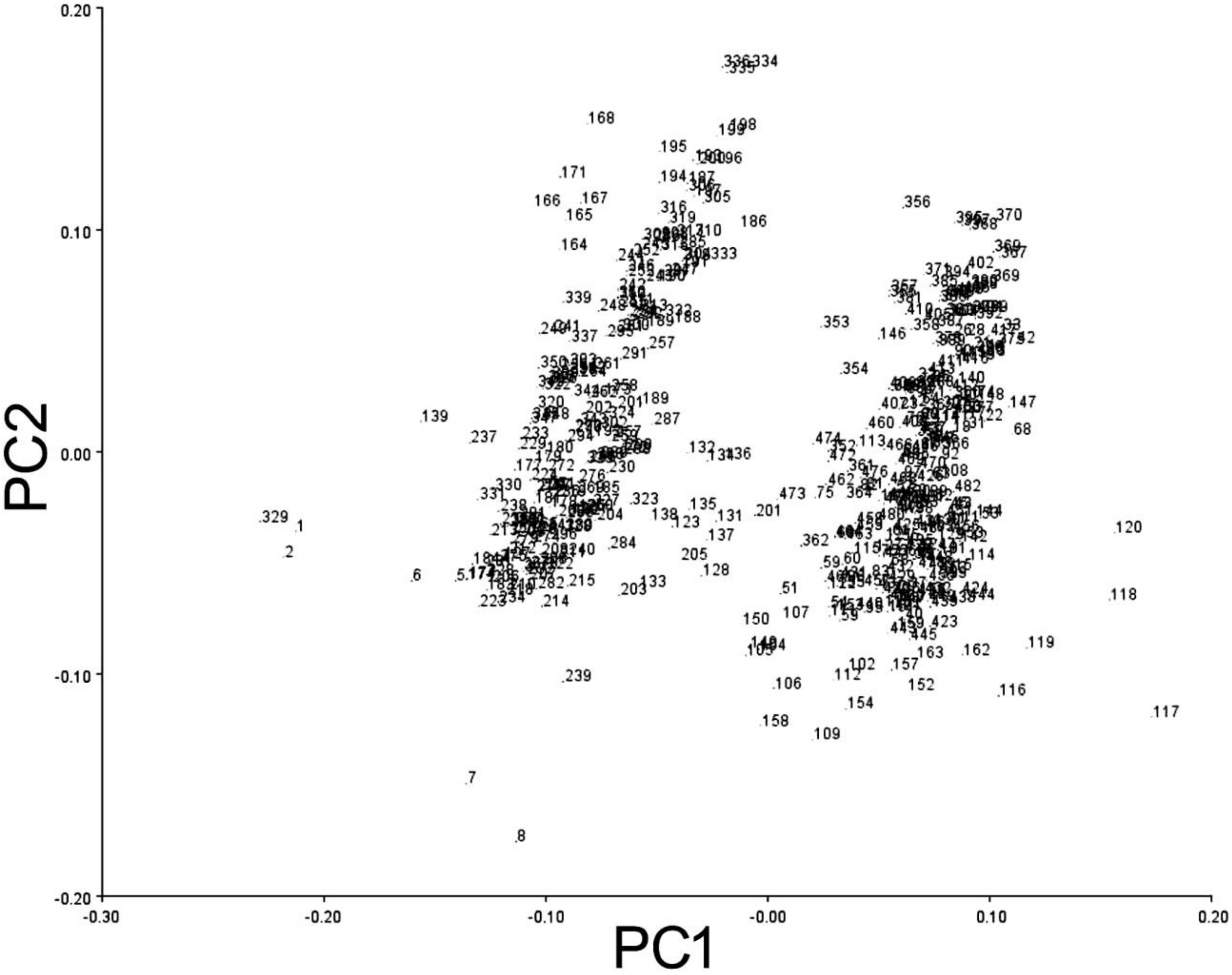
**Appendix 5.** Geometric morphometric plots of full body analysis with principle components 1 and 4. Percentage in parentheses in each axis denotes percent variation explained by that principle component.



**Appendix 6.** Geometric morphometric plots of full body analysis with principle components 1 and 5. Percentage in parentheses in each axis denotes percent variation explained by that principle component.



**Appendix 7.** Geometric morphometric plots (small dots) of precaudal body analysis with species codes (see Appendix 1; cf. Fig. 4C). Overlapping numbers are appreciably difficult or impossible to read, but this illustration is intended to at least show codes of species present at extremities or representing outliers.



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**Appendix 8.** Geometric morphometric plots (small dots) of caudal fin analysis with species codes (see Appendix 1; cf. Fig. 4D). Overlapping numbers are appreciably difficult or impossible to read, but this illustration is intended to at least show codes of species present at extremities or representing outliers.