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MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS OF RECENT AND FOSSIL CARCHARHINIFORM SHARK VERTEBRAL CENTRA

By

John H. Burris

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ABSTRACT

MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS OF RECENT AND FOSSIL CARCHARHINIFORM SHARK VERTEBRAL CENTRA

By

John H. Burris

The cross–sectional anatomy of secondary calcifications of shark vertebral centra has featured in phylogenetic hypotheses, although never in a rigorous cladistic framework. In this study, the internal calcification patterns, along with the external morphology, of fossil and Recent shark centra of the Order Carcharhiniformes have been coded and subjected to a cladistic analysis to address the utility of centrum features for revealing relationships. Carcharhiniform sharks were selected as a study group because they are a monophyletic clade with reasonably well understood intraordinal relationships, a rich fossil record, and readily available Recent comparative skeletal material.

External characters include centrum proportions, the presence and distribution of cartilage canals, and the size, shape, and spacing of the foramina for the basidorsal and basiventral arch components. The internal calcification features evaluated include the morphology and spacing of the four intermedialia, the four noncalcified areas, and the four diagonal calcifications.

Centrum characters were analyzed both separately and combined with other morphological characters from previous analyses. Results of the cladistic analysis show that shark centrum characters are useful for elucidating phylogeny. Tree topology was very similar for both analyses, and similar to recent molecular databased phylogenies. The addition of centrum data to shark phylogenetic analyses will allow for a more objective means of determining the interrelationships of fossil and extant carcharhiniform

sharks than studies based on teeth alone, with their well–documented difficulties. The data gathered will also be important for future studies to interpret the relationship between centrum morphology and swimming characteristics in extant and, ultimately, extinct taxa.

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INTRODUCTION

Fossilized sharks have been studied for over a hundred and seventy years, (e.g. Agassiz, 1833–1843), though most of these studies focus only on isolated teeth, particularly for Mesozoic and Cenozoic sharks. The shark skeleton is composed entirely of cartilage, with a low potential for preservation. While articulated fossil shark skeletons are known from the Paleozoic (e.g. Coates and Sequeira, 2001; Lund, 1985; Maisey, 1989), skeletons from the Mesozoic and Cenozoic are rare. Fossilized shark teeth, however, are the most common and abundant vertebrate fossil in the entire fossil record (Maisey, 1984). These teeth are abundant due to their hard enamel covering, and the tremendous numbers produced during the life span of these animals.

Fossil shark teeth present many difficulties for study and identification, especially due to the fact that nearly all sharks display heterodonty in their dentition. This heterodonty is often monognathic, where the teeth in a single jaw have different morphologies depending on position within that jaw (Compagno, 1970). Most sharks display dignathic heterodonty, where teeth of the upper and lower jaws have different morphologies (the most commonly observed form of heterodonty in Carcharhiniformes [Cappetta, 1987], the focus group of this study). In many cases, a single individual may have both conditions. Additionally, young often display different tooth morphologies than adults, and sexual dimorphism is also displayed in the teeth of many sharks (e.g. *Scyliorhinus, Carcharhinus*, and *Galeus*) (Cappetta, 1987). The difficulty of using shark teeth is heightened by convergence in tooth morphology among different species of sharks specialized in similar feeding habits. Researchers studying fossil shark teeth often described new genera and species based on small samples of teeth. This practice, coupled with the scarcity of comparative material among the living sharks, has led to many invalid shark taxa (Cappetta, 1987; Compagno, 1988). In one example, Case and Cappetta (1997) described 44 fossil shark species from a single Late Cretaceous locality; to put this into context, there are only approximately 350 total extant species of sharks worldwide.

Teeth are not the only shark skeletal element to be preserved, however. Neoselachians secondarily calcify regions of their vertebral centra with a bone–like tissue (e.g., Applegate, 1967), and the centra are commonly found as fossils. Hasse (1879–1885) and Ridewood (1921) both recognized the potential for study of the calcification patterns within shark vertebral centra. Shark centra are morphologically distinct between different orders, but are also distinct among different genera within a single family. Because of the well–documented problems with fossil shark teeth, these additional fossil elements are potentially an important source for additional data, but fossilized shark centra are rarely studied or even identified. This study describes the morphology of the vertebral centra from four carcharhiniform families, and discusses their usefulness for identification and systematics.

The Order Carcharhiniformes, sistergroup to the Order Lamniformes, is the focal clade for this project (Figure 1a). Carcharhiniformes includes eight families and over sixty fossil and extant genera, and represents about 55% of the approximately 350 living shark species and 25% of all living elasmobranchs (Compagno, 1988; Naylor, 1992). Carcharhiniform sharks are the most numerous in species, and also likely in individuals, of all sharks. They predominate in warmer seas over continental shelves and slopes, but are distributed worldwide, ranging from tropical to polar seas, and inhabit both benthic

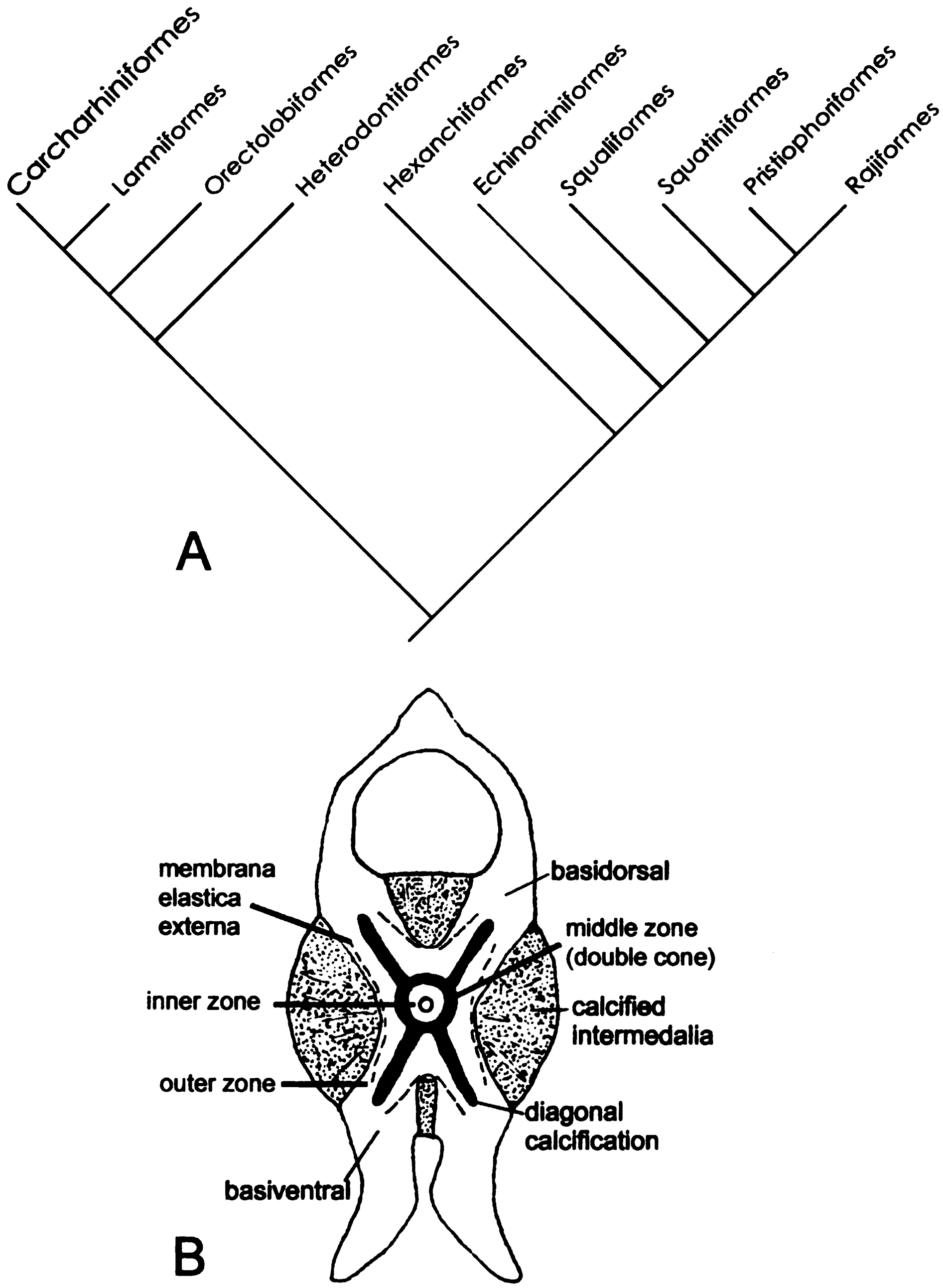


Figure 1. A. Ordinal relationships of the Recent Elasmobranchii. Modified from Carvalho (1996). **B.** Cross section of S*phynra* centrum. Modified from Ridewood (1921).

and pelagic regions (Compagno, 1984). Comparative Recent material is relatively easy to obtain as a result of their abundance.

Carcharhiniform sharks are also an old group, with their first appearance in the Jurassic (Cappetta, 1987). More advanced carcharhinids first appear in the Paleogene, but did not achieve their high diversity until the Neogene (Maisey, 1984). Carcharhiniform fossils, including vertebral centra, are common in deposits along both the East and West Coasts of North America, and are also found worldwide in other shallow marine deposits.

Despite their high taxonomic diversity, carcharhiniform sharks are far less diverse morphologically than other shark orders, and have few highly specialized sharks (Compagno, 1988). With the exception of the hammerheads, members of this order are less distinct from each other than are lamniform or orectolobiform sharks. Carcharhiniform sharks form a morphological gradient, with scyliorhinids at one extreme, and highly derived carcharhinids and sphyrnids at the other, with all the other members between these extremes (Compagno, 1988). This "gradient" makes additional techniques for clarifying carcharhiniform taxonomy essential.

This study focuses on ten genera among four families of carcharhiniform sharks, including the Triakidae (houndsharks), Hemigaleidae (weasel and snaggletoothed sharks), Carcharhinidae (requiem sharks), and Sphyrnidae (hammerhead sharks). These four families are the most derived of the order, are common as fossils, and (with the exception of Hemigaleidae) have readily obtainable Recent comparative specimens. The four families not included are the Scyliorhinidae (catsharks), Proscylliidae (finback catsharks), Pseudotriakidae (false catsharks), and Leptochariidae (barbeled houndsharks). Members of these four families are rare as fossils and Recent comparative material is difficult to obtain. Scyliorhinids, proscylliids, and pseudotriakids are all deepwater sharks or are found on continental slopes, environments that offer a low probability of fossilization. In addition, proscylliids, pseudotriakids, and leptochariids have low diversity, with only six genera among the three families.

SHARK CENTRA

The vertebral column of neoselachian sharks, including the Order Carcharhiniformes, consists of a central axis of centra, with a series of neural arches on the dorsal surface, and ventral ribs (anteriorly) or haemal arches (posteriorly) on the ventral surfaces. The neural arch encloses the dorsal nerve chord, and the haemal arches protect the dorsal aorta, and the posterior cardinal vein in the caudal region. The vertebral centrum is the major unit of the vertebral column, housing the notochord or its remnants and providing structural support for the shark. Shark centra are amphicoelous to varying degrees, with concave anterior and posterior faces, giving them a bobbin– or spool–like shape. The notochord passes through the center of the centra which may be constricted and reduced to intervertebral lenses through ontogeny (Cappetta, 1987). Consecutive centra are firmly united by fibrous rings, or intervertebral ligaments, and by white fibrous tissue that occur between the cartilage of the neural and haemal arches. Unlike teleosts, neoselachians do not have zygapophyseal processes for articulation of the vertebrae (Ridewood, 1921).

Neoselachian sharks have a cartilaginous skeleton, virtually lacking true bone. The vertebral column, likewise, is composed of cartilage. Neoselachians secondarily calcify regions of their vertebral centra, adding rigidity and strength to the column as an adaptation to the compressive forces experienced during locomotion through the dense aquatic environment (Ridewood, 1921; Daniel, 1934; Budker, 1971). This secondary calcification often forms distinct antero–posterior cross–sectional patterns within different lineages. Much discussion has occurred on the systematic significance and usefulness of the calcification patterns for elasmobranch classification (e.g., Gill, 1893; Jordan and Evermann, 1896; Jordan, 1923; White, 1938; Fowler, 1941; and Smith, 1949), which will be revisited in this dissertation.

Development

Information on development of the elasmobranch vertebral column is derived mainly from Hasse (1879–1885) and Ridewood (1921). In the early stages of development, a chordal cell–produced sheath invests the notochord. This sheath differentiates into two regions; forming externally is the membrana elastica externa, and on the interior a thick, fibrous sheath forms called the membrana elastica interna. This layer of cells forms the innermost portion of the notochordal sheath. Skeletogenous tissue is applied to the lateral surfaces of the notochordal sheath as the sclerotomes differentiate from the myotomes. This skeletogenous tissue is not continuous on the dorsal and ventral surface of the notochordal sheath. The arch–cartilages differentiate later in the upper and lower parts of the tracts while the middle part of each tract becomes reduced to a layer roughly two cells thick (Figure 1b).

During early development, the membrana elastica interna differentiates into three regions, known as the inner, middle, and outer zones (Figure 1b). The middle zone is composed of fibrous cartilage, which calcifies and forms the double cone of the centra.

The inner zone is composed of hyaline cartilage, and is mostly found at the apices of the double cone. The outer zone initially consists of hyaline cartilage, and comprises a large volume of the centrum. This outer zone may become secondarily calcified in adults by the development of an investing layer immediately external to the double cone. The outer zone may also secondarily develop longitudinal calcified laminae, either in a radiating star–like pattern (e.g., Lamniformes) or in a series of concentric tubes (e.g., Squatiniformes). These secondary outer zone calcifications are independent of the primary double cone calcification.

Skeletogenous cells next invade the inner fibrous sheath of the notochord through foramina in the membrana elastica externa, especially from the arch–bases, and produce a layer of cartilage between the membrana elastica externa and the inner fibrous sheath (or membrana elastica interna). The once continuous elastica interna differentiates into rings of hyaline cartilage set end to end. These rings continue to grow and develop into centra. The remaining areas of the chordal sheath ultimately develop into the fibrous intervertebral ligaments articulating adjacent centra together. As the centra continue to rapidly grow and develop, the notochord becomes constricted at the apices of the double cone by the hyaline cartilage of the inner zone, but continues to increase in size in the intervertebral spaces. Any calcification outside of the notochordal sheath layers is termed peripheral calcification (Ridewood, 1921).

The neural and haemal arches develop independently of the centra, with the exception of the skeletogenous cells immigrating to the inner fibrous sheath through foramina at the arch–bases. The neural and haemal arches are, for the most part, morphologically distinct and external to the centra. The arches do become continuous with the sheath cartilage at the areas where the arches attach to the centra as a result of the foramina in the membrana elastica externa. Each centrum has a pair of dorsal and a pair of ventral foramina for the attachment of arch cartilages.

A complete neural arch in elasmobranch fishes is composed mainly of the basidorsal and interdorsal cartilages, and to a lesser degree, small, unpaired supradorsals and suprainterdorsals (Figure 2). The basidorsal cartilage is typically immediately dorsal to the centrum, with the exception of the transition zone (i.e., the transition from monospondylous to diplospondylous vertebrae). The interdorsal cartilages are immediately dorsal to the intervertebral ligaments. The haemal arches are composed mainly of basiventral cartilages. The interventral cartilages appear with less regularity than do their dorsal counterparts. While the haemal arches are complete and closed in the caudal region, those vertebrae anterior to the cloaca are incomplete, and the basiventral cartilages in this more anterior region are known as transverse processes and form ventral ribs (Cappetta, 1987).

Centrum Morphology

As mentioned earlier, a single vertebral centrum has a cylindrical shape that varies from a bobbin– to spool–like shape. The lateral sides of a centrum may be concave, somewhat resembling an hourglass, straight, or slightly convex (Kozuch and Fitzgerald, 1989). Kozuch and Fitzgerald (1989) classify four basic shapes for shark centra. The centrum may be a cylinder, where the sides are nearly flat, with perhaps slight concavity or convexity to the outer wall. The modified cylinder is like the cylinder, except it has concave sides that recurve slightly near the rim. A fluted cylinder is a long,

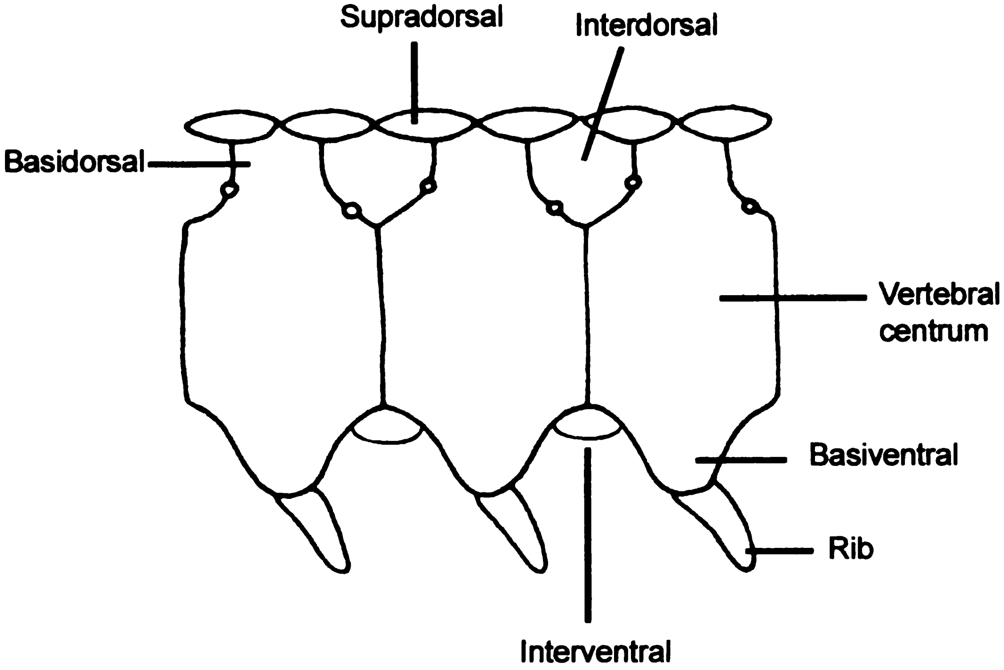


Figure 2. Lateral view of a section of a shark vertebral column. Modified from Cappetta (1987).

slender centrum that flares at each end. Finally, some centra have a strong hourglass shape with a pinched middle area and sides that are strongly recurved at the rims (Figure 3).

As mentioned earlier, shark centra vary in length regionally (i.e., MP centra tend to be much longer than DP or DC centra), but also vary among different genera. Fluted cylinder–shaped centra tend to be relatively the longest centra, along with hourglass–shaped centra. Cylinder– and modified–cylinder shaped centra tend to be of moderate to short length.

In articular view, shark centra are most often round. The centra of many genera are ovoid in articular view, with a medio–lateral breadth that is greater than dorso–ventral height. Less commonly, some centra are larger in dorso–ventral height than medio–lateral breadth.

An obvious feature on both Recent and fossil carcharhiniform centra is the foramina on the dorsal and ventral surfaces of the centra. In life, these foramina housed the cartilage of the basidorsal and basiventral cartilages. These foramina are typically oval, rectangular, or square, and have varying width and length proportions depending on genus, or, to a lesser degree, the region within the column. In some genera, the foramina extend fully into the rims, while in others, the foramina are not sufficiently long. The interforaminal wall, that is, the space between the two dorsal or two ventral foramina, also varies in width. The width of the dorsal interforaminal wall tends to be more consistent within the column than the width of the ventral interforaminal wall, which widens dramatically towards the caudal regions of the column.

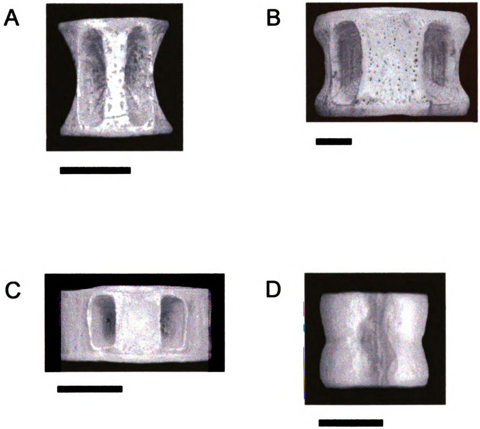


Figure 3. Four common shapes of carcharhiniform centra. **A.** Fluted cylinder (UCMP 148061, *Triakis*, dorsal view), **B.** Modified cylinder (CAS 65084, *Galeocerdo*, dorsal view), **C.** Cylinder (ANSP LCM 27, *Carcharhinus*, dorsal view), **D.** Hourglass (AMNH 93843, *Sphyrna*, dorsal view).
Scale bars = 10 mm. After Kozuch and Fitzgerald (1989).

Another physical characteristic of carcharhiniform centra is the size and spacing of the small pores found between the foramina. These pores vary in size from species to species, and follow a variety of patterns (Kozuch and Fitzgerald, 1989). These pores may be scattered along the external surface, may follow the outline of the rim and the foramina, may be concentrated in irregular clusters at the rim, or may be found midway between the rims along the sides of the centra (Kozuch and Fitzgerald, 1989) (Figure 4). Hoenig and Walsh (1982) identify these pores as cartilage canals, rod–shaped or branching structures penetrating the intermedialia, external to the notochordal sheath. These canals are especially well developed in the carcharhiniform families Carcharhinidae and Sphyrnidae. These structures are found throughout the intermedialia in mature individuals, though the presence of newer cartilage surrounding and filling some canals suggests destruction by chondrogenesis. These cartilage canals may serve nutritive roles, providing blood to the cartilage, or as part of the mechanism that regulates the levels of calcium in the serum and tissues, though the function is not clearly understood (Hoenig and Walsh, 1982). Hoenig and Walsh (1982) did, however, rule out any bone–forming role of these canals.

In some shark centra, a notochordal canal remnant is still present at the very center of the centrum. This canal remnant is typically very small in carcharhiniform sharks, and is more often completely closed over with calcified cartilage and reduced to intervertebral lenses (Cappetta, 1987). It is most often present in less derived neoselachians that have less calcified skeletons (Cappetta, 1987).

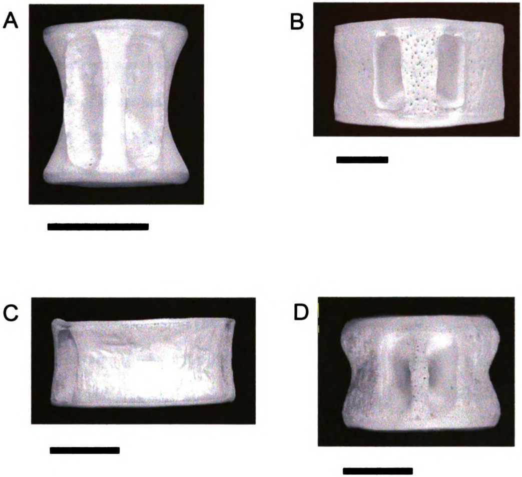


Figure 4. Variation in presence and distribution of cartilage canals (pores) in carcharhiniform centra. **A.** Pores absent (CAS 25825.13, *Triakis*, dorsal view), **B.** Scattered (G. Hubbell Collection *Sphyrna mokarran*, dorsal view), **C.** Dense at rim (G. Hubbell Collection *Prionace glauca* #1, lateral view), **D.** Encircling (AMNH 99058.52, *Sphyrna*, dorsal view). Scale bars = 10 mm.

Due to the secondary calcification of shark vertebral centra, their internal structure is complex and varied. In the past, the easiest method of studying these structures in a vertebra was to make a cross–section through the narrowest portion of the notochordal canal of a centrum and at right angles to the length of the vertebral column (e.g., Hasse, 1879, 1882). More recent advances in x–radiography provides a superior and non–destructive method of studying these same patterns in shark centra (e.g., Ridewood, 1921; Compagno, 1988; Gottfried, 1999).

In most carcharhiniform sharks, hyaline cartilage fills the areas between the basidorsals and basiventrals, the latter of which may be displaced by calcifications from the periphery of the centrum or from the double cone. These sharks likewise have an area of poorly calcified cartilage that extends inwards to the double cone from the basidorsals and basiventrals. There are also four calcified areas, found between the each of the arch cartilages; one between the two basidorsals on the dorsal surface of the centrum, one between the two basiventrals on the ventral surface, and one on each side of the centrum found between a basidorsal and basiventral. These four calcified areas are known as intermedialia, and are found in nearly all carcharhiniform sharks as well as in a number of other shark clades.

Intermedialia can vary in their expansion into the chondrified body of the centrum, but do broaden with age (Ridewood, 1921). Intermedialia grow radially and in a centrifugal manner, so that the newest calcifications in these wedges are on the most external surface (Ridewood, 1921).

Carcharhiniform intermedialia vary greatly in their shape and size both ontogenetically and between taxa, but Compagno (1988) was able to classify them into three basic types. The first, rudimentary intermedialia, form thickened calcified pads but are not expanded as wedges into the centrum. This type of intermedialium is found in some scyliorhinids and all proscylliids. The second type, hollow intermedialia, are strong wedges of calcification that extend into the centrum, but have hyaline cartilage cores. These hollow intermedialia are found in the scyliorhinids *Atelomycterus* and *Aulohalaelurus*. The third type, solid intermedialia, likewise forms strong wedges or trapezoids that extend varying distances into the centrum (Figure 1b). The solid intermedialia are the most important elements in the "Maltese cross" or "carcharhinoid" vertebral calcification type of Applegate (1967) (see "Nomenclature" discussion below). This Maltese cross pattern is present in all members of the Triakidae, Hemigaleidae, Carcharhinidae, and Sphyrnidae and *Leptocharias* (Compagno, 1988). The rudimentary intermedialia are present in many members of Scyliorhinidae and in all members of Proscylliidae. Some scyliorhinids have short, wedge–shaped intermedialia that extend only a part of the way into the vertebral body, and are transitional between the rudimentary and solid types.

In addition to the calcified intermedialia, carcharhiniform shark centra also have diagonal calcifications. These calcification are a set of four extensions of the calcified double cone into the basal cartilages (Compagno, 1988). These are absent in many scyliorhinids, some proscylliids, a few triakids and carcharhinids, and in *Pseudotriakis*, but are otherwise widespread in the order. In some scyliorhinids and proscylliids, these take the form of thick, rounded diagonal calcified knobs. In most carcharhiniform sharks, these diagonal calcifications are thin plates, termed diagonal calcified lamellae (Ridewood, 1921) (Figure 1b).

Massare and Sharkey (2003) studied the effect drying had on the morphology of vertebral centra. When comparing a radiograph of a fresh skeleton with the dried skeleton of *Carcharhinus limbatus* (Black–tip sharks), they found that the overall morphology was essentially the same. Some shrinkage did occur in the dried skeleton, but no other distortion in centrum proportions was observed. Drying the skeleton actually allowed regional variations to become more apparent.

Age Determination using Centrum Growth Rings

Ridewood (1921) noted the presence of concentric growth rings in shark vertebral centra, which were later predicted to have a potential use as age indicators (e.g., Haskell, 1949; Urist 1961; Applegate, 1967). These growth rings have subsequently been used in successful shark age determination (e.g., Tanaka and Mizue, 1979; Thorson and Lacy, 1982; Parsons, 1985; Branstetter and McEachran, 1986; Officer et al, 1996; Wintner, 2000). The nature of the systematic physiological disturbances that forms the growth rings is not well understood, however (Clement, 1992).

A growth ring is usually defined as a pair of bands, an opaque, calcified band and a translucent, less–calcified band (e.g., Cailliet et al., 1985; Wintner, 2000). The annual deposition of a band pair has been verified (Smith, 1984; Parsons, 1993), with the opaque bands deposited in the summer, and the translucent bands in the winter (Cailliet et al., 1985). Brown and Gruber (1988), however, demonstrate that band pairs are not necessarily annual in all genera, and the need exists to determine the timing of band pair formation for each species.

Using growth rings for shark age determination has other difficulties. Different increment readers may obtain significantly different counts for the same vertebrae (Officer et al., 1996). Fortunately, many different techniques exist for enhancing the growth rings for the increment readers, such as alcohol or oil immersion, xylene impregnation, alizarin red staining, x–radiography, and x–ray spectroscopy (Cailliet et al., 1985). No significant variation in growth counts is apparent between at least some of the different techniques (e.g., using alizarin red staining versus x–radiography) (Officer et al., 1996). The variation in counts also decreases with more experienced increment readers (Officer et al., 1996).

Officer et al. (1996) discovered significant variation of increment counts from different regions of an individual vertebral column. Counts from centra within a single region of the column, however, were not significantly different. Natanson and Cailliet (1990) concluded that in Pacific angel sharks, these regional increment count differences were due to differences in vertebral development. Officer et al. (1996) found that it was not possible to determine whether the regional count variations in the triakids they studied were due to vertebral development or due to the methodology used to display the increments.

Because sharks lack the scales, otoliths, and bones used in age determination in bony fish, growth ring counts in vertebral centra remains the best widely applicable method for age determination in sharks. Continued validation of the timing of band development and evaluation of the methods employed are necessary to improve the results, however.

Regions of the Vertebral Column

Krefft (1968) and Compagno (1970) have divided the shark vertebral column into three regions. The first region is made up of monospondylous precaudal centra (MP). These include those vertebrae from the occipital centrum to the transition between monospondylous and diplospondylous centra. This transition is typically at or just posterior to the pelvic girdle in carcharhiniform sharks (Compagno, 1988). Monospondylous centra gradually increase in length posteriorly in the vertebral column, and are typically longest just anterior to the MP–DP transition (Springer and Garrick, 1964). The first several centra typically have extremely wide ventral foramina, that progressively narrows to the width found in the remaining centra. The second region includes the diplospondylous precaudal centra (DP), beginning at the MP–DP transition to the caudal fin. The transition between the MP–DP zones in many carcharhiniform sharks is marked by an abrupt decrease in centrum length, often with a centrum of intermediate length separating the two zones (Compagno, 1988). Finally, the diplospondylous caudal centra (DC) are the centra of the caudal fin. These vertebrae are readily recognizable by their expanded haemal arches for support of the hypural lobe of the caudal fin (Compagno, 1988). With the exception of the MP–DP transition, centrum proportions gradually change from one centrum to next with the changes cumulative.

The formation of diplospondylous vertebrae occurs during embryonic growth of the shark, when vertebral basal cartilages and centra in the postpelvic tail double to produce two vertebrae for every myomere. The centra and basal cartilages transform by elongating, dividing, and reforming into two vertebrae, with new interdorsal cartilage between the basidorsals (Ridewood, 1899b; Šecerov, 1911; Goodrich, 1930; and

Compagno, 1988). The diplospondylous centra are short, typically three–quarters to one–half the length of the longest monospondylous centra. In larger carcharhiniform sharks with numerous short centra, such as carcharhinids and sphyrnids, the diplospondylous centra are nearly as long as the monospondylous centra (Compagno, 1988). The multiplication of the vertebrae in the caudal region may increase the flexibility of the tail, useful for the caudal propulsion exercised by sharks (Regan, 1906; Daniel, 1934; Goodrich, 1930; Cappetta, 1987).

In a number of carcharhiniform species, the diplospondylous region begins with a transition zone of alternating long and short centra, also known as the stutter zone (Compagno and Springer, 1971; Compagno, 1973a, b). This transition zone may extend well into the caudal fin (Compagno, 1988). Isolated long centra may also be found in the diplospondylous precaudal region. The posterior–most region of the vertebral column becomes highly specialized. The basal cartilages become irregular and replaced by fused blocks of cartilage that form a continuous rod enveloping the posterior extremity of the notochord (Goodrich, 1930).

Vertebral counts and ratios of the different regions have been identified for most extant carcharhiniform sharks (e.g. Springer and Garrick, 1964), but do not help when studying isolated fossil centra. While counts can be variable among the different species, a definite increase in total vertebral counts occurs in the succession from Scyliorhinidae to Proscylliidae to Triakidae to Hemigaleidae and finally to Carcharhinidae and Sphyrnidae (Compagno, 1988), suggesting an increase in vertebral count is a derived feature. Compagno (1988) identified the mean total of vertebrae for each of these families: scyliorhinids 128.4, proscylliids 139.4, triakids 145.8, hemigaleids 154.6, carcharhinids 178.0, and sphyrnids 175.7. Among carcharhiniform sharks, *Leptocharias* and *Pseudotriakis* have very high vertebral counts and do not fit the above succession, having 198–223 and 180–186 vertebrae respectively.

Composition and Function

Elasmobranchs typically have two types of cartilage in their vertebral centra: uncalcified hyaline cartilage, which does not have a high preservation potential, and calcified cartilage, which is much sturdier. Hyaline cartilage is found in the inner zone of the centra, and also initially in the outer zone, prior to its secondary calcification. This non–calcified cartilage also extends into the neural and haemal arches. The calcified cartilage that makes up the centra in elasmobranchs is formed as a result of the "impregnation of the intercellular material with a complex mixture of calcium phosphate and carbonates…" (Budker, 1971). Urist (1961) and Applegate (1967) examined these calcified deposits using x–ray diffraction and found the resulting pattern was essentially identical to the apatite found in bone in other vertebrates, though Clement (1992) suggests all tissues containing mineralized collagen have essentially indistinguishable x–ray diffraction patterns. No osteocytes have been found in the calcified cartilage, however, and elasmobranchs cannot definitively be said to have true bone in their centra (Clement, 1992). The only skeletal material that appears to be true bone is found at the bases of teeth and dermal denticles (e.g., Moss, 1970). The presence or absence of bone in shark cartilage is a subject of continuing debate. The similarity of vertebral cartilage to bone in other vertebrates increases the potential for elasmobranch centra preservation, especially when compared to the non–calcified portions of their skeleton (Kozuch and Fitzgerald, 1989).

Ridewood (1921) hypothesized that the development of calcified cartilage in the vertebrae of sharks was a response to the stresses associated with locomotion in water. Strengthening of the cartilage skeleton was necessary in certain areas to withstand these rigors while still retaining motility. In addition to being related to activity, calcification is also related to habitat, as discussed above with the deepwater forms, and size (Budker, 1971; Compagno, 1988). Larger sharks would need the calcification due to the strong swimming muscles of their trunk, working in association with the vertebral column (Budker, 1971). A related area for further study would be the mechanical and functional differences between sharks with radiating areas of calcification (e.g., Lamniformes and Carcharhiniformes) versus those with concentric bands (e.g., Squatiniformes).

Nomenclature

Hasse (1879–1885) attempted to classify the Neoselachii into three groups using the patterns seen in the cross–section of their vertebrae. The first group were those with cyclospondylous vertebrae, which are simple cylinders with a ring of calcified cartilage around the notochordal sheath. This group includes the squalids and hexanchids. Tectospondylous vertebrae have calcified cylinders deposited concentrically around the double cone, found in the squatinids. Asterospondylous vertebrae, found in the galeomorph sharks, have strong secondary calcifications formed either as solid intermedialia (the Maltese cross of carcharhiniform sharks) or radii (thin branching plates found in lamniform sharks). Woodward (1889), Regan (1906), Goodrich (1930), Ridewood (1921), Applegate (1967), and Compagno (1988) have discussed the problems associated with the use of Hasse's terms. Ridewood (1921) felt that though these patterns were "… very striking and may prove to be of some taxonomic value, Hasse did not succeed in expressing and coordinating the facts in a scheme that adequately meets the requirements of the case." (p. 337–338). Ridewood also found that the terms were used inconsistently in the literature. Applegate (1967) suggested that classification based on these vertebral types lumps unrelated groups together.

Applegate (1967) saw some value in using vertebral centra for classification, and tried to remedy the problems of Hasse's system with his own terminology, which reflected the genera in which the different morphologies occurred. He proposed eight morphotypes that could in turn be further subdivided, three of which characterized carcharhiniform sharks. The first of these are the pristiuroid vertebrae found in some members of the Scyliorhinidae (e.g., *Pristiurus* and *Cephaloscyllium*). A strongly calcified middle zone with a surrounding weakly calcified outer layer characterizes these vertebrae. The second type, atelomycteroid vertebrae, is also found in some members of the Scyliorhinidae (e.g., *Atelomycterus*), and Applegate envisions these as transitional between the pristiuroid type and those found in the Carcharhinidae. In this type, both the middle and outer zones are calcified with strongly developed radii into the basalia areas and peripheral calcification of the intermedialia. The final type is the carcharhinoid type, found in the families Triakidae, Carcharhinidae, and Sphyrnidae. Applegate envisioned this vertebral type as the culmination of a trend started in the atelomycteroid type. In the carcharhinoid vertebrae the notochordal sheath may vary in size. The four radii in the basalia are strongly developed, and the intermedialia are well calcified.

Hasse (1879) first suggested that there might be an identifiable trend in the development of secondary calcification patterns in the carcharhiniform sharks. Hasse and others (e.g., White, 1937; Nakaya, 1975) assumed that the cyclospondylic (or Applegate's pristiuroid) centra are primitive in carcharhiniform sharks, and the Maltese cross (or carcharhinoid) centra are the culmination of the trend. Nakaya (1975) especially envisioned a distinct trend starting with primitive centra with only thin, rudimentary intermedialia and no diagonal calcifications. As this trend continues, diagonal knobs and intermedialia form and eventually develop into large solid intermedialia and diagonal lamellae (Figure 5).

Dissenters (e.g., Regan, 1906; Ridewood, 1921) suggested that some cyclospondylic centra, such as in *Galeus,* may have secondarily developed from more heavily calcified centra similar to the type seen in *Atelomycterus*. Applegate (1967) suggested that cyclospondyly in scyliorhinids and squaloids evolved in parallel through reduction in a deepwater habitat. Weak rudimentary intermedialia exist today in sharks more specialized for deepwater environments, while shallow–water forms typically have strong rudimentary, solid, or hollow intermedialia (Compagno, 1988). Compagno (1988) used neither Hasse nor Applegate's system of vertebral classification, and instead discussed only the different types of elements of vertebral centra. Compagno (1988) suggests that the primitive carcharhiniform calcification pattern might consist of low but strong solid or thick rudimentary intermedialia and diagonal calcification (either lamellae or knobs), and that extreme cyclospondylic centra are not necessarily primitive. Compagno (1988) also notes that intermedialia size can vary and sometimes overlap between families, such as between some triakids and carcharhinids. Diagonal calcified

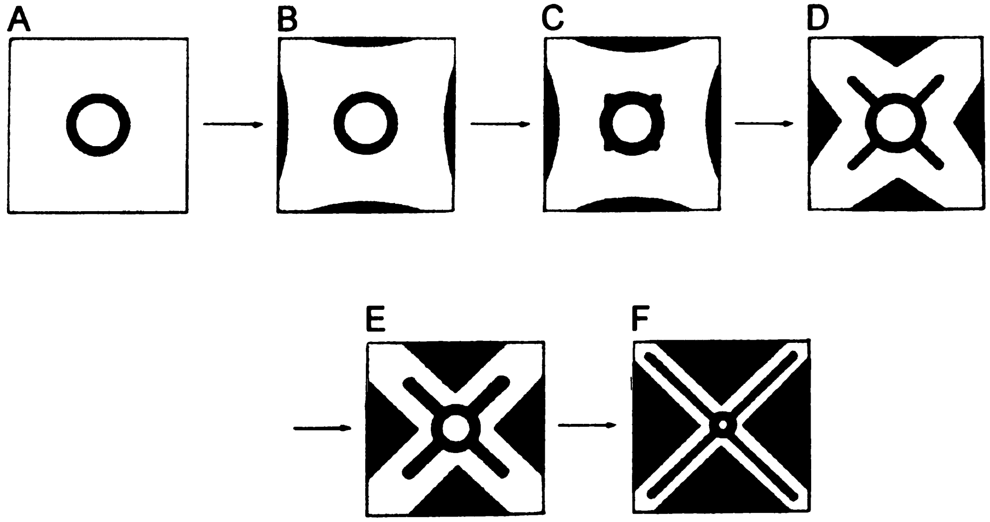


Figure 5. Trend in cross sectional calcification pattern of carcharhiniform vertebral centra according to Nakaya, (1975). A. *Cephaloscyllium, Scyliorhinus*; B. *Apristurus, Galeus*; C. *Halaelurus, Proscyllium*; D. *Mustelus, Triakis*; E. *Scoliodon, Rhizoprionodon*; F. *Pterolamiops*. Modified from Nakaya (1975).

lamellae likewise are quite variable in size in these two families, from long and well developed to completely absent.

MATERIALS AND METHODS

Radiographs

Radiographs were prepared at the MSU Department of Radiology in a triple phase general radiographic room produced by General Electric, using DuPont Quanta Detail screens, with exposures at 52–58 kilivolts and 2.0–10.0 milliamperes. Isolated fossil and Recent vertebrae were radiographed in articular view.

Photographs

Photographs of vertebral centra were taken on an Olympus C3000 digital camera, and manipulated in Adobe Illustrator 9.0 and Adobe Photoshop 5.0.

Centrum measurements

Eleven measurements were taken on each fossil and Recent centrum. Centra were measured to a hundredth of a millimeter using digital calipers. The measurements include (Figure 6):

1. Diameter 1: Diameter of centrum measured from lateral side to side at the rim. Because anterior and posterior are impossible to determine in isolated centra, the larger of the two rim measurements was recorded for centrum width 1.
2. Diameter 2: Diameter of centrum measured from lateral side to side at the rim. The smaller of the two diameter measurements was recorded for centrum diameter 2.

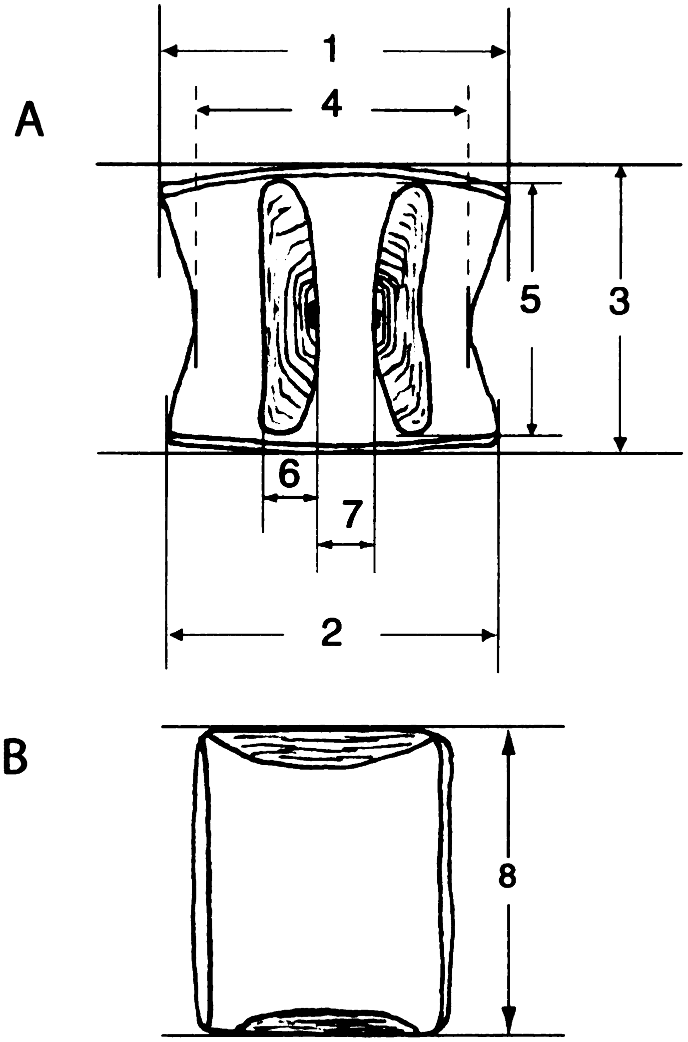


Figure 6. Carcharhiniform cenrum measurements. **A.** Dorsal view; **1)** Diameter 1, **2)** Diameter 2, **3)** Length, **4)** Width at apices of double cone, **5)** Dorsal foramen length, **6)** Dorsal foramen width, **7)** Dorsal interforaminal width. Note: measurements 5-7 repeated for ventral foramina. **B.** Lateral view; **8)** Height. After Kozuch and Fitzgerald (1989).

3. Centrum length: The length of the centrum measured from anterior to posterior rim.
4. Centrum width at apices of the double cone: Width of the centrum at the apices of the double cone. Centrum walls at this location are concave to convex in varying degrees.
5. Centrum height: Height of centrum measured at apices of the double cone.
6. Dorsal foramen length: Length measured from anterior to posterior margin of a single dorsal foramen. Because fossil centra are sometimes imperfectly preserved, the length was measured on whichever of the two foramina that was preserved best.
7. Dorsal foramen width: Maximum width of the same dorsal foramen that was measured for length.
8. Dorsal interforaminal width: Width of the wall separating the two dorsal foramina.
9. Ventral foramen length: Length measured from anterior to posterior margin of a single ventral foramen. Because fossil centra are sometimes imperfectly preserved, the length was measured on whichever of the two foramina that was preserved best.
10. Ventral foramen width: Maximum width of the same ventral foramen that was measured for length.
11. Ventral interforaminal width: Width of the wall separating the two ventral foramina.

These measurements were recorded into Microsoft Excel, and later transferred to SYSTAT for analysis (see Discriminant Analysis).

Specimens available for study

Fossil and Recent specimens were studied at or borrowed from eleven institutions and individuals. The list of institutions and their abbreviations are listed below. Lists of examined specimens are found in the Systematic Description and Appendix A.

Specimen cataloging system

Institutional catalog numbers are used for specimens when available. When multiple centra are assigned a single catalog number, the number is expanded to include decimal numbers to identify individual centra. For example, five associated *Negaprion* specimens with the catalog number UF 3245 become UF 3245.1, 3245.2…3245.5. Unofficial numbers are assigned to fossil specimens that are uncataloged, as follows:

ANSP GM 1–8: Academy of Natural Sciences specimens collected from Gardinier Mine, Bone Valley, Florida.

ANSP AF 1–18: Academy of Natural Sciences specimens collected from Agrico Fort Green Mine, Bone Valley, Florida.

ANSP LCM 1–104: Academy of Natural Sciences specimens collected from Lee Creek Mine, Aurora, North Carolina.

ANSP BVA 1–5: Academy of Natural Sciences specimens collected from Bethany, Virginia.

Recent specimens without catalog numbers are distinguished by the identification of the shark and the individual who loaned or donated the specimens, and then individually numbered, as follows:

Gordon Hubbell, private collector in Gainesville, Florida. For example: G. Hubbell Collection, *Carcharhinus perezi* 1–3.

Lisa Whitenack, student at University of Southern Florida. For example: L. Whitenack donation, *Sphyrna mokarran*, 1–8.

Abbreviations of Institutions

AMNH: American Museum of Natural History, New York, New York.

ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania.

BMNH: The Natural History Museum, London, England.

CAS: California Academy of Sciences, San Francisco, California.

CMMV: Calvert Marine Museum, Solomons, Maryland.

SDNHM: San Diego Natural History Museum, San Diego, California.

UCMP: University of California Museum of Paleontology, Berkeley, California.

UF: Florida Museum of Natural History, Gainesville, Florida.

USNM: Smithsonian Institution, National Museum of Natural History, Washington, D.C.

G. Hubbell Collection: private collection of Gordon Hubbell, Gainesville, Florida.

L. Whitenack Collection: donation from Lisa Whitenack, University of Southern Florida, Tampa, Florida.

SYSTEMATIC DESCRIPTION

The following section is formatted into "systematic paleontology" style, but it combines information for fossil and Recent centra of a single genus under one heading. This information was combined to make the comparisons more manageable. In addition, a description of *Hemipristis* based solely on fossil specimens and descriptions of two additional morphotypes of unknown identification are included. Definition and description of the morphological terms employed can be found in the Background on Shark Centra and Materials and Methods.

Class CHONDRICTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order CARCHARHINIFORMES Compagno, 1973c (Carcharhinida White, 1936)

TRIAKIDAE: Gray, 1851

***Triakis* Müller and Henle 1838A**

Figure 7

Triakis Müller and Henle 1838A, p. 36; 1838c, p. 84 (no species mentioned); 1839, p. 63.

Description of modern *Triakis* centra

Recent Referred Specimens. — CAS 25825 – *T. semifasciata*, entire skeleton; UCMP 136058 – *T. semifasciata*, entire skeleton.

Centrum Proportions. — Centra of *Triakis* include both cylinders and fluted cylinders, depending on location within the vertebral column. The largest centra, those

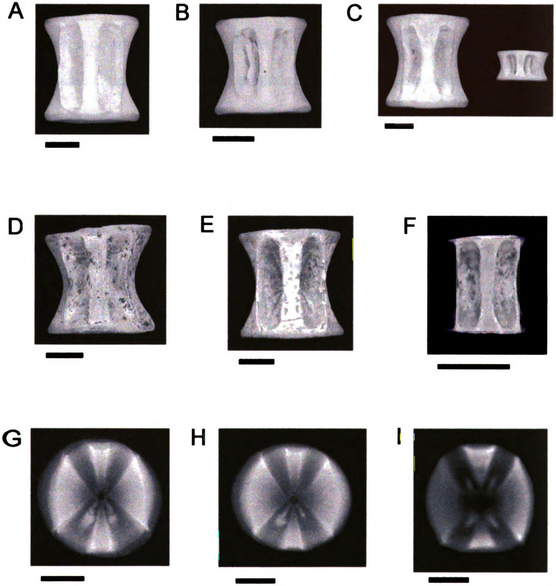


Figure 7. Recent and fossil centra of *Triakis*. **A-C:** Recent centra. **A.** CAS 25825.13, dorsal view, **B.** CAS 25825.21, dorsal view, **C.** CAS 25825.13 (left), ventral view, and CAS 25825.37 (right), dorsal view. **D-F:** Fossil centra. **D.** SDNHM 71142.05, dorsal view, **E.** UCMP 148061, dorsal view, **F.** UCMP 148078, dorsal view. **G-I:** X-radiographs. **G.** CAS 25825.14, articular view, **H.** CAS 25825.36, articular view, **I.** UCMP 148059, articular view. Scale bars = 5 mm.

found in the mid–trunk region before the MP–DP transition, are of the fluted variety. The length of these centra is greater than the width, which is partly responsible for the fluted cylinder classification. *Triakis* has proportionately the longest centra of any carcharhiniform observed. These fluted cylinder centra have strongly concave lateral walls at the apices of the double cone. The smaller centra are cylinders, and are found either in the anterior–most region or in the posterior diplospondylous regions. The cylinders have greater width than length. These centra likewise display strongly concave lateral walls at the apices of the double cone, though to a lesser degree than the fluted cylinders. This concavity decreases with decreasing centrum length. All centra lack any recurve at the rims. The medio–lateral breadth is greater than the dorso–ventral height.

Foraminal Proportions. — The dorsal foramina are typically straight, elongate ovals, while the ventral foramina are straight rectangles. All foramina are wide, dominating the either the entire dorsal or ventral surfaces of the centra. As is normal for carcharhiniform centra, the ventral foramina on anterior centra are especially wide. The dorsal and ventral interforaminal walls are typically narrower than the width of a single foramen, though the anterior centra have ventral interforaminal walls wider than the width of a single, ventral foramen. With a few exceptions, the foramina do not extend into the rims of the centra.

Pore Characteristics. — No pores are present on these centra.

Notochord Canal Characteristics. — The canal for the notochord at the apices of the double cone varies from centrum to centrum, but is mostly open and large.

Calcification Pattern. — The radiographs of CAS 25825 (*Triakis semifasciata*) reveal four strongly calcified intermedialia, extending nearly completely to the calcified double cone. The intermedialia have the typical carcharhiniform wedge shape, coming to a point at the center of the centrum. The angle of this interior point in the lateral intermedialia makes approximately a right angle, or a slightly obtuse angle. The external surfaces of the lateral intermedialia are slightly convex, though straighter than the intermedialia of other genera, especially those with little concavity of the lateral walls at the apices of the double cone. The dorsal intermedialia (the intermedialia between the two dorsal foramina) and ventral intermedialia (the intermedialia between the two ventral foramina) are very narrow, and the outside surface is strongly concave. The foraminal areas are long and straight in these centra, narrowest next to the calcified double cone and increasing in width to the outside surface of the centra. The ventral foraminal areas are wider than dorsal in these centra and are spaced further apart.

The calcified double cone is clear in centra on these radiographs, but is delicate and small. It is, however, comparatively larger than the calcified double cone in carcharhinids and sphyrnids. Extending from the calcified double cone are four diagonal calcified lamellae. These have an unusual form in *Triakis*. Instead of four narrow lamellae of approximately equal length, *Triakis* has dorsal and ventral lamellae of dramatically unequal length. The two dorsal lamellae are very short, extending less than a quarter of the length of the foramina, and are very narrow. The two ventral lamellae are much longer, extending almost half the distance of the foramina. These lamellae are thicker at the base than the dorsal lamellae, and end with an extreme increase in thickness. In cross–sectional view, these almost appear as knobs on the end of the thinner base.

Description of fossil *Triakis* centra

Referred specimens. — SDNHM 61933.12, 61933.13, 71142.05, 71142.10, 71142.20; UCMP 148039, 148058, 148059, 148061, 148066, and 148078.

Age and distribution. — Paleocene to Recent in the West Indies, Europe; Recent in East South Atlantic, Eastern Pacific, Western North Pacific, South Pacific, and Western Indian Oceans (Compagno, 1984, 1988; Cappetta, 1987).

Discussion. — Fossilized *Triakis* centra were rare among the specimens examined for this study. All fossil *Triakis* centra were from California localities, which is consistent with their modern and fossil North American distribution. The eleven fossil *Triakis* centra were very similar to the Recent comparative material. All were long, fluted cylinders with strongly concave lateral walls. Cylinder–shaped *Triakis* centra were not identified among the fossil centra on loan to the MSU Museum, though identification of these cylinder–shaped centra to the generic level can be difficult due to a lack of diagnostic characters. Foraminal aspects of the fossil centra were likewise similar to Recent centra. The foramina were wide, typically long rectangles or ovals, with narrow interforaminal walls. In a few specimens, a single foramen extended completely into the rim, though this was not the normal case. The notochordal canal was visibly open only in SDNHM 71142.20. The canal was obscured with sediment in all other *Triakis* specimens. The medio–lateral breadth was larger than the dorso–ventral height in all specimens except UCMP 148061, which was round in articular view. UCMP 148043 was crushed during preservation, though it possesses a fluted cylinder shape and triakid–like foramina.

UCMP 148059 and 148061 were the only fossil *Triakis* centra with x–radiograph images available for study. The radiographs of these specimens are very similar to the x–radiograph of Recent specimen CAS 25825. The lateral intermedialia have interior angles that are slightly obtuse, and have slightly convex external surfaces. The centra of CAS 25825 have relatively straight external surfaces compared to other triakid centra, but those of UCMP 148061 are straighter. The dorsal and ventral intermedialia are also very narrow with concave external surfaces. The foraminal dimensions of the specimens are also similar.

The calcified double cone of UCMP 148061 is visible, but is small and delicate. Four short and slender diagonal lamellae extend from this double cone. Unlike CAS 25825, these lamellae are all of equal length, and extend roughly a quarter of the length of the foramina. UCMP 148061 lacks any evidence of thickened lamellae in the ventral foramina. UCMP 148059, however, has four robust diagonal lamellae of approximately equal length, extending approximately one–quarter to one–third of the distance to the surface of the centrum.

Mustelus **Linck, 1790**

Figure 8

Mustelus Linck, 1730, p. 31.

Description of modern *Mustelus* centra

Material Examined. — CAS 53006 – *M. californicus* entire skeleton; G. Hubbell Collection – *M. canis*, 3 centra; UCMP 136060 – *M. californicus* or *lunulatus,* entire skeleton; UCMP 128660 – *M. henlei,* entire skeleton.

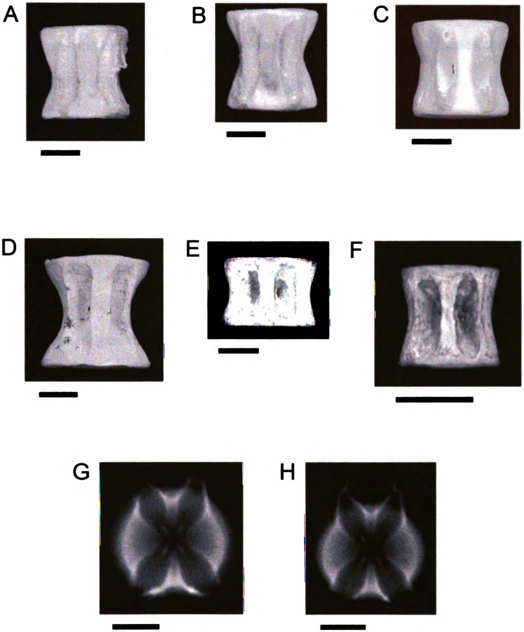


Figure 8. Recent and fossil centra of *Mustelus*. **A-C:** Recent centra. **A.** CAS 53006.26, dorsal view, **B.** CAS 53006.28, dorsal view, **C.** G. Hubbell Collection *Mustelus canis*, dorsal view. **D-F:** Fossil centra. **D.** SDNHM 71142.02, dorsal view, **E.** UCMP 148041, dorsal view, **F.** UCMP 148053, dorsal view. **G-H:** X-radiographs. **G.** G. Hubbell Collection *Mustelus canis* 1, articular view, **H.** G. Hubbell Collection *Mustelus canis* 2, articular view. Scale bars = 5 mm.

Centrum Proportions. — Centra of *Mustelus* include both cylinders and fluted cylinders, depending on location within the vertebral column. The largest centra, those found in the mid–trunk region before the MP–DP transition, are fluted cylinders. The length of these centra is greater than the width, partly responsible for the fluted cylinder classification. These fluted cylinder centra also have strongly concave lateral walls at the apices of the double cone, with a tendency to recurve towards their prominent rims. The smaller centra are cylinders, and are found either in the anterior–most region or in the posterior diplospondylous regions. These cylinders have greater width than length. These centra likewise display strongly concave lateral walls at the apices of the double cone, though to a lesser degree than the fluted cylinders and with less recurve at the rims. This concavity decreases with decreasing centrum length. The medio–lateral breadth is much greater than dorso–ventral height, giving these centra a very ovoid shape in articular view.

Foraminal Proportions. — Dorsal and ventral foramina on centra of *Mustelus* are usually straight, elongate ovals. Ventral foramina on the large, fluted cylinder centra are typically slightly bowed medially. Foramina vary in width. Dorsal foramina are typically moderate in width, while ventral are wider. Both have an interforaminal wall that is wider than the width of a single dorsal foramen. Both the sets of foramina are comparatively narrower than in other triakids. The foramina are long, and extend fully into the rims.

Pore Characteristics. — No pores are present on these centra.

Notochord Canal Characteristics. — The size of the canal for the notochord at the apices of the double cone varies from centrum to centrum, though is only rarely closed.

Calcification Pattern. — Radiographs of G. Hubbell Collection *Mustelus* centra reveal four strongly calcified intermedialia, as in *Triakis*. The interior angles of the two lateral intermedialia are either approximately right angles or slightly acute. The outside surface of these intermedialia are very convex and rounded, adding to the overall round appearance of the cross sectional view of the centra. The dorsal and ventral intermedialia are narrow as in *Triakis*, but much shorter. This shortness is related to the ovoid shape of the centra in articular view. The surfaces of the dorsal and ventral intermedialia are sharply concave, almost appearing gouged. The non–calcified areas previously housing the arch cartilage are not long and straight as is commonly seen in carcharhiniform centra. Instead, they are short and wide. These foraminal areas flare out rapidly until reaching a maximum width near the surface of the centrum and then recurve heavily, giving the foraminal area a bulbous shape. Calcified ridges, connected to the intermedialia, follow and define the foraminal areas past the surface of the centrum.

The calcified double cone is small and delicate in this genus, as in *Triakis*, with four very short and thin diagonal lamellae extending from its surface. These lamellae extend about a quarter to a third of the distance to the surface of the centra.

Description of fossil *Mustelus* centra

Referred specimens. — SDNHM 28495, 61933.05, 61933.07, 61933.14, 71142.01–71142.03, 71142.11, 71142.14, 71142.15, 71142.21, 71142.26; UCMP 148041, 148053, and 148056.

Age and distribution. — Lower Eocene through Recent in Europe and North America; Recent in all tropical and temperate seas (Compagno, 1984, 1988; Cappetta, 1987; Purdy et al., 2001).

Discussion. — The fossil centra identified as *Mustelus* vary between the cylinder and fluted cylinder shapes, but are recognizable based on other characters. All of the fossil *Mustelus* centra have strongly concave lateral walls that recurve at the rims. The medio–lateral breadth is also usually greater than the dorso–ventral height, especially in the longer, fluted cylinders. The foramina are elongate oval, still tend to be narrower than in other triakid centra, and are often bowed medially in the fluted cylinders. The canal for the notochord remnant is open in the Recent specimens, though only open in three fossil *Mustelus* centra. The remaining centra either have a closed notochordal canal or are obstructed with sediment. No x–radiographs of fossil *Mustelus* centra were available for study.

Galeorhinus Blainville, 1816

Figure 9

Galeorhinus Blainville, 1816, p. 121.

Description of modern *Galeorhinus* centra

Material Examined. — CAS 25822 – *G. zyopterus*, entire skeleton; G. Hubbell Collection – *G. galeus,* 1 centrum.

Centrum Proportions. — *Galeorhinus* centra are mostly cylinders, though once again the largest few may be classified as fluted cylinders. The fluted cylinders in

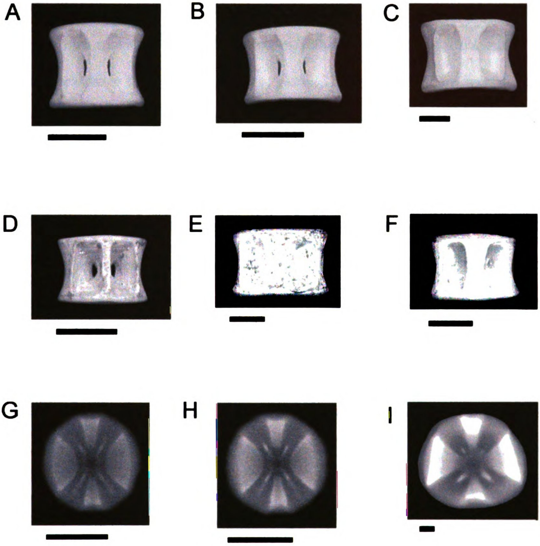


Figure 9. Recent and fossil centra of *Galeorhinus*. **A-C:** Recent centra. **A.** CAS 25822.46, dorsal view, **B.** CAS 25822.41, dorsal view, **C.** G. Hubbell Collection *Galeorhinus galeus*, dorsal view. **D-F:** Fossil Centra. **D.** SDNHM 61933.03, dorsal view, **E.** SDNHM 71142.09, dorsal view, **F.** UCMP 148048, dorsal view.
G-I: X-radiographs. **G.** CAS 25822.1, articular view, **H.** CAS 25822.2, articular view, **I.** UCMP 148045, articular view. Scale bars = 5 mm.

Galeorhinus have concave walls at the apices of the double cones, but not to the same degree as in other triakids. The smaller cylinders likewise have concave walls, but in decreasing measure as the size decreases posteriorly. These centra lack any recurve at the rims. *Galeorhinus* centra are also shorter than other triakids. Length of the centra never exceeds width, giving them a stocky appearance. The proportions as seen from the articular view exhibit considerable variation. The *Galeorhinus* specimen from the G. Hubbell Collection has a medio–lateral breadth that is quite a bit larger than dorso–ventral height, as do many of the anterior centra from CAS 25822. A few centra in CAS 25822, however, have a dorso–ventral height that is larger than medio–lateral breadth. The bulk of these specimens are round in articular view.

Foraminal Proportions. — The dorsal and ventral foramina are either rectangular (on the fluted centra) or square (on the cylinders). The squared–edges of all the foramina are due to the fact that they extend fully into the rims, so much so that the rims make the dorsal and ventral boundaries of the foramina. The foramina are very wide in *Galeorhinus* centra, more so than observed in any other triakid, and dominate the dorsal and ventral surfaces. The dorsal interforaminal walls are always narrower than the width of an adjacent dorsal foramen, sometimes less than 1 mm in width. These walls are so narrow in some that they are barely present. The ventral interforaminal walls are likewise narrower than the width of a ventral foramen, except in the anterior–most centra where the wall is quite wide, even exceeding the width of an adjacent foramen.

Pore Characteristics. — No pores are present on these centra.

Notochord Canal Characteristics. — The canal of the notochord remnant is open in the available specimens, in most cases quite large compared to the size of the centrum.

Calcification Characteristics. — Centra from CAS 25822 and G. Hubbell Collection *G. galeus* were radiographed for this study. The intermedialia of *Galeorhinus* are well–calcified, as in the previous two triakid genera, but are unique in that this calcification does not appear connect with the calcified double cone. Instead of coming to a sharp angle at the very center of the centrum, these intermedialia stop short, and have a very blunt or rounded medial surface. The outside surface of the two lateral intermedialia are only slightly convex, giving the centra laterally compressed appearances. The dorsal and ventral intermedialia are extremely narrow and rod–shaped. The outside surfaces of these intermedialia are slightly concave. The non–calcified foraminal areas are narrow near the center of the centrum and flare out towards the surface, where they are quite wide.

Like other triakids, the calcified double cone is small and delicate, with four clear diagonal lamellae projecting from it. These lamellae are likewise narrow and delicate. The two lamellae projecting into the dorsal foraminal areas are the shorter pair, extending roughly a quarter of the distance to the surface of the centrum. The ventral lamellae are longer, extending two–thirds of the distance to the surface of the centrum.

Description of fossil *Galeorhinus* centra

Referred specimens. — ANSP 3331, 15415.07; SDNHM 61933.01–61933.04, 61933.06, 61933.07, 61933.09–61933.11, 61933.15, 71142.06, 71142.08, 71142.09, 71142.12, 71142.13, 71142.16, 71142.17, 71142.22–71142.25, 71142.28, 71142.29; UCMP 148020, 148021, 148028, 148029, 148031, 148033, 148045, 148047, 148048, 148050, 148054, 148062, 148064, 148065, 148069, 148070, 148072–148074, and 148080.

Age and distribution. — Upper Cretaceous through Recent in Europe, North America, and North and West Africa; Recent in all seas (Compagno, 1984, 1988; Cappetta, 1987; Purdy et al., 2001).

Discussion. — Many more fossil centra have been identified as *Galeorhinus* than the other two triakid genera described in this study (*Triakis, Mustelus*). Centra of this genus are distinguished by their relatively short, stocky appearance and very wide foramina. It must be acknowledged, however, that the cylinder–shaped centra of *Triakis* and *Mustelus* may appear very similar to those of *Galeorhinus*, and possibly some centra that were identified as *Galeorhinus* may, in fact, be diplospondylous centra from one of these genera. In those cylinder–shaped centra, the wide foramina may be the only character useful for identification.

The above centra all have cylinder to fluted cylinder–shaped centra, and appear relatively stocky compared to other triakid centra. The foramina are also wide in these centra, though some are relatively narrower than those observed on Recent *Galeorhinus* centra, making identification less certain. In the two Recent specimens, the foramina were always rectangular or square and extended into the rims. In the some of the fossil centra identified as *Galeorhinus*, many of the foramina were oval, and often did not extend into the rims (e.g. ANSP 3331, UCMP 148021).

Only seven of the forty–five fossil *Galeorhinus* centra had an open notochordal canal. The remaining centra were either completely closed or obscured by sediment. In the centra where the opening remained, the canal remnants were wide and obvious.

X–radiographs of UCMP 148028, 148031, and 148045 were available for study. The cross–sectional views of these centra are consistent with the Recent specimens, CAS 25822 and G. Hubbell Collection *G. galeus*. One of the major differences is the medial surface of the intermedialia. On the Recent specimens, the intermedialia have a rounded and blunt medial surface that does not extend to the calcified double cone. The medial surfaces of the intermedialia on the three fossil centra form a sharp corner that extends to the double cone. The dorsal and ventral intermedialia are somewhat wider than on the Recent specimens, but do have concave external surfaces. The non–calcified foraminal areas are wide, and flare towards the surfaces of the centra.

The calcified double cone and four diagonal lamellae are visible on all fossil *Galeorhinus* specimens. These calcifications on UCMP 148028 very closely resemble those of CAS 25822, but UCMP 148031 and 148045 have much thicker diagonal lamellae. The lengths of the lamellae are comparable to CAS 25822.

Summary of Triakidae

Centra of these three genera have many similarities. All three include both cylinder and fluted cylinder shapes. The smaller centra are usually the cylinder shape, and are short to medium in length. These cylinders appear both in the anterior–most region of the column, and in the diplospondylous region. Their shorter lengths give them a more disk–like appearance, though all do have at least some constriction at the apices of the double cones. The largest, fluted cylinder centra are extremely long for their diameter, and have strongly concave lateral walls. Of the three, *Triakis* centra are relatively the longest and narrowest, while *Galeorhinus* have the thickest, most robust centra. *Mustelus* centra are the only to show any consistent recurve at the rims.

The foramina vary depending on location of the centra within the column, but typically are very wide, dominating the dorsal and ventral surfaces of the centra. The ventral foramina are especially wide in the anterior–most region of the column, separated by a wide ventral interforaminal wall. Foraminal shape is not consistent in triakid centra. Elongate oval, rectangular, and square shaped foramina are found in centra of this family, sometimes multiple shapes in a single genus. Overall, the *Mustelus* foramina appear to be narrower for their length than those of *Triakis*. The ventral foramina in the fluted cylinders of *Mustelus* bow so that the apices of the curves face each other medially, while those in *Triakis* are straight. Foramina on *Triakis* centra do not extend into the rims, while foramina on *Mustelus* and *Galeorhinus* centra do. *Galeorhinus* centra have extremely wide foramina compared to the other two genera.

The cross–sectional patterns of secondary calcification in Recent triakid centra are distinct from one another. The only arguable similarity, beyond those similarities common to all carcharhiniform sharks, is the amount of widening of the non–calcified foraminal areas towards the surface of the centra. The shapes of the intermedialia and diagonal lamellae are unique to each genus.

Unlike carcharhinids or sphyrnids, triakid centra completely lack pores. This feature, along with the presence of fluted cylinders and wide foramina are the most reliable characters for distinguishing triakid centra from centra of other carcharhiniform sharks. Great care must be taken, however, when identifying isolated fossil triakid centra to the generic level. The fluted cylinder–shaped centra are generally distinct from one another. These distinctions diminish in more posterior regions of the column, as the centra become relatively shorter.

HEMIGALEIDAE: Hasse 1879 (1885B)

Hemipristis Agassiz 1843B

Figure 10

Hemipristis Agassiz, 1843B, p. 237.

Referred specimens (fossil). — ANSP 7055–7061, LCM 3, 9, 18, 51, 91, 96; USNM 464, 288017, 288020, 288023, 288039, 288042, 288045, 290319, 467529, 467530; UCMP 148001, and 148008.

Age and distribution. — Middle Eocene through Pleistocene in Europe, North and South America, North and West Africa, India, and Indonesia; Recent in Indian and western Pacific Oceans (Cappetta, 1987; Compagno, 1984).

Description of fossil *Hemipristis* centra

Centrum Proportions. — *Hemipristis* centra are very short, disk–like cylinders. They are, along with *Prionace* centra, consistently the shortest of carcharhiniform centra. The lateral walls are typically straight, though are sometimes slightly concave. All *Hemipristis* centra have wide, distinct rims. These centra are usually round in articular view, though the largest centra are often ovoid due to a larger medio–lateral breadth than dorso–ventral height.

Foraminal Proportions. — Foramina are the most unique feature of *Hemipristis* centra. Each foramen is perfectly bisected by a thick diagonal lamella that extends completely to the surface of the centrum. As a result, each foramen appears as two adjacent elongate oval openings. Each of these adjacent openings appears narrow by themselves, but the foramina, as a whole, tend to be quite wide. These foramina generally do not extend into the rims. Dorsal interforaminal walls are narrower than the foramina. Ventral foramina are usually narrower than the foramina, though on some of the larger centra these can be slightly wider than the foramina.

Pore Characteristics. — All *Hemipristis* centra have medium to large pores. These pores typically encircle the rims and foramina closely, though a small percentage of the pores are scattered over the entire external surface.

Notochordal Canal Characteristics. — The notochordal canal is filled with sediment in these centra. The only exception is USNM 288023, where the canal is very large and open.

Calcification Pattern. — USNM 467529, ANSP LCM 3, and LCM 51 were radiographed for this study. The pattern of secondary calcification in *Hemipristis* centra is easily recognizable, for reasons mentioned above. The intermedialia are unremarkable. The lateral intermedialia have obtuse interior angles and very convex exterior surfaces. The narrower dorsal and ventral intermedialia have straight to slightly convex exterior surfaces. The non–calcified foraminal areas are quite wide, and are completely bisected by thick diagonal lamellae that extend completely to the surface. This is the only genus to consistently have lamellae that are so fully formed. The calcified double cone is not visible in these radiographs.

Discussion. — Recent *Hemipristis* skeletal material was not available for comparative purposes. Fossil centra of this genus were recognized by Purdy et al. (2001)

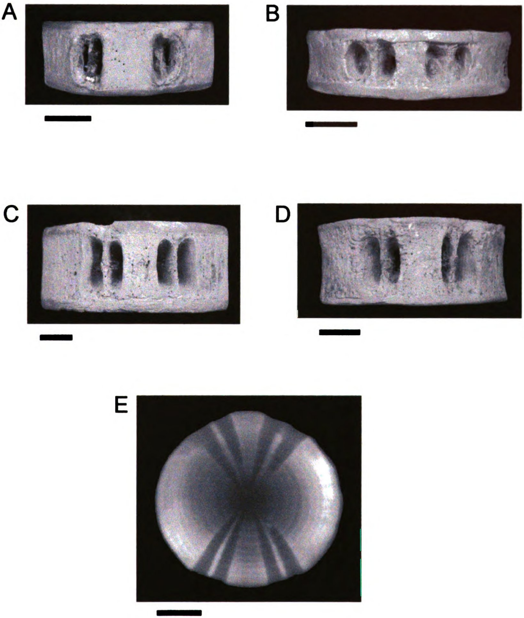


Figure 10. Fossil centra of *Hemipristis*. **A.** ANSP 7060, dorsal view, **B.** UCMP 148001, dorsal view, **C.** USNM 288042, dorsal view, **D.** USNM 288045, dorsal view, **E.** X-radiograph of USNM 467529, articular view. Scale bars = 10 mm.

in association with fossil teeth at Lee Creek Mine, North Carolina, and were used for comparison. *Hemipristis* centra are difficult to confuse with centra from other genera, because of the distinct characteristics described above. While *Carcharhinus* centra are also short cylinders with straight walls and encircling pores, *Hemipristis* centra have thicker rims and very distinct foramina with diagonal lamellae.

CARCHARHINIDAE: Jordan and Evermann 1896

Galeocerdo Müller and Henle 1837

Figure 11

Galeocerdo Müller and Henle, 1837, p. 115.

Description of modern *Galeocerdo* centra

Material Examined. — CAS 65084 – *G. cuvier*, 3 centra; AMNH 99048 – *G. cuvier*, entire skeleton.

Centrum Proportions. — All of the observed *Galeocerdo* centra have a distinct modified cylinder shape, that is, a cylinder with concave sides that recurve at the rims. Even the small caudal centra have this shape. The lateral walls are very concave, though never to the degree seen in triakids. The centra are medium in length, though the length is less than the width. When compared to length, *Galeocerdo* centra are comparatively longer than most *Carcharhinus* centra, and slightly shorter than *Sphyrna* centra. *Galeocerdo* centra have robust anterior and posterior rims. The centra are round from an articular view.

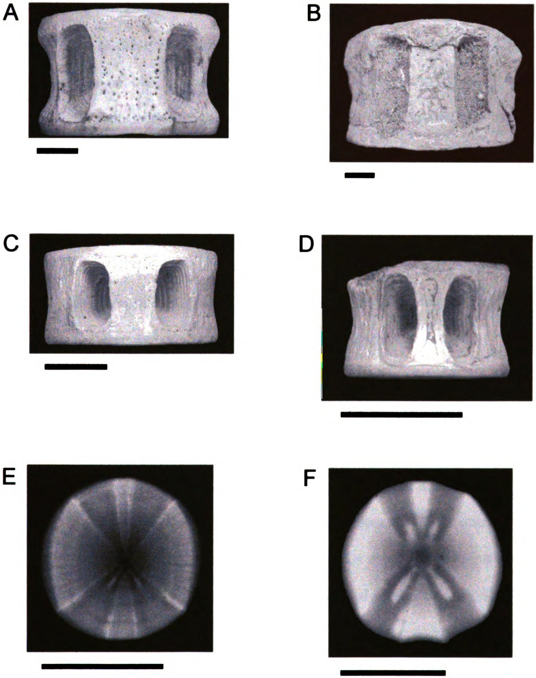


Figure 11. Recent and fossil centra of *Galeocerdo*. **A.** Recent centrum CAS 65084.1, dorsal view. **B-D:** Fossil centra. **B.** USNM 494467, dorsal view, **C.** ANSP LCM 52, dorsal view, **D.** ANSP LCM 53, dorsal view. **E-F:** X-radiographs. **E.** CAS 65084.3, articular view, **F.** UCMP 148068, articular view. Scale bars = 10 mm.

Foraminal Proportions. — Dorsal and ventral foramina are mostly rectangular, approaching a square shape in the shorter centra of the anterior–most and caudal regions. Oval foramina were not observed. (Kozuch and Fitzgerald (1989) observed oval foramina exclusively in *Galeocerdo,* though this author disagrees with their classification based on the photographed specimen they included.) Foramina are medium width. The interforaminal walls are usually narrower than the foramina, though may be wider dorsally close to the MP–DP transition. The foramina never reach the rims.

Pore Characteristics. — *Galeocerdo* centra have many extremely large pores, the largest of any specimen studied. The pores encircle the rim and foramina in a regular pattern, with a few scattered on the lateral walls and interforaminal spaces.

Notochord Canal Characteristics. — The canal for the notochord is completely sealed in all observed specimens.

Calcification Characteristics. — Centra of CAS 65084 were radiographed for this study. The four intermedialia in *Galeocerdo* centra are fairly typical in their overall appearance. They all originate at the very center of the centrum next to the opening for the notochord. The two lateral intermedialia have an interior angle of approximately 90° with slightly convex outside surfaces. The dorsal and ventral intermedialia are thin wedge shapes with straight outer surfaces. The non–calcified foraminal areas are straight, and widen rapidly towards the surface. The ventral foraminal areas are wider and spaced further apart than the dorsal foraminal areas.

The calcified double cone from which the diagonal lamellae extend is not visible in *Galeocerdo* centra, and the opening for the notochord is much smaller than in the centra of triakid genera. Two diagonal lamellae extend ventrally about one third of the distance to the surface. These lamellae are thin at the base and widen slightly at the distal end. No dorsal lamellae are present.

Description of fossil *Galeocerdo* centra

Referred specimens. — ANSP LCM 52, 59, 60; USNM 494467; UCMP 148002, 148068, 148079; and BMNH 1309.

Age and distribution. — Lower Eocene through Recent in Europe, North and South America, North, West, and South Africa, Celebes, India, and Japan; Recent in all warm–temperate and tropical seas (Compagno, 1984, 1988; Cappetta, 1987).

Discussion. — Centra of *Galeocerdo* were rare among the fossils available for study. The eight fossil centra identified as *Galeocerdo* share the long, modified cylinder–shape and large, encircling pores found in Recent centra of the genus. The main dissimilarity is the presence of oval foramina found in UCMP 148079. The remaining fossil centra had rectangular foramina, as was observed in all Recent *Galeocerdo* centra. Kozuch and Fitzgerald (1989), however, observed oval foramina in *Galeocerdo* centra, suggesting that either rectangular or oval foramina may be present. In ANSP LCM 60, the pores are large, but very scarce. USNM 494467, on the other hand, has large pores in abundance, mostly encircling the rims and foramina, but also covering the lateral walls. This specimen is somewhat weathered, however, which may obscure the true nature of pore distribution.

UCMP 148068 was the only fossil *Galeocerdo* centrum for which an x–radiograph was available. The cross–section of UCMP 148068 is similar to that of the Recent specimens, CAS 65084, in most ways, but with a few notable differences. The interior angle of the lateral intermedialia is approximately 90° in the Recent specimen, but is clearly obtuse in the fossil centrum. The dorsal and ventral intermedialia, however, are quite similar. The calcified double cone is not visible in the Recent centrum, and has two slender diagonal lamellae extending into the ventral non–calcified areas. In the fossil centrum, the calcified double cone is visible and robust, as are four diagonal lamellae. The two ventral lamellae are approximately twice the length of the dorsal lamellae. It must be noted that these discrepancies might be better understood with additional x–radiographs of *Galeocerdo* centra, especially considering both specimens are relatively short and small, and are mostly likely diplospondylous caudal centra.

Rhizoprionodon **Whitley 1929**

Figure 12

Rhizoprionodon Whitley, 1929, p. 354.

Description of modern *Rhizoprionodon* centra

Material Examined. — AMNH 22826 – *R. terraenovae,* entire skeleton; G. Hubbell Collection – *R. terraenovae* 5 centra; L. Whitenack Collection – *R. terraenovae*, 10 centra.

Centrum Proportions. — The centra of *Rhizoprionodon* are unlike those of any other carcharhinid. Their centra, in fact, more closely resemble triakid centra. The centra range from cylinder to fluted cylinder in overall shape and are longer than typical carcharhinid vertebrae. The size tends to be small compared to other carcharhinids. The lateral walls of the centra are strongly concave. The centra have a medio–lateral breadth

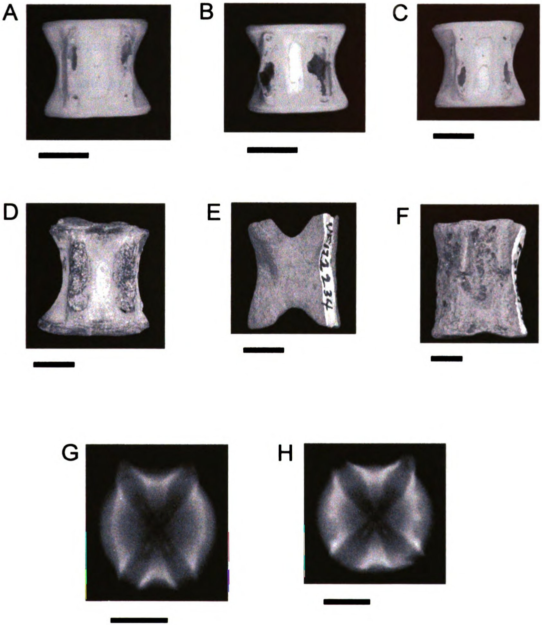


Figure 12. Recent and fossil centra of *Rhizoprionodon*. **A-C:** Recent centra. **A.** G. Hubbell Collection *Rhizoprionodon terraenovae* 1, dorsal view, **B.** G. Hubbell Collection *Rhizoprionodon terraenovae* 2, dorsal view, **C.** G. Hubbell Collection *Rhizoprionodon terraenovae* 5, dorsal view. **D-F:** Fossil centra. **D.** ANSP AF 19, dorsal view, **E.** UF 122234, dorsal view, **F.** UF 123154, dorsal view. **G-H:** X-radiographs. **G.** G. Hubbell Collection *Rhizoprionodon terraenovae* 2, articular view, **H.** G. Hubbell Collection *Rhizoprionodon terraenovae* 4, articular view. Scale bars = 5 mm.

larger than dorso–ventral height, sometimes extremely so. This gives the centra an ovoid appearance from articular view.

Foraminal Proportions. — Foramina on these centra are also unlike any other carcharhiniform centra observed. They are almost completely closed over by what appears to be calcified cartilage or remnants of the arch–cartilage. The foramina are all elongate ovals, and tend to be quite narrow. Due to this narrowness, the interforaminal walls are all wider than the foramina, sometimes greatly so. Wall width varies with region of column as is normal for carcharhiniform centra.

Pore Characteristics. — No pores were visible on any *Rhizoprionodon* centra, even with a dissecting microscope. This makes them the only carcharhinid centra observed without pores.

Notochord Canal Characteristics. — The canal for the notochord was closed in every centrum of *Rhizoprionodon.*

Calcification Characteristics. — Centra from G. Hubbell Collection *R. terraenovae* were radiographed for this study. The cross–sectional pattern of secondary calcification in *Rhizoprionodon* is almost indistinguishable from the pattern seen in *Mustelus*. The most obvious difference is the shape of the lateral intermedialia. In *Rhizoprionodon*, the interior angle of these intermedialia are at right angles to obtuse angles, while they tend to be acute in *Mustelus*. The external surfaces of these intermedialia in *Rhizoprionodon* are very convex, giving a very round appearance to the centra in the radiograph. The dorsal and ventral intermedialia are quite similar to those of *Mustelus*, both are quite narrow and short. In *Rhizoprionodon* the surface of these two intermedialia are sharply concave. The non–calcified areas previously housing the arch cartilage are not long and straight as is commonly seen in carcharhiniform centra, but are rather short and wide. These foraminal areas flare out rapidly until reaching a maximum width near the surface of the centrum and then recurve heavily, giving the foraminal area a bulbous shape. *Rhizoprionodon* does not have this shape to the same degree as *Mustelus*. Calcified ridges, connected to the intermedialia, follow and define the foraminal areas past the surface of the centrum.

The calcified double cone is not visible in the radiographs of these centra, though four small diagonal lamellae do extend into the non–calcified foraminal areas. These lamellae are thin at the base and wider distally, and extend a quarter to a third of the distance into the foraminal areas.

Description of fossil *Rhizoprionodon* centra

Referred specimens. — ANSP AF 19; UF 122858, 122234, and 123154.

Age and distribution. — Lower Eocene through Recent in Europe, North Africa, and North America; Recent in warm–temperate to tropical Atlantic and Indo–Pacific Oceans (Compagno, 1984, 1988; Cappetta, 1987; Purdy et al., 2001).

Discussion. — These four fossil specimens are poorly preserved. Their identification as *Rhizoprionodon*, however, is certain. Key morphological features are still visible on these centra that are common to *Rhizoprionodon*. The centra are all long, fluted cylinders with strongly concave lateral walls. The medio–lateral breadth is much greater than the dorso–ventral height, giving the centra an ovoid shape in articular view. The fossil centra also display the same unusual foramina seen in the Recent centra. The foraminal surfaces are closed over with what appears to be arch–cartilage. On the fossil specimens, this is observed as thin ridges where the foramina are normally located. No pores are visible on the UF specimens, but the poor quality of these fossils would preclude any possibility of observing pores. ANSP AF 19 has what appears to be a few small pores adjacent to the foramina, though preservational quality of this specimen is poor enough to make this uncertain. The presence of pores on this specimen would make it the only *Rhizoprionodon* specimen with this character.

An x–radiograph was available for UF 123154, but no internal detail was visible. The only information that was visible was the ovoid cross–sectional shape, similar to the shape observed in the x–radiographs of the G. Hubbell Collection *Rhizoprionodon* centra.

Prionace **Cantor 1849**

Figure 13

Prionace Cantor, 1849 p. 1399.

Description of modern *Prionace* centra

Material Examined. — G. Hubbell Collection – *Prionace glauca*, 5 vertebrae.

Centrum Proportions. — *Prionace* centra are disk–like cylinders. For their diameters, they are the shortest carcharhiniform centra. Despite their shortness, they still have strongly concave lateral walls. Their rims are quite pronounced, giving them a very unique appearance compared to other carcharhinids. *Prionace* centra are round in articular view. These centra also seem more delicate than other carcharhiniform centra. The cartilage has a low density and chalky texture. The walls also have a somewhat fibrous appearance. These centra are from an adult animal that measured 9’6”, so lower

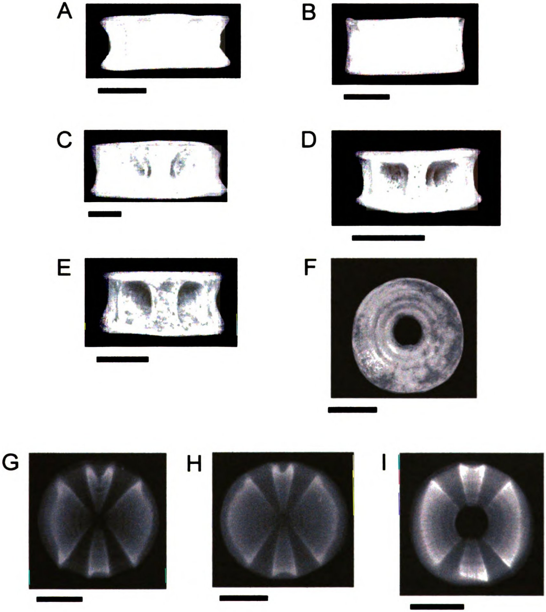


Figure 13. Recent and fossil centra of *Prionace*. **A-B:** Recent centra. **A.** G. Hubbell Collection *Prionace glauca* 1, dorsal view, **B.** G. Hubbell Collection *Prionace glauca* 1, lateral view. **C-F:** Fossil centra. **C.** CMMV 815, dorsal view, **D.** ANSP LCM 64, dorsal view, **E.** ANSP 308.2, dorsal view, **F.** ANSP 308.2, articular view. **G-I:** X-radiographs. **G.** G. Hubbell Collection *Prionace glauca* 4, articular view, **H.** G. Hubbell Collection *Prionace glauca* 5, articular view, **I.** ANSP 308.2, articular view. Scale bars = 10 mm.

density is not a result of the animal being juvenile with little calcification of the cartilage. These centra should be compared with centra from other *P. glauca* specimens.

Foraminal Proportions. — In all of the centra examined, the foramina are short, wide rectangles. Their short length is due to the overall short length of the centra, but the width of the foramina is comparable to other carcharhinids. The foramina extend fully into the rims. The interforaminal walls are generally quite narrow, much narrower than the foramina.

Pore Characteristics. — Pores are present and abundant on these centra. The pores are miniscule, making magnification necessary to see them clearly. The pores are found surrounding the foramina in fairly low density and in a single, regular line following the rims. This pattern is unique to *Prionace* centra.

Notochord Canal Characteristics. — The canal for the notochord is not entirely closed, but small enough to be barely noticeable. Like *Negaprion*, the Canal appears to have been more open recently, but is now closed over by cartilage.

Calcification Characteristics. — Centra from G. Hubbell Collection *P. glauca* were radiographed for this study. As in the external view of the *Prionace* centra, the cross–sectional calcification patterns are unique. The interior angles of the lateral intermedialia are always obtuse and extend completely to the opening for the notochordal remnant. The external surfaces of these intermedialia all have a unique shape. These surfaces have the normal convex, rounded appearance, but recurve strongly near the foramina, giving them a gentle “W” shape. The dorsal and ventral intermedialia are long, but vary quite a bit in width. The external surfaces on all of these intermedialia are very concave, sometimes dramatically so, and to a degree more so than in any other observed carcharhiniform shark centra. The four non–calcified foraminal areas are narrow at the base and flare towards the external surfaces.

No calcified double cones are visible in *Prionace* centra, nor are there any diagonal calcified lamellae.

Description of fossil *Prionace* centra

Referred specimens. — CMMV 815; ANSP 308.1–308.4, and ANSP LCM 64.

Age and distribution. — Pliocene of Italy; Recent in all tropical and temperate seas (Cappetta, 1987). *Prionace* is the widest ranging modern cartilaginous fish (Compagno, 1984, 1988).

Discussion. — Six fossil centra from the eastern United States have been tentatively identified as *Prionace*. Of these six, ANSP 308.1–308.4 are associated and likely from the same individual. These six centra have only been tentatively identified, because *Prionace* centra are not otherwise known from Neogene deposits in North America. Cappetta (1987) lists the only known fossil occurrence for *Prionace* as the Pliocene of Italy.

These six fossil centra closely resemble the Recent *Prionace* centra that were available for comparison. All were short, disk–like cylinders with strongly concave lateral walls, strong rims, and were round in articular view. The foramina were all short, wide rectangles that extended into the rims. The Recent *Prionace* centra were observed to be very delicate compared to other carcharhinid centra. They seemed to have a lower density cartilage, and an almost fibrous texture. All six fossil centra likewise seemed much more delicate, despite mineralization during fossilization.

The Recent centra have unique pore characteristics compared to other carcharhinid sharks. Their pores are miniscule and closely followed the rims in a single line. The pores on these six fossil centra are larger, and encircle the foramina and rims, though not in the regular, single line observed on the Recent centra.

Of special note is the opening for the notochordal canal in ANSP 308.1–308.4. These openings are enormous, ranging from 3.4 mm to 6.5 mm in diameter. In other carcharhiniform centra, the openings for the notochordal remnants usually resemble tiny pinholes, and are not generally measurable. The reason for the unusually large openings in these four centra is not clear, though it does not appear to be the result of weathering or poor preservation.

CMMV 815 and ANSP 308.1–308.4 had x–radiographs available for study. In overall appearance, the cross–sectional views of the fossil and Recent centra appear similar, but differ in a few characteristics. The Recent *Prionace* centra have lateral intermedialia with a convex outer surface that recurve strongly near the foramina that give them a gentle "W" shape. This feature is only visible on one lateral intermedialium on CMMV 815, and only to a small degree. This centrum is heavily worn, however, and the condition could have been present when the centrum was in better condition. ANSP 308.1–308.4 have only a hint of this shape on the lateral intermedialia. The strongly concave external surfaces of the dorsal and ventral intermedialia seen in the Recent centra are also apparent in ANSP 308.1–308.4, but not in CMMV 815, though the poorer condition of preservation could have obscured this feature.

No calcified double cone or diagonal lamellae are visible on the G. Hubbell Collection *Prionace* specimens. ANSP 308.1–308.3 also lack any evidence for these calcifications. ANSP 308.4, however, has two small diagonal lamellae extending into the dorsal non–calcified areas. CMMV 815 has four thick diagonal lamellae extending over half of the distance towards the surface of the centrum.

***Negaprion* Whitley 1940**

Figure 14

Negaprion Whitley, 1940, p. 11.

Description of modern *Negaprion* centra

Material Examined. — G. Hubbell Collection – *N. brevirostris,* 2 centra.

Centrum Proportions. — *Negaprion* centra have a cylinder shape with concave lateral walls. In one specimen, this concavity is minor, with a small amount of recurvature at the rims. The second specimen has strongly concave lateral walls and a large amount of recurve. *Negaprion* centra are short, though longer than the average *Carcharhinus* centrum. Both centra are round in articular view. In overall appearance, they are very similar to centra of *Carcharhinus*. There may, indeed, be no unique character possessed by either that can distinguish them from each other. The sample size of two centra is too small, and more centra are needed to draw final conclusions.

Foraminal Proportions. — Foramina are all rectangular with medium width and length that do not extend into the rims of the centra. Both the dorsal and ventral interforaminal spaces are wider than the foramina.

Pore Characteristics. — These *Negaprion* centra have numerous pores closely following the rims and foramina. The pores are miniscule, almost too small to be seen

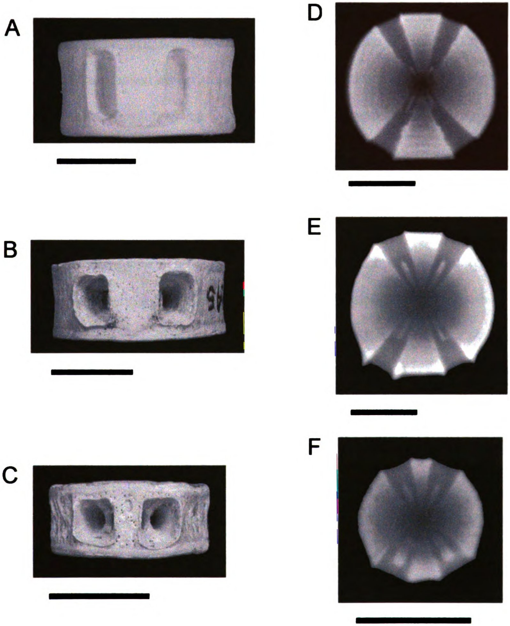


Figure 14. Recent and fossil centra of *Negaprion*. **A.** Recent centrum G. Hubbell Collection *Negaprion brevirostris* 1, dorsal view. **B-C:** Fossil centra. **B.** UF 3245.2, dorsal view, **C.** UF 3245.5, dorsal view. **D-F:** X-radiographs. **D.** G. Hubbell Collection *Negaprion brevirostris* 1, articular view, **E.** UF 3245.2, articular view, **F.** UF 3245.5, articular view. Scale bars = 10 mm.

without magnification. Kozuch and Fitzgerald (1989) record *Negaprion* pores as being scattered over the surface, which is clearly not the case in the G. Hubbell Collection specimens. As mentioned earlier, more centra are needed to increase the sample size.

Notochord Canal Characteristics. — Both centra still have a small opening for the notochord, but they are miniscule, smaller even than the pores on the surfaces. This opening was clearly larger earlier in the life of the shark, but is now closed over by cartilage.

Calcification Characteristics. — Centra from G. Hubbell Collection *N. brevirostris* were radiographed for this study. The pattern of secondary calcification in *Negaprion* centra is very similar to that of *Carcharhinus.* The lateral intermedialia have a very obtuse interior angle with moderately convex outer surfaces. These intermedialia extend completely to the center of the centra where they connect with the openings for the notochordal remnant. The dorsal and ventral intermedialia are long, wide wedges with straight to slightly concave exterior surfaces. The non–calcified foraminal areas are narrow wedge shapes. The dorsal foraminal areas are slightly shorter than the ventral foraminal areas, and are straight. The longer ventral foraminal areas are slightly bowed laterally.

The calcified double cone is not visible in the radiographs of these centra. Four diagonal lamellae extend from the center of the centra. These lamellae are comparatively wide and quite short, extending less than a quarter of the distance to the surface of the centrum.

Description of fossil *Negaprion* centra

Referred specimens. — UF 3245.1–3245.5.

Age and distribution. — Middle Eocene through Recent in Europe, North and South America, and West Africa; Recent in warm–temperate to tropical Atlantic and Indo–Pacific Oceans (Compagno, 1984, 1988; Cappetta, 1987).

Discussion. — The five fossil *Negaprion* centra are associated with teeth identified as *Negaprion brevirostris*, and are likely from a single individual. UF 3245.4 and 3245.5 appear to be diplospondylous caudal centra. They are smaller than the other three fossil centra, and are very short. All five of the fossil centra are shorter than the two Recent *Negaprion* centra. The three larger fossil centra may be diplospondylous precaudal centra. The fossil and Recent centra closely resemble one another in most other ways. The fossil centra have slightly concave later walls and prominent rims, and are round in articular view. The foramina are rectangular with wide interforaminal walls. All the fossil centra have fine pores scattered on the lateral walls and surrounding the foramina. No opening for the notochordal remnant was observed on any of the fossil centra.

All five fossil *Negaprion* centra were radiographed for this study. The cross–sectional view is very similar to that of G. Hubbell Collection *Negaprion brevirostris*. The intermedialia have the same obtuse interior angle and convex outer surfaces. The dorsal and ventral intermedialia likewise are long, wide wedges with slightly concave exterior surfaces. All four non–calcified were narrow and straight. The calcified double cone is not visible in the fossil specimens, though all have four thick diagonal lamellae. In the three fossil centra that appear to be diplospondylous precaudal, the lamellae extend a quarter to a third of the distance to the external surface of the centra. In the diplospondylous caudal centra, the lamellae extend two–thirds to three–quarters of the distance to the surface, and are thicker than the lamellae in the precaudal centra.

The unfortunately small sample size of Recent *Negaprion* centra greatly limits the identification of fossil centra of the same genus. UF 3245.1–3245.5 would most have most likely been identified as *Carcharhinus* centra had it not been for the associated *Negaprion brevirostris* teeth. Hundreds of fossil centra have been identified as *Carcharhinus* below, though a few *Negaprion* centra may be present. *Carcharhinus* is much more abundant and diverse in both modern waters and in the fossil record (e.g., almost 30 extant species of *Carcharhinus* versus 2 extant species of *Negaprion.* (Compagno, 1984)). Another difficulty with the comparison of the fossil and Recent *Negaprion* centra is that the specimens were from different regions within the vertebral column. G. Hubbell Collection *Negaprion brevirostris* centra are monospondylous centra, while all of the fossil centra appear to be diplospondylous. Variations along the column were most certainly responsible for some of the differences seen between the two sets of specimens.

***Carcharhinus* Blainville 1816**

Figure 15

Carcharhinus Blainville, 1816, p. 121.

Description of modern *Carcharhinus* centra

Material Examined. — AMNH 218147 – *C. leucas,* entire skeleton; G. Hubbell Collection – *C. leucas*, 3 centra; G. Hubbell Collection – *C. leucas*, 5 centra; G. Hubbell Collection – *C. leucas*, 2 centra; AMNH 93846 – *C. brevipinna,* entire skeleton; AMNH 218150 – *C. acronotus,* entire skeleton; G. Hubbell Collection – *C. altimus*, 2 centra; G. Hubbell Collection – *C. falciformis*, 4 centra; G. Hubbell Collection – *C. falciformis*, 5 centra; G. Hubbell Collection – *C. limbatus*, 3 centra; G. Hubbell Collection – *C. limbatus*, 3 centra; L. Whitenack Collection – *C. limbatus*, 15 centra; L. Whitenack Collection – *C. limbatus*, 12 centra; G. Hubbell Collection – *C. perezi*, 4 centra; G. Hubbell Collection – *C. perezi,* 3 centra; G. Hubbell Collection – *C. perezi*, 4 centra; G. Hubbell Collection – *C. plumbeus*, 5 centra; G. Hubbell Collection – *C. signatus*, 4 centra.

Centrum Proportions. — Specimen availability for this genus was better than for any other carcharhiniform shark. *Carcharhinus* is also the most diverse carcharhiniform genus. Their centra display some of this diversity, but the morphology of the centra for the different species is similar. All species observed have cylinder–shaped centra. *C. brevipinna* is unique among the observed specimens in having a few of the largest centra that could be classified as fluted cylinders. *C. falciformis*, *C. altimus*, and *C. signatus* have a few centra with a slight amount of recurve at the rims, approaching a modified cylinder shape. Overall, *Carcharhinus* centra are very short relative to their diameters, giving them a disk or bobbin–like appearance. Some of the largest centra, found just prior to the MP–DP transition, are longer and more similar in length to those of *Sphyrna* or *Galeocerdo*. *Carcharhinus* centra have less concave lateral walls than any other genus.

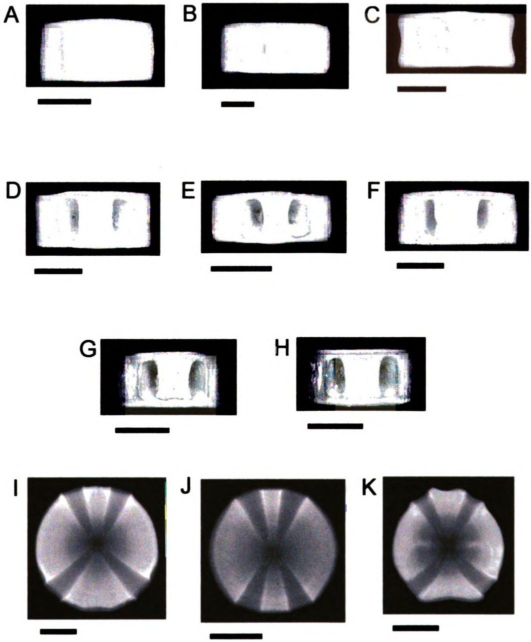


Figure 15. Recent and fossil centra of *Carcharhinus*. **A-C:** Recent centra. **A.** G. Hubbell Collection *Carcharhinus perezi* 3, dorsal view, **B.** G. Hubbell Collection *Carcharhinus leucas* 2.1, dorsal view, **C.** G. Hubbell Collection *Carcharhinus signatus* 4, dorsal view. **D-H:** Fossil centra. **D.** ANSP LCM 27, dorsal view, **E.** ANSP LCM 46, dorsal view, **F.** ANSP LCM 47, dorsal view. **G-H.** Associated specimens. **G.** USNM 24914.04, dorsal view, **H.** USNM 24914.12, dorsal view. **I-K.** X-radiographs. **I.** G. Hubbell Collection *Carcharhinus leucas* 2.1, articular view, **J.** G. Hubbell Collection *Carcharhinus signatus* 4, articular view, **K.** BMNH 4546.1, articular view. Scale bars = 10 mm.

While this concavity does exist in some species, it is minor, with the exception of *C. brevipinna* and a few centra of *C. acronotus*. Centra typically have straight or even convex lateral walls. *Carcharhinus* centra are usually round in articular view, though may vary between medio–lateral breadth greater than dorso–ventral height or dorso–ventral height greater than medio–lateral breadth.

Foraminal Proportions. — Foraminal shape is quite variable in *Carcharhinus* centra. Most foramina are oval or rectangular, though square foramina are found in some of the shortest caudal centra. Foramina are medium in width, and never extend into the rims. Except on the anterior–most centra, the ventral interforaminal width is narrower than the width of the foramina. Dorsal interforaminal width, however, can be both narrower and wider than the width of the foramina in a single individual.

Pore Characteristics. — Pores are always present on *Carcharhinus* centra, though in varying numbers. The pores are very small to medium in size, never as large as those found on *Galeocerdo* centra. The pores are commonly scattered over the entire external surface or encircle the rims and foramina.

Notochord Canal Characteristics. — The passage for the notochord is rarely intact. When it is open, it is quite small and barely visible without magnification. The area typically looks to have been previously larger and closed over with cartilage.

Calcification Characteristics. — Centra from G. Hubbell's *C. signatus, C. perezi,* and *C. leucas* were radiographed for this study. While centra of *Carcharhinus* do not have any characters of the calcification pattern that are unique, the overall pattern is identifiable. This pattern, unfortunately, does closely resemble the pattern seen in *Negaprion* centra. The four intermedialia are unremarkable. The lateral intermedialia each have an obtuse interior angle, and a very rounded, convex exterior surface. The dorsal and ventral intermedialia vary in width, as in all carcharhiniform centra, and have a straight to gently concave exterior margin. The non–calcified foraminal areas are fairly narrow. The dorsal foraminal areas are typically shorter than the ventral, and are straight. The longer ventral foramina are either straight or curve laterally gently.

The calcified double–cone is faintly visible in these radiographs, and is quite narrow, especially considering the medium to large size of these centra. Extending from the double–cone are four delicate, short diagonal lamellae. These four lamellae are equal in length, and extend a fourth or fifth of the distance towards the exterior of the centra. The lamellae are thinnest at the base, increase slightly in width distally, and taper at the end.

Description of fossil *Carcharhinus* centra

Referred specimens. — CMMV 1013, 1131, 1133, 1575, 1577, 1578, 1581, 1582, 1652.01–1652.11, 1784, 1887; ANSP GM 1, 4, 5, ANSP 308.5, 6480, 7054, 8111, 8113, 8122, 8125, 8131, 8040, 14698, 15415.02–15415.06, 15415.08, 15433, 20148.1, ANSP AF 5, 11, 13, ANSP LCM 2, 4, 5, 7, 8, 12, 14, 21, 23, 26–30, 44–50, 53–58, 62, 63, 65–67, 72–75, 79, 81–83, 85–88, 90, 92, 93, 94, 97, 104, ANSP BVA 1–5; USNM 24914.01–24914.13, 288037, 369890, 435324.01, 435324.02, 467532, 494463.01–494463.11; SDNHM 25782, 61937.01–61937.03, 63154, 65993–65995, 71142.04; UF 92276, 92277, 92280–92282, 92291, 128906; UCMP 148003, 148005–148007, 148009–148012, 148015, 148017, 148018, 148025–148027, 148032, 148035, 148044; BMNH 4645.1, 4645.2, 4645.4, 4645.6, 5571.1–5571.4, 35611a.1–35611a.8, and 13799.

Age and distribution. — Middle Eocene through Recent of Europe, North America, North and West Africa, Australia, Japan, New Zealand, and India; Recent in all warm–temperate and tropical seas (Compagno, 1984, 1988; Cappetta, 1987).

Discussion. — *Carcharhinus* is abundant and diverse today, as it was during much of the Cenozoic. Fossil centra from *Carcharhinus* are much more abundant than any other genus among the material examined for this study. While some diversity in their morphology is expected, their centra are still readily identifiable (though *Negaprion* centra may easily be mistaken for *Carcharhinus*). All of the fossils examined are short, cylinder–shaped, and have slightly concave to convex lateral walls. Also similar to Recent *Carcharhinus* centra, the foramina on the fossil centra vary from round to rectangular, though they never consistently extend into the rims. The remnant for the notochordal canal was closed in every fossil centrum. Pores are always present (when fossil preservation is sufficiently good), either scattered over the entire external surface, or found encircling the rims and foramina. UCMP 148010 is the only observed exception. The pores on this centrum followed the rims in single, regular lines. This pattern is similar to that of *Prionace* centra, though these pores were much larger. UCMP 148010 did not resemble *Prionace* centra in any other characteristic.

Over 50 fossil *Carcharhinus* centra were x–radiographed for this study. The cross–sectional patterns on these fossils are very similar to those of Recent *Carcharhinus* centra. One feature that is especially distinct on the fossil centra is the shape of the ventral non–calcified areas. At times, these non–calcified areas are straight and narrow, but in many, they curve laterally (e.g. CMMV 1013, 1652.02, 1652.07, ANSP 20148).

This characteristic was noted on Recent *Carcharhinus* centra, but not as often, nor to the same degree (with the exception of a single *C. leucas* centrum).

The calcified double–cone is rarely visible in the radiographs. When it is visible, it is faint and delicate, similar to those of Recent *Carcharhinus* centra. Diagonal lamellae are always present and well developed. The lengths of these lamellae vary between extending one–quarter to three–quarters of the distance to the surface of the centrum. Like those observed on Recent *Carcharhinus* centra, the lamellae are thinnest at the base, increase slightly in width distally, and taper at the end.

Summary of Carcharhinidae

The members of Carcharhinidae are numerous and diverse, and this diversity is visible in the morphology of the vertebral centra. Of the five genera examined, only *Carcharhinus* and *Negaprion* centra closely resemble each other, and distinguishing the two will be difficult.

Galeocerdo centra are among the most easily recognized of the carcharhinids. These centra have distinct modified cylinder shapes with large encircling pores. In radiographs, the presence of only two diagonal lamellae is a unique feature found in only *Galeocerdo,* though more samples may prove otherwise.

Carcharhinus centra are very common as fossils, and are generally not difficult to recognize. The combination of their extremely short, disk–like cylinder shape, typically straight to slightly convex lateral walls, and scattered to encircling distribution of tiny pores is enough to identify them. Those centra that are longer are more difficult to distinguish, as they may be confused with *Negaprion* or perhaps *Galeocerdo* if the lateral walls are strongly concave or display any recurve at the rims. Long centra of unknown identification will have to be examined on a case–by–case basis and compared to centra of known identification.

The morphology of *Rhizoprionodon* centra is quite distinct from the morphologies of other carcharhinid centra. Their strongly concave lateral walls and length alone are enough to distinguish them. Their lack of pores is also very distinct among carcharhinids. Distinguishing these centra from triakid centra poses more of a problem. Both have similar shapes, lack pores, and often have elongate oval foramina. The cartilage that closes over the foramina will be the key identifying feature. This cartilage does appear to be preserved in fossils, as in ANSP AF 19, UF 122858, 122234, and 123154.

Negaprion centra closely resemble the centra of *Carcharhinus*. Both have similar cylindrical shapes, and while *Negaprion* centra have more heavily concave lateral walls, these concave walls are still sometimes found in *Carcharhinus* centra. The shapes in articular view and foraminal characteristics are likewise similar. The most distinguishing characteristic of *Negaprion* centra is their greater length. Comparisons of the two genera were hampered by a lack of an appropriate sample size of *Negaprion* centra.

Prionace centra are really quite unique among carcharhiniform centra. Their lengths are among the shortest of any carcharhinid, a family that is has many taxa with short centra. Their strongly concave walls, unique pore distribution, and shape of their intermedialia also make them distinct. Finally, their delicate cartilage is unlike the centra of any other carcharhiniform shark. From a taphonomical sense, these centra seem unlikely to be preserved as fossils. Six fossil centra have been tentatively identified as *Prionace* because of their similar morphologies and delicate cartilage.

SPHYRNIDAE: Gill 1872

Sphyrna *Rafinesque 1810*

Figure 16

Sphyrna Rafinesque, 1810A p. 46, 60.

Description of modern *Sphyrna* centra

Material Examined. — AMNH 93843 – *S. tiburo,* entire skeleton; AMNH 99058 – *S. zygaena,* entire skeleton; AMNH 99064 – *S. lewini,* entire skeleton; G. Hubbell Collection – *S. mokarran*, 1 centrum; L. Whitenack donation – *S. mokarran*, 8 centra; UCMP 136052 – *S. lewini,* entire skeleton.

Centrum Proportions. — *Sphyrna* centra are usually cylinders to modified cylinders, often exhibiting strong recurve at the rims. The centra of *S. tiburo* are the sole examples of the hourglass shaped centra. These centra are pinched in the middle and have sides recurving strongly at the rims. All centra of *Sphyrna* have concave walls at the apices of the double cones, though in many centra this is fairly minor. The concavity is never as pronounced as in triakids. Centra are medium in length, typically longer than carcharhinids but shorter than triakids. Centrum length never exceeds centrum width except for a few centra from UCMP 136052, a juvenile *S. lewini*. The centra are usually round in articular view to slightly greater in dorso–ventral height than medio–lateral breadth, with the exception of *S. tiburo*. Most of *S. tiburo* centra around round, though the largest centra located near the MP–DP transition are much larger in medio–lateral

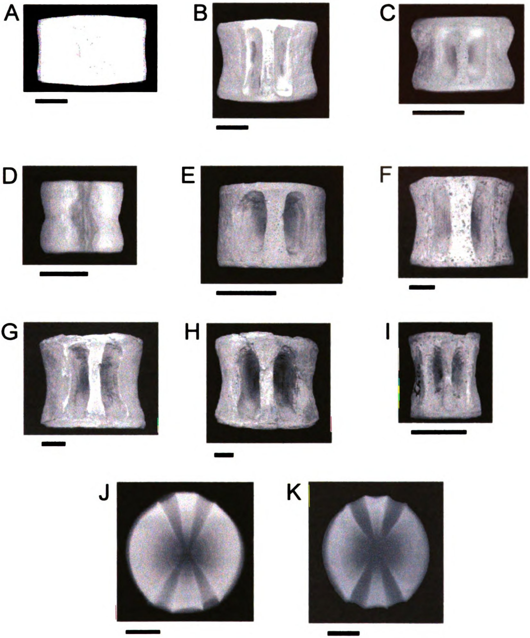


Figure 16. Recent and fossil centra of *Sphyrna*. **A-D:** Recent centra. **A.** G. Hubbell Collection *Sphyrna mokarran*, dorsal view, **B.** AMNH 99058.52, dorsal view, **C.** AMNH 99064.65, dorsal view, **D.** AMNH 93843.37, dorsal view. **E-I:** Fossil centra. **E.** USNM 288057, dorsal view, **F.** ANSP LCM 68, dorsal view, **G.** SDNHM 71143, dorsal view, **H.** UCMP 148049, dorsal view. **I.** USNM 494466, dorsal view. **J-K:** X-radiographs. **J.** G. Hubbell Collection *Sphyrna mokarran*, articular view, **K.** X-radiograph of SDNHM 71143, articular view. Scale bars = 10 mm.

breadth than dorso–ventral height. With the proportions discussed, *Sphyrna* centra appear stocky and robust.

Foraminal Proportions. — Foramina are almost always rectangular. The one exception is found on *S. tiburo*, where the few foramina that were not covered with arch cartilage displayed strongly bowed, elongate oval foramina. *Sphyrna* foramina are wide in all cases except *S. tiburo*. The dorsal interforaminal wall is wider than the width of the dorsal foramina, while the ventral interforaminal wall is narrower than the ventral foramina. The foramina do not extend into the rims.

Pore Characteristics. — All *Sphyrna* centra have abundant pores, and are usually very small, though may reach medium to large sizes in rare cases. The pores are scattered, and do not form a recognizable pattern over the outer wall. The pores on *S. tiburo* are sparse, and are small enough that magnification is required to see them.

Notochord Canal Characteristics. — In every centrum, the notochord canal is completely closed.

Calcification Characteristics. — G. Hubbell Collection *S. mokarran* centrum was radiographed for this study. The pattern of secondary calcification in *Sphyrna* is similar to most carcharhinids, but does have a unique enough morphology to be distinguishable. The lateral intermedialia have obtuse interior angles, with well rounded, obtuse exterior margins. The dorsal and ventral intermedialia are narrow wedge–shapes with straight to slightly concave exterior surfaces. The dorsal intermedialium is long, adding a distinct hump–shape to the dorsal margin in cross–sectional view, and is partly responsible for the dorso–ventral height being larger than the medio–lateral breadth. The four non–

calcified foraminal spaces are very long, narrow, and straight. With the dorsal and ventral intermedialia being so narrow, the foraminal spaces are closely spaced.

The calcified double–cone is very small in *Sphyrna*, similar to that of *Carcharhinus*. The opening for the notochordal remnant likewise has a small diameter. Four very tiny diagonal lamellae extend from the calcified double–cone. These diagonal calcifications are extremely short, projecting approximately 1 mm into the non–calcified areas.

Description of fossil *Sphyrna* centra

Referred specimens. — CMMV 1139; ANSP GM 2, 3, ANSP AF 3, 6, 7, ANSP LCM 1, 6, 10, 13, 17, 19, 20, 25, 31, 68–71, 76, 80, 84, 89; USNM 288026, 288027, 288041, 288043, 288049, 288051, 288055, 288056.1, 288056.2, 288057, 494464–494466, 495870; SDNHM 71143; UF 92289; UCMP 148049; and BMNH 13795.

Age and distribution. — Lower Miocene through Recent in Europe, Asia, and North America; Recent in all warm–temperate and tropical seas (Compagno, 1984, 1988; Cappetta, 1987; Purdy et al., 2001).

Discussion. — Identification of fossil *Sphyrna* centra has been very difficult, as there are few characteristics common in centra of all members of this genus. Many of the specimens on loan arrived with the identification of *Sphyrna*, though none were associated with teeth. These centra were always compared with Recent *Sphyrna* centra, and always were similar in most of the characteristics. In the process of identifying these fossil *Sphyrna* centra, several inconsistencies did arise. *Sphyrna* centra are always medium to long, and almost always have recurve at the rims. The amount of recurve, however, varies dramatically among the centra. Some of the centra have only slight recurve (to almost none whatsoever (e.g. CMMV 1139, ANSP AF 6, 7)), while others have very strong recurve (e.g. NMNH 288026, 494465).

An hourglass shaped centrum appears to be diagnostic of *Sphyrna*, but not all members of this genus have centra with this shape. Kozuch and Fitzgerald (1989) found this shape only in *Sphyrna tiburo*, and was only found in this species among the Recent comparative material examined for this study. A few fossil centra possess the long, hourglass shape consistent with the morphology of *Sphyrna tiburo* (e.g. ANSP LCM 19, UCMP 148049).

The recent *Sphyrna* centra on loan typically have rectangular foramina, while oval were more common on the fossil centra. The ventral interforaminal wall is very narrow on many fossil centra, similar to those of Recent centra. Some of the largest specimens resemble one another very closely, but are very distinct when compared to other fossil *Sphyrna* centra. These have very heavily concave lateral walls, heavy recurve at the rims, and a medio–lateral breadth that is much greater than dorso–ventral height. No fossil specimen were observed with an opening for the notochordal canal.

The most stable characteristics of *Sphyrna* centra are the pore size and distribution. The pores are almost always minute, enough so that magnification is often necessary for proper observation. The pores are also scattered over the entire surface of the centrum.

Fossil *Sphyrna* centra are most similar to *Galeocerdo* centra, as both have modified cylinder shapes. *Galeocerdo* centra have large, encircling pores and generally more strongly concave lateral walls (with the exception of the largest specimens).

CMMV 1139, ANSP GM 2, 3, ANSP AF 3, 6, 7, USNM 288056, 494466, SDNHM 71143, and UCMP 148049 were all radiographed for this study. The overall morphology of these cross–sectional views varied to a small degree, which is not surprising considering the diversity of shapes observed in centra from *Sphyrna*. Each centrum has one interforaminal wall that is very narrow, which is also observable on the external surface. The most diagnostic characteristic shared by every fossil centrum is the complete lack of diagonal calcifications, and no visible calcified double cone. The only instance of diagonal lamellae being observed on a *Sphyrna* specimen was the Recent G. Hubbell Collection *S. mokarran* centrum. In this centrum, four very small and delicate lamellae are slightly visible on the x–radiograph. Every other carcharhiniform genus observed have well–developed diagonal lamellae in their centra, with the exception of *Prionace*. Ridewood (1921), however, notes that in *Sphyrna*, along with *Carcharhinus* and *Galeocerdo*, the diagonal lamellae are the most developed. While well–developed diagonal lamellae were expected, they were never observed.

Indeterminate Carcharhiniform 1

Figure 17

Fossil Material Examined. — BMNH 1965, 5752.1, 5752.2, 13794, 13796, 13797.

Centrum Proportions. — The six centra that comprise indeterminate carcharhiniform 1 are very distinct from any other carcharhiniform centrum examined in this study. They are best classified as robust cylinders with a medium length. Their lateral walls tend to be somewhat irregular, without showing any concavity. The rims are

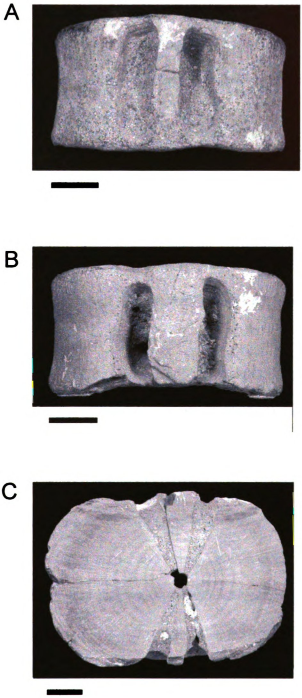


Figure 17. Fossil centra of Indeterminate Carcharhiniformes 1. **A.** BMNH 5752.1, dorsal view, **B.** BMNH 5752.1, ventral view. **C.** Cross section of BMNH 5752.2, articular view. Scale bars = 10 mm.

visible, but not conspicuous. The medio–lateral breadth is much greater than the dorso–ventral height, giving these centra a pronounced ovoid shape in articular view. These centra resemble flattened *Carcharhinus* centra. All of these centra are very large, with the smallest having a width of about 50mm.

Foraminal Proportions. — The foramina are long, straight ovals in all of these centra. The dorsal interforaminal wall is typically narrower than the width of a single foramen, while the ventral interforaminal wall is wider.

Pore Characteristics. — Pores are difficult to see on most of the centra due to poor preservation of the external surface. Small pores are visible encircling the rims and foramina on BMNH 5752.1, however.

Notochordal Canal Characteristics. — The notochordal canal is closed in every centrum, though this may be in part due to poor preservational quality.

Calcification Pattern. — All of these centra are heavily mineralized, and the foramina are filled with matrix, so no radiographs are available. BMNH 5752.2 has been sectioned in the same plane as the radiographs, however. The lateral intermedialia are large, have an obtuse interior angle, and a very convex external surface. The dorsal and ventral intermedialia are very narrow, with rounded external surfaces. The non–calcified areas are narrow and straight. No calcified double cone is visible, nor are any diagonal lamellae. The lack of these structures may be a result of poor preservations.

Discussion. — These six specimens arrived from The Natural History Museum with the identification of *Galeus*. This identification is unlikely. *Galeus* is a small scyliorhinid, rarely reaching even 90cm (Compagno, 1984). These centra are far too large for this genus. *Galeus* was a synonym for *Galeorhinus* (Cuvier, 1817), though this identification would also be unlikely. Fossil and Recent *Galeorhinus* centra have been examined, and are not morphologically similar to these unknown centra. These centra are far too large to be consistent with the size of *Galeorhinus*, which reach a maximum size of about 190cm (Compagno, 1984). The unknown centra have pores on the external surface, which are lacking in all observed triakid centra, including *Galeorhinus*.

Indeterminate Carcharhiniform 2

Figure 18

Fossil Material Examined. — ANSP AF 1, 2, ANSP LCM 16, 22, 24, 32–43, 61, 78, 102, 103; USNM 288014.

Centrum Proportions. — The centra of this indeterminate carcharhiniform are quite distinct. The centra are very long cylinders, and with gently concave lateral walls. Strong recurve at the rims is present in some of the centra, while in others recurve is completely lacking. The rims are narrow but distinct. All of the centra are markedly greater in medio–lateral breadth than dorso–ventral height, giving the centra a wide ovoid shape in articular view.

Foraminal Proportions. — The foramina are also unique on these centra. The centra have elongate oval foramina that never extend into the rims. The foramina are usually straight on the shorter centra of this morphotype, and strongly bowed on the longer centra. These bowed foramina are positioned with the apices facing medially. The foramina often have what appear to be remnants of cartilage closing over the openings, similar to the condition seen in *Rhizoprionodon* centra.

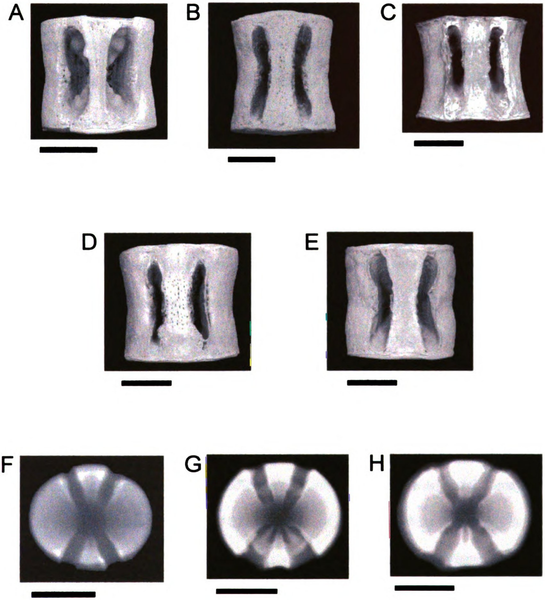


Figure 18. Fossil centra of Indeterminate Carcharhiniformes 2. **A.** ANSP LCM 37, dorsal view, **B.** ANSP LCM 39, dorsal view, **C.** ANSP LCM 32, dorsal view, **D.** ANSP LCM 34, dorsal view, **E.** ANSP LCM 36, dorsal view. **F-H:** X-radiographs. **F.** ANSP LCM 16, articular view, **G.** ANSP LCM 37, articular view, **H.** ANSP LCM 39, articular view. Scale bars = 10 mm.

Pore Characteristics. — Pores are present on all of these centra, though in varying numbers. The pores are small, and are usually scattered over the surface of the centrum. In a few centra, the pores are more heavily concentrated in the interforaminal areas.

Notochordal Canal Characteristics. — The notochordal canal is closed in every example of this morphotype.

Calcification Pattern. — ANSP AF 1, 2, and ANSP LCM 16, 33, 37, and 39 were radiographed for this study. The intermedialia are well–developed and unremarkable in cross–sectional view. The lateral intermedialia are wide and well–developed, with obtuse interior angles, and strongly convex external surfaces. The dorsal and ventral intermedialia are narrow with either straight or gently concave external surfaces. The non–calcified areas are more distinct in these images. Instead of straight or flaring, as is usually observed in carcharhiniform centra, these narrow non–calcified areas have irregular, undulating margins. No calcified double cone is visible in any of the images, nor are any diagonal lamellae. ANSP LCM 37 is unusual among these six centra in that is has what appear to be calcified growths along the anterior and posterior margins of the non–calcified areas. In cross–sectional view, this is seen as a thick, knobby projection in each non–calcified area.

Discussion. — These indeterminate centra are most similar to centra of *Rhizoprionodon*. Both are much longer than other carcharhinid centra, and both have a greater medio–lateral breadth than dorso–ventral height. Both also have long, oval foramina that are often covered or encrusted with additional cartilage. These unknown fossil centra differ from *Rhizoprionodon* centra in a number of ways, though.

Rhizoprionodon centra have heavily concave lateral walls and completely lack any recurve at the rims. The unknown fossil centra, however, generally have only slightly concave lateral walls, and often have heavy recurve at the rims. These fossil centra also have distinct pores scattered on the external surfaces, while no pores were ever observed in *Rhizoprionodon*, even with magnification.

These fossil centra also resemble centra from *Sphyrna* in a few minor ways. Both often have long centra, though these unknown centra tend to be far longer. *Sphyrna* centra also have recurve at the rims, though again not usually to the degree observed in the unknown centra. Both appear to usually lack diagonal lamellae in the radiographs, though the Recent *Sphyrna mokarran* centrum has minute lamellae, and ANSP LCM 37 has some extra calcification in the non–calcified areas. These unknown fossil centra most likely do not belong to *Sphyrna*.

All of these centra are from the Lee Creek Mine, and would most likely be from a genus represented by teeth in the Lee Creek Mine deposits, but matching the centra to a genus has not yet been possible. While the centra appear to be carcharhiniform, they do not resemble *Hemipristis, Galeocerdo, Carcharhinus,* or *Sphyrna* centra, genera that are well represented by teeth at Lee Creek, and of sufficient size. The indeterminate centra do not resemble scyliorhinid or triakid centra. About 50 *Paragaleus* (Hemigaleidae) teeth are present in these deposits, from sharks between 1.5 and 1.7 m in total length (Purdy et al., 2001). Recent *Paragaleus* are usually smaller and reach a maximum size of only 1.4 m, (Compagno, 1984). Sharks of these sizes would be small for the size of the indeterminate centra. Five teeth of *Triaenodon* are also present in the Lee Creek Mine deposits. These sharks are somewhat larger than *Paragaleus*, reaching maximum sizes of about 2.1 m, but are rarely larger than 1.6 m (Compagno, 1984). Because teeth are sturdy and durable, more *Triaenodon* teeth would be expected if these twenty–two indeterminate centra were from *Triaenodon*.

DISCRIMINANT ANALYSIS TESTING CLASSIFICATION OF FOSSIL CENTRA

Introduction to Discriminant Analysis

Discriminant analyses are generally employed for one of two reasons. The first relates to interpretation when studying the ways in which groups differ. The discriminant analysis will identify which variables contribute most to discriminating cases among groups. The second purpose involves classification: that is, predicting the group membership in naturally occurring groups for cases of unknown membership (Klecka, 1980; Tabachnick and Fidell, 1983). The analysis involves two types of variables. The grouping variable defines the groups into which the cases are being classified, and the discriminating variables are used to distinguish between groups. In discriminant analyses the variables are not defined as dependent or independent. If causation were indicated, the analysis would be analogous to a multiple regression analysis (Klecka, 1980).

Several assumptions exist when conducting this type of analysis (Klecka, 1980):

- The grouping variable must involve two or more mutually exclusive groups, with at least two cases per group.
- The analysis must involve at least two more cases than discriminating variables.
- The discriminating variables must be interval or ratio scale variables.

- Discriminating variables may not be linear combinations of other discriminating variables, and may not be perfectly correlated. To include this type of variable would involve redundant information in the analysis.
- The covariance matrices for each group must be approximately equal.
- The discriminating variables must have a normal distribution.

The data used in these analyses meet all of the above assumptions.

When the analysis is run, a classification matrix is produced that indicates the number of cases that were predicted correctly. The classification matrix also indicates the number of incorrectly classified cases, and the groups into which they were predicted. The classification matrix is especially useful when using discriminant analysis as a means of predicting the group membership for cases with unknown membership. The classification matrix can also be used to test the ability of the discriminating variables to classify cases of known grouping. An analysis can be conducted on the known cases, and the percent correctly classified indicates the accuracy of the procedure (Klecka, 1980). The more successful the discriminating variables are for distinguishing between groups, the higher the percentages in the classification matrix. In the following analyses, morphological measurements of various shark vertebral centra characteristics serve as the discriminating variables and identification at the family or genus level is used as the grouping variable. The ability of the independent variables to successfully discriminate for identification was first tested by performing analyses using only Recent centra where identification was already known. Once established, fossil centra with hypothetical identifications were added to test whether these centra were identified as predicted in the analysis.

A value called Wilks' Lambda is produced with the output of a discriminant analysis, which is a measure of the level of discrimination in the analysis. Values of lambda that are near zero denote high discrimination. When lambda approaches a maximum value of 1.0, it is denoting less discrimination (Klecka, 1980). To test significance, Wilks' Lambda is converted to an F value (provided in the output of the analysis) and compared to a standard statistical table.

A jackknifed classification matrix is also included with the output of the analysis. Bias enters the discriminant analysis when the data from the case being classified is included when developing the classification equation (Tabachnick and Fidell, 1983). When all variables are included in the jackknifed classification, each case is then classified on the basis of all data except the specific case being classified, and biased is removed (Tabachnick and Fidell, 1983). The results of a jackknifed classification can be viewed as a more realistic estimate of the ability of the discriminating variables to distinguish between groups (Tabachnick and Fidell, 1983).

The following analyses were conducted to test the identification and significance of identification given to individual fossil centra, predict identification for unknown centra, and provide a testable model to the identification of sometimes morphologically similar fossils.

Methods

The data used in the statistical analyses include eleven interval scale variables, measuring external centrum and foraminal proportions of the shark vertebrae. These eleven measurements were taken from all accessible centra from thirty–eight Recent individuals and 507 fossil centra that were either on loan to the MSU Museum or were examined during collection visitations. The eleven variables, listed by the variable names used in SYSTAT, include:

1. DIAMETER_1: The larger of the two diameter measurements, measured from lateral side to side at the rim.
2. DIAMETER_2: The smaller of the two diameter measurements, measured from lateral side to side at the rim.
3. MAX_LENGTH: The length of the centrum measured from anterior to posterior rim.
4. WAIST_WIDTH: Width of the centrum at the apices of the double cone. The centrum walls at this location are concave in varying degrees.
5. WAIST_HEIGHT: Height of centrum, measured at the apices of the double cone.
6. D_FORAM_L: Length of one dorsal foramen.
7. D_FORAM_W: Width of one dorsal foramen, measured at its maximum.
8. D_WALL_W: Width of the dorsal interforaminal space.
9. V_FORAM_L: Length of one ventral foramen.
10. V_FORAM_W: Width of one ventral foramen, measured at its maximum.
11. V_WALL_W: Width of the ventral interforaminal space.

These measurements were recorded into Microsoft Excel, and later transferred to SYSTAT. The analyses of these centra were designed to examine the overall morphology of centra from different genera. Centra may dramatically differ in size, however, even within a single genus. The differences in size mask the overall morphology in a discriminant analysis, and centra would be classified based primarily on their size. Because of this, the interval scale variables have been transformed into ratio scale variables. Variables 2–11 were divided by DIAMETER_1. DIAMETER_1 was chosen over MAX_LENGTH because the latter can vary dramatically depending on the location of the centrum within the vertebral column. Centrum length is relatively the longest just anterior to the monospondylous–diplospondylous transition. Length decreases rapidly in the caudal region. The diameter of the centra is more consistent with overall size. Following are the names of the ten transformed variables used in SYSTAT.

12. T_DIAMETER_2
13. T_MAX_LENGTH
14. T_WAIST_WIDT
15. T_WAIST_HEIG
16. T_D_FORAM_L
17. T_D_FORAM_W
18. T_D_WALL_W
19. T_V_FORAM_L
20. T_V_FORAM_W
21. T_V_WALL_W

Two nominal variables were included for use as grouping variables in the discriminant analyses.

22. GENUS
23. FAMILY

Nine genera were measured and included in the data matrix, and were given the following nominal classification in the GENUS variable:

1. *Galeorhinus*
2. *Mustelus*
3. *Triakis*
4. *Carcharhinus*
5. *Galeocerdo*
6. *Negaprion*
7. *Prionace*
8. *Rhizoprionodon*
9. *Sphyrna*

Three families were measured and included in the data matrix, and were given the following nominal classification in the FAMILY variable:

1. Triakidae
2. Carcharhinidae
3. Sphyrnidae

The raw data used in these analyses is found in Appendix A. Transformed data is available upon request. SYSTAT output, including Wilks' Lambda, Approximate F values, and classification matrices, is found in Appendix C.

Discriminant analyses testing identification of modern centra:

The first discriminant analysis performed was on data that included only measurements of Recent centra of known identification. This was designed to test the ability of the analysis to successfully discriminate centra using the morphological variables listed above. Many of the cases were not included in the final discriminant analyses for several reasons. First, varying numbers of centra were available from each individual shark, ranging from the entire column of over one hundred centra to as few as one or two centra from an individual. In order to prevent a few specimens with hundreds of centra from overwhelming the data set, a maximum of ten centra with complete measurements were randomly included from a single individual. Second, only centra from the monospondylous region were included in the data set. The MP–DP transition is marked by an abrupt decrease in centrum length. Diplospondylous centra converge in morphology posteriorly, even among different families. To prevent these morphological similarities from obscuring the differences in the larger, more anterior centra, they were removed from the data matrix. Two genera were not included in the analysis because of an exceedingly small sample size. Only two monospondylous centra were available for the genus *Negaprion* and, excluding fluid–preserved specimens, three monospondylous centra of *Rhizoprionodon* (two being the minimum number of cases in a group allowed by a discriminant analysis (Klecka, 1980)). Finally, any centrum that had missing data was not included. Remnants of the neural and haemal arches were sometimes present on the vertebral columns of the Recent skeletons. These remnants often prevented measurements from being recorded, especially WAIST_HEIGHT, D_FORAM_W, and D_WALL_W. The final data set of Recent centra includes 116 centra from 28 individuals.

A correlation table of the transformed variables demonstrates that these variables are not perfectly correlated, supporting the assumption necessary for discriminant analyses (Appendix B). The most highly correlated variables are T_D_FORAM_L and T_MAX_LENGTH with correlation coefficients of 0.95, T_V_FORAM_L and T_MAX_LENGTH at 0.96, and T_D_FORAM_L and T_V_FORAM_L at 0.97. All other variables were correlated with coefficients less than 0.82.

Discriminant analyses were generally performed using the complete estimation option, which includes all variables in the solution. Stepwise options are available, which test the contribution of individual variables to the discriminating process. Those that do not discriminate the cases well are removed. This option is particularly useful for exploratory purposes, or when the goal is to interpret the ways the groups differ.

The first discriminant analysis performed on the data from the Recent centra used all ten transformed ratio variables, with FAMILY as the grouping variable. The analysis used 0.01 tolerance and the complete estimation option, and the distances were saved. The Wilks' Lambda was 0.0729, and Approximate F was 28.1148, which is significant below the 0.001 level. 100% of triakid centra were predicted correctly (31 total), as were 100% of sphyrnid centra (16 total). Of the sixty–nine carcharhinid centra, 96% were discriminated properly, with three incorrectly predicted as sphyrnid centra. Overall, 97% of the centra were correctly classified, with 94% correctly classified in the jackknifed classification matrix.

For exploratory purposes, a backward stepwise discriminant analysis was performed on the same ratio variables. This analysis begins with all variables used in the discriminant function, and removes variables when the F score drops below the identified threshold. FAMILY was once again the grouping variable in this analysis, and 0.15 as the to Alpha–to–enter and Alpha–to–remove. Wilks' Lambda was 0.0617, and the F score was 54.4438 (significant below the 0.001 level) for this analysis. In this analysis one *Carcharhinus* centrum was classified as a *Sphyrna* centrum. The total correct predictions was 99%, with 96% correctly predicted in the jackknifed classification matrix. Of the ten variables, T_WAIST_HEIG, T_D_WALL_W, T_D_FORAM_L, T_V_FORAM_L, T_V_FORAM_W, and T_V_WALL_W were useful in discriminating the families. T_DIAMETER_2, T_MAX_LENGTH, T_WAIST_WIDT, and T_D_FORAM_W were not entered into the solution by SYSTAT.

To further test the use of the transformed ratio variables for classification, all ten variables were included in a discriminant analysis with GENUS as the grouping variable. The analysis used 0.01 tolerance and the complete estimation option, and the distances were saved. The Wilks' Lambda was 0.0120, and Approximate F was 11.6830 (significant below the 0.001 level). The included variables discriminated for genus very well, though not with quite the same success as for family. Among the triakids, only

Mustelus centra (5 total) were discriminated properly 100% of the time. *Galeorhinus* centra (11 total) were predicted correctly 91% of the time, with one centrum predicted as a *Galeocerdo* centrum. *Triakis* centra had the lowest number of correctly classified centra, with 80% being properly predicted. Of the 15 centra, 12 were predicted correctly, with two predicted as *Galeorhinus* and one as *Mustelus*. The centra from triakid genera tend to be very similar to each other, and identification is difficult. The discriminant analyses consistently had the most difficulty correctly predicting the classification of triakid genera when fossil centra were added to the data matrix.

Of the three carcharhinid genera, *Galeocerdo* (12 total) and *Prionace* (5 total) centra were both predicted correctly 100% of the time. *Carcharhinus* centra (52 total) were classified correctly 85% of the time, with two centra classified as *Galeorhinus* centra, three as *Galeocerdo*, and three as *Sphyrna*. *Sphyrna* centra (16 total) were classified correctly 100% of the time. Overall, 90% of the centra were correctly classified.

The Jackknifed classification matrix scores for triakids were somewhat lower, as they were in the family discriminant analysis. The percent classified correctly remained the same for *Galeorhinus* and *Mustelus* (91%, 100%, respectively), but decreased to 67% for *Triakis* centra. Five of these centra were misclassified, with two centra predicted as *Galeorhinus*, two as *Mustelus*, and one as *Galeocerdo*.

All three carcharhinid genera had lower percentages of correctly classified centra. *Carcharhinus* centra were predicted correctly at 83%, as one additional centrum was misclassified as *Sphyrna*. *Galeocerdo* centra dropped to 92%, with one centrum predicted as *Carcharhinus*. *Prionace* centra were predicted correctly at only 60%, with one centrum classified as *Mustelus* and one as *Carcharhinus*. *Sphyrna* centra were correctly predicted 88% of the time, with one centrum predicted as *Carcharhinus* and one as *Galeocerdo*. The total correct predictions were 83% in the Jackknifed classification matrix for genera.

For exploratory purposes, a backward stepwise discriminant analysis was also performed on the same ratio variables, with genus once again as the grouping variable, and 0.15 to enter and remove. Wilks' Lambda was 0.0076, and the Approximate F score was 17.8044 (significant below the 0.001 level) for this analysis. This new analysis successfully classified 93% of the centra, with 88% correctly predicted in the jackknifed classification matrix. Of the ten variables, T_MAX_LENGTH, T_WAIST_WIDT, T_WAIST_HEIG, T_D_FORAM_L, T_D_WALL_W, T_V_FORAM_L, T_V_FORAM_W, and T_V_WALL_W, were useful in discriminating the families. T_DIAMETER_2 and T_D_FORAM_W were not entered into the solution by SYSTAT.

After the above analyses were run, *Negaprion* and *Rhizoprionodon* centrum measurements were included into the data set. Some fossil centra were available that were consistent with the morphology observed in those two genera (especially fossil centra from FMNH). Despite having a small sample size of centra from the Recent genera, they proved necessary for comparison. Two discriminant analyses were performed on the file including the *Negaprion* and *Rhizoprionodon* centrum measurements.

The first analysis used FAMILY as the grouping variable. The Wilks' Lambda was 0.0726, and the Approximate F was 29.5631 (significant below the 0.001 level). The overall percentage of the classification matrix was 98%, and the Jackknifed classification matrix was 96% predicted correctly. Three *Carcharhinus* centra were misclassified as sphyrnids.

The second analysis used GENUS as the grouping variable. The Wilks' Lambda was 0.0067, and Approximate F was 9.9247 (significant below the 0.001 level). 85% of the centra were classified correctly, with 74% correctly classified in the Jackknifed matrix. The new genera, with their small sample sizes increased the error in the predictions. One of the two *Negaprion* centra was misclassified as a *Carcharhinus* centrum and two of the three *Rhizoprionodon* centra were misclassified as *Prionace*. The addition of these two genera also lowered the percentage of correct predictions for *Carcharhinus* and *Prionace*, as some of these centra were predicted as the added genera.

Discriminant analyses including fossil centra

The results of the discriminant analysis on modern shark centra justify the use of the transformed ratio variables as a test for identification, with correct classifications being in the ninety–percent range for both family and genus classification. When adding fossil centra measurements to the Recent centra data set, the existing classification problems continued, and therefore lowered the overall percent predicted correctly for the following analyses. For example, centra from *Carcharhinus acronotus* and *C. brevipinna* were often misclassified in the above analyses. Their centra are unusually long compared to other *Carcharhinus* centra, and resemble triakid centra based on measurements alone. The analyses continued to misclassify these centra after fossil centra data was added.

Measurements of fossil centra were recorded in the same manner as for Recent centra. These centra were also transformed into ratio scale variables by dividing

DIAMETER_1 into each variable. Before the fossil centra were included in the data matrices for discriminant analyses, they were first given tentative identification based on characteristics compared with the modern centra. As above, centra that were missing data (i.e., incomplete centra) or centra that were from the diplospondylous regions were not included in the analyses.

Calvert Marine Museum fossil centra

Added to the data set of modern shark centra (not including *Negaprion* or *Rhizoprionodon*) were twenty–two fossil centra from the Calvert Marine Museum. Once constructed, the data set was subjected to discriminant analyses. The first analysis involved all transformed ratio variables with FAMILY used as the grouping variable. Wilks' Lambda for this analysis was 0.1027, and the Approximate F was 26.7246 (significant below the 0.001 level). The classification matrix had an overall score of 96% predicted correctly, and the jackknifed classification matrix had 92% correct predictions. For the fossil centra, only one was predicted contrary to the tentative identifications given them. CMMV–1139 was identified as a sphyrnid in the nominal variable FAMILY, but was predicted as a triakid. This centrum is a fluted cylinder, that is, a long cylinder with strongly concave lateral walls and no recurve at the rims. This centrum is large, however, with a diameter of almost 40 mm, and has very small, scattered pores similar to those present on recent *Sphyrna* centra.

The same data set was also subjected to a discriminant analysis with GENUS as the grouping variable. The Wilks' Lambda for this analysis was 0.0183, and the Approximate F was 12.2994 (significant below the 0.001 level). The classification matrix had an overall score of 91%, and the jackknifed matrix was 83% predicted correctly. As for the discriminant analysis with FAMILY as the grouping variable, only CMMV–1139 was predicted differently than its initial identification. While identified as a *Sphyrna* centrum, it was predicted as *Triakis*. Again, the fluted cylinder morphology of this centrum probably led to this classification. Overall size and pore distribution are not being analyzed during the discriminant analyses.

Of interest is CMMV–815. This centrum is large, with a short, disk–like cylinder shape, has a large amount of concavity at the apices of the double cone, and small to medium size pores that closely follow the rims. This centrum seems less dense and more delicate than other fossil centra, and is not preserved as well. These characteristics closely match those of modern *Prionace* centra. Because of these similarities, this centrum was classified as *Prionace* in the GENUS variable, and was predicted as the same genus in the discriminant analysis. Cappetta (1987) lists the only known fossil *Prionace* specimens from the Pliocene of Italy. CMMV–815 was found as float at the Calvert Cliffs in Maryland, known for its Miocene shark fossils.

Florida Museum of Natural History fossil centra

Fossils from the Florida Museum of Natural History include sixteen centra from the Late Miocene through Pleistocene of Florida. Five of the centra were associated with three teeth and were identified as *Negaprion brevirostris*. Of the seventeen centra from the University of Florida collection, six were caudal centra and not included. Three other centra of poor quality were excluded due to a lack of complete measurements. Eight centra remained, of which three were associated.

The University of Florida centra measurements were combined with the data set that included *Negaprion* and *Rhizoprionodon* Recent centra. This new data set was subjected to a discriminant analysis using the complete estimation option and included all transformed ratio variables and used FAMILY as the grouping variable. The Wilks' Lambda for this analysis was 0.123 and the approximate F was 21.6587 (significant below the 0.001 level). The classification matrix had 92% of centra predicted correctly, and a jackknifed matrix with 88% predicted correctly.

Of the eight fossil centra added to the matrix, five were discriminated correctly. Of the three misclassified, UF 92281, identified as *Carcharhinus*, was predicted as a sphyrnid. UF 92289, identified as *Sphyrna*, was predicted as a carcharhinid. Finally, UF 123154, identified as *Rhizoprionodon*, was predicted as a triakid.

The same data were subjected to a discriminant analysis using the complete estimation option that included all transformed ratio variables and used GENUS as the grouping variable. The Wilks' Lambda for this analysis was 0.0155 and the approximate F was 8.2754 (significant below the 0.001 level). The classification matrix had 83% of centra predicted correctly, and a jackknifed matrix with 71% predicted correctly.

Four of the eight fossil centra were discriminated incorrectly for genus. UF 3245.2, one of the *Negaprion brevirostris* centra, was classified as *Carcharhinus*, while the other two were predicted correctly. This is puzzling, as the three associated centra closely resemble each other, and have similar dimensions. The unfortunately small sample size for *Negaprion* centra (five total) likely played a role. UF 123154 may have had similar problems. In this case, the sample size for *Rhizoprionodon*, including UF 123154, was only four centra. While identified as *Rhizoprionodon*, this centrum was classified as *Mustelus*. Both genera have long, fluted cylinder shaped centra and a medio–lateral breadth that is greater than dorso–ventral height, which could have led to the misclassification. UF 123154 is clearly a *Rhizoprionodon* centrum based on examination of the foramina. UF 128906, identified as *Carcharhinus*, was predicted as *Rhizoprionodon*, which again may be attributed in part to the confusion introduced due to the small sample of *Rhizoprionodon* centra. UF 92289 was tentatively identified as *Sphyrna*, but was classified as *Galeocerdo*. This centrum is quite small, and does resemble *Galeocerdo* in some aspects, but is missing the characteristic large pores and modified cylinder shape. Neither of these characteristics would be apparent in the measurements taken from the centra and included in this data set.

The Natural History Museum (London) fossil centra

Sixteen fossil centra from The Natural History Museum were analyzed using discriminant analyses. Four centra from this collection were excluded because they are unlike any recent comparative material available for this study. These centra were previously identified as *Galeus* sp. Other centra were excluded due to incomplete specimens or because they were caudal centra.

The measurements from the sixteen centra were added to the data set of Recent centra that excluded the *Negaprion* and *Rhizoprionodon* centra, as there were no fossil centra in this set that resembled those two genera. The new data set was subjected to a discriminant analysis using the complete estimation option and using all transformed ratio variables and FAMILY as the grouping variable. The Wilks' Lambda was 0.0860, and the approximate F was 28.9251 for this analysis (significant below the 0.001 level).

The classification matrix had 96% of the centra predicted correctly, with a jackknifed matrix with 92% predicted correctly. The only fossil centrum misclassified was BMNH 13795, which was identified as Sphyrnidae and classified as Carcharhinidae.

The same data were subjected to a discriminant analysis using the complete estimation option, and again using all transformed ratio variables and GENUS as the grouping variable. The Wilks' Lambda was 0.0146, and the approximate F was 12.6585 for this analysis (significant below the 0.001 level). The classification matrix had 91% of the centra predicted to genera correctly, with a jackknifed matrix with 85% accuracy. Once again BMNH 13795 was misclassified. While identified as a centrum from *Sphyrna*, the analysis predicted it as a *Carcharhinus* centrum. While the measurements may suggest the latter classification, simple observation suggests this is actually a centrum from *Sphyrna*. The centrum is relatively much longer than *Carcharhinus* centra tend to be, and is closer to the relative length of *Sphyrna*. The centrum did arrive from The Natural History Museum with a carcharhinid identification, however. BMNH 1309 was also misclassified in the analysis. This centrum was entered as a *Galeocerdo* centrum, and was predicted as *Carcharhinus*. This centrum is not entirely complete, which will affect measurements to some degree. The centrum has a somewhat shorter relative length than most *Galeocerdo* centra, but has a slightly modified cylinder shape and large pores. The centrum arrived from The Natural History Museum with the identification *Galeocerdo*.

San Diego Natural History Museum fossil centra

The vertebral centra on loan from the San Diego Natural History are unusual by having a heavy concentration of triakid centra, and little else. Carcharhinidae, and especially *Carcharhinus* centra, are usually more abundant. Triakid centra tend to be difficult to identify to genus due to similarities on overall morphology, and lack of any distinct characters.

Measurements from thirty–nine complete, non–caudal centra were included in the data set of modern carcharhiniform centra measurements. The transformed ratio variables were subjected to a discriminant analysis with the complete estimation option using FAMILY as the grouping variable. The Wilks' Lambda for this analysis was 0.1375, and the approximate F was 24.2635 (significant below the 0.001 level). The classification matrix shows 95% of centra classified correctly, with a jackknifed matrix with 91% correct classification. Only two fossil centra were misclassified in this analysis. One was SDNHM 61933.06, classified as a carcharhinid and predicted as a triakid. The other was SDNHM 61933.09 (not associated with SDNHM 61933.06), classified as a triakid, but predicted as a carcharhinid.

The same transformed ratio variables were subjected to a discriminant analysis with the complete estimation option, using GENUS as the grouping variable. The Wilks' Lambda was 0.0229, and the approximate F was 12.9108 (significant below the 0.001 level). The classification matrix had 86% predicted correctly, with a jackknifed classification matrix with 81% correct predictions. Nine of the thirty–nine fossil centra were misclassified. SDNHM 61933.06 was once again misclassified. It was identified as *Carcharhinus* and was predicted as a *Galeorhinus* centrum. It is very possible that the initial classification of this specimen was incorrect, and the discriminant analysis has predicted it correctly. The specimen is a small, short cylinder with heavily concave lateral walls. It also lacks pores, which is a triakid character. This specimen may be a centra from the diplospondylous region, misleading the initial classification. SDNHM 61933.08 (not associated with the other centra in lot SDNHM 61933) was initially classified as *Carcharhinus*, but was predicted as *Galeocerdo*. The small size of this specimen makes classification difficult, especially if it is a carcharhinid, as it was likely from a juvenile. This centrum has a cylinder shape that is approaching a modified cylinder. The lateral walls are very concave, and the length is relatively long for a carcharhinid centrum. Pores are present, but due to the small size of the vertebra, are difficult to observe clearly. While clearly a carcharhinid, the identification to the generic level is uncertain.

SDNHM 61933.09 (not associated with other centra in lot SDNHM 61933) was identified as *Galeorhinus* and predicted in the analysis as *Galeocerdo*. The initial identification of *Galeorhinus* is more likely in this case. The centrum is a small cylinder with strongly concave lateral walls and no hint of recurve at the rims. The relative length compared to diameter would be similar to that of *Galeocerdo* but is also consistent with *Galeorhinus*. This specimen also completely lacks pores on its lateral surface and interforaminal areas, once again suggesting the *Galeorhinus* prediction is correct.

SDNHM 61933.14 (not associated with other centra in lot SDNHM 61933) was initially identified as *Galeorhinus*, and was predicted as *Mustelus* during the analysis. While this specimen is clearly a triakid centrum, generic classification is not as clear. The centrum has foramina that are narrower than is usually seen in *Galeorhinus* centra, and there is some recurve at the rims. Both of these characteristics are common to *Mustelus*. In this instance, the predicted classification of *Mustelus* is most likely correct.

Specimens SDNHM 61933.15 (not associated with other centra in lot SDNHM 61933), 71142.08, and 71142.28 (specimens from lot SDNHM 71142 are not associated) were initially described as *Galeorhinus* and were predicted as *Galeocerdo*. These specimens are approaching a fluted cylinder classification, lack recurve at the rims, have wide foramina that extend into the rims, and completely lack pores. These specimens are clearly not *Galeocerdo* centra. The reason for this prediction during the analysis is not clear.

SDNHM 61933.16 (not associated with other centra in lot SDNHM 61933) was initially classified as *Triakis*, and was predicted to be *Galeorhinus* as a result of the analysis. The ventral interforaminal area on this centrum is extremely wide, suggesting this centrum was from the anterior–most region of the vertebral column. Centra from this region tend to converge in morphology among different genera, and are difficult to identify. This centrum is clearly from a triakid, but generic identification is not certain.

SDNHM 71142.14 was initially identified as *Mustelus*, but was predicted as *Triakis* during the analysis. The reason for the initial identification of *Mustelus* was the presence of slight recurve at the rims. The centrum has foramina that are wider than normal for a *Mustelus* centrum, but they do extend into the rims. Triakid foramina do not appear to extend into the rims, nor do they have any recurve at the rims, suggesting this centrum actually is from *Mustelus*.

Academy of Natural Sciences of Philadelphia fossil centra

Measurements from ninety–seven fossil centra were included in the following analyses. Two hundred and thirty–four specimens are on loan from the Academy of Natural Science, but many of them are incomplete or are clearly caudal centra. Also, several centra that have been identified as *Hemipristis* sp. were not included because of a lack of recent centra of that genus for comparison. Finally, one morphotype was present in this sample that did not match any other centra from modern sharks, and any centrum with this morphology was not included in the discriminant analysis.

Measurements from the ninety–seven complete, non–caudal centra were included in the data set of modern carcharhiniform centra measurements. The transformed ratio variables were subjected to a discriminant analysis with the complete estimation option using FAMILY as the grouping variable. The Wilks' Lambda for this analysis was 0.2039, and the approximate F was 24.4166 (significant below the 0.001 level). The classification matrix had 88% of centra classified correctly, with a jackknifed matrix with 85% correct classification. The percent of correctly classified centra is lower for this analysis than in other analyses. Several centra that were identified as Sphyrnidae had long, fluted cylinder shapes and were predicted as triakid centra. These centra had small, scattered pores on the lateral walls and interforaminal areas, however, which are never present on triakid centra. Other centra were commonly confused between Carcharhinidae and Sphyrnidae.

The same transformed ratio variables were subjected to a discriminant analysis with the complete estimation option, using GENUS as the grouping variable. The Wilks' Lambda was 0.0660, and the approximate F was 11.7652 (significant below the 0.001

level). The classification matrix had 86% predicted correctly, with a jackknifed classification matrix with 80% correct predictions. Twelve of the ninety–seven fossil centra were misclassified in this analysis.

The same problems that occurred in the first analysis were also present in this analysis. LCM 19, 70, 71, and 80 were identified as *Sphyrna* centra, but predicted as a variety of triakid genera. These centra had long, fluted cylinder shapes, which is sometimes present in *Sphyrna* centra, but more common in triakid centra. These centra had small, scattered pores covering their surfaces, and the identification of *Sphyrna* is more likely correct.

One centrum of *Sphyrna* (LCM 25) was predicted as *Galeocerdo*, which is understandable. The two genera both have modified cylinder shapes. One of the main observable differences between them is the difference in pore size and distribution. *Sphyrna* centra typically have small pores scattered over their surfaces, while *Galeocerdo* centra have large, encircling pores. This character was not tested during the discriminant analyses.

ANSP 308.1 and 308.2 were identified as *Carcharhinus* and were predicted as *Prionace*. These centra do superficially seem very similar to *Prionace*, but lack the single line of pores along each rim, and are more likely *Carcharhinus* centra. LCM 64, 66, 86, 97 was tentatively identified as *Prionace* for the analysis. Its morphology and pore distribution closely resembles that of *Prionace*. This centrum was predicted as *Prionace* in the analysis.

Agrico Fort #4 was identified as *Galeorhinus* and predicted as *Triakis*. While this centrum is triakid, it is possible that it could belong to either genus. It resembles

Galeorhinus in its short, stocky shape, but it has heavily concave lateral walls and rather narrow foramina, similar to that seen in *Triakis*. Generic classification may not be confidently made in this case.

ANSP 15415.06 and 15415.08 (not associated) and Lee Creek 15 were all identified as *Carcharhinus* and predicted as *Sphyrna* in the analysis. ANSP 15415.08 is clearly a centrum of *Carcharhinus*, with its short, cylinder shape. The other two are more problematic. Both ANSP 15415.06 and Lee Creek 15 are cylinder shape, though are slightly longer than most *Carcharhinus* centra. Their foramina are relatively large for their diameter. It is possible these are actually *Sphyrna* centra, but identification is not certain.

Finally, LCM 50 was identified as a *Galeocerdo* specimen, but was predicted to be *Carcharhinus*. Upon further examination, the initial identification is still likely correct. This centrum is a large, modified cylinder with noticeable recurve at both rims. The length of this centrum exceeds that which is normally seen in *Carcharhinus*, though is shorter than most *Galeocerdo* centra. The pores are encircling, but smaller than is usually observed in *Galeocerdo*.

National Museum of Natural History fossil centra

A total of forty–one fossil centra on loan from the National Museum of Natural History were included in the data matrix with modern shark centra. These fossils are unusually high in *Carcharhinus* and *Sphyrna* centra. No triakid centra were observed.

A discriminant analysis of the new data matrix was conducted with the complete estimation option using all transformed ratio variables and FAMILY as the grouping variable. The Wilks' lambda for this analysis was 0.1469 and the approximate F was 23.3286 (significant below the 0.001 level). 87% of the centra were predicted according to the FAMILY variable, with 83% correct predictions in the jackknifed classification matrix. The centra misclassified in this discriminant analysis were similar to that of the following discriminant analysis, and will be discussed more thoroughly below.

The same data matrix was subjected to a discriminant analysis, with the complete estimation option, using GENUS as the grouping variable. The Wilks' lambda was 0.0483, with an approximate F of 9.8783 (significant below the 0.001 level). The classification matrix had 83% of the centra predicted correctly, with 76% correct in the jackknifed matrix. Of the forty–one fossil centra, seven were misclassified. Most of these misclassifications were expected, however. USNM–V–288049, 288055, 459870, 494465, and 494466 were all identified as *Sphyrna*. These centra are all extremely large, relatively long, and have extremely concave lateral walls at the apices of the double cone. With the effects of overall size eliminated as a result of transformation of the data, the morphology of these centra is very similar to that of triakid centra. These fossil centra are clearly not triakid, however. They all have well–developed pores, and are much too large. It is most likely these centra are actually monospondylous centra from *Sphyrna*.

USNM–V–288041 was identified as *Sphyrna*, but predicted as *Galeocerdo*. These two genera have similar centra, but this particular centrum closely matches the five centra listed above. It is long and has extremely concave lateral walls. *Galeocerdo* centra have large, encircling pores, while this specimen has small, scattered pores.

USNM–V–494467 was identified as *Galeocerdo*, but was predicted as *Sphyrna*. This specimen is not as relatively long as most *Sphyrna* centra tend to be, but is longer than *Carcharhinus* centra. The centrum has a modified cylinder shape, with large, well–developed pores that appear to be mostly encircling, though the outer surfaces of this centra are poorly preserved.

The remaining centra all were predicted as identified. USNM–V–24914 has 13 associated centra, and USNM–V–494463 has 11 associated centra, and the predictions were consistent among all of these specimens.

University of California Museum of Paleontology fossil centra

A total of forty–seven fossil centra on loan from the University of California Museum of Paleontology were included in the data matrix of modern shark centra. A discriminant analysis of the new data matrix was conducted with the complete estimation option using all transformed ratio variables and FAMILY as the grouping variable. The Wilks' lambda for this analysis was 0.1222 and the approximate F was 26.4336 (significant below the 0.001 level). 91% of the centra were predicted according to the FAMILY variable, with 90% correct predictions in the jackknifed classification matrix. The centra predicted incorrectly in this discriminant analysis were similar to that of the following discriminant analysis, and will be discussed more thoroughly below.

The same data matrix was subjected to a discriminant analysis with the complete estimation option, using GENUS as the grouping variable. The Wilks' lambda was 0.0264, with an approximate F of 12.9225 (significant below the 0.001 level). The classification matrix had 86% of the centra predicted correctly, with 79% correct in the jackknifed matrix. Of the forty–seven fossil centra included in the analysis, seven were misclassified.

UCMP 14802 is one of the largest specimens on loan from the University of California Museum of Paleontology. It was identified as *Galeocerdo* due to its large encircling pores and modified cylinder morphology. This centrum was predicted to be a *Galeorhinus* centrum as a result of the analysis, which it clearly is not. This centrum appears to have some damage that occurred during preparation, which could alter the specimen enough to result in a misclassification.

UCMP 148003 is a short, cylinder–shaped centrum with straight lateral walls, and resembles *Carcharhinus* centra in all observable characteristics. It was, however, predicted as a *Sphyrna* centrum during the analysis. The initial identification of *Carcharhinus*, however, is more likely.

UCMP 148041 was initially identified as *Mustelus*, but was classified as *Galeorhinus* during the analysis. This centrum is a small cylinder to modified cylinder with strongly concave lateral walls that recurve towards the rims. The medio–lateral breadth is larger than the dorso–ventral height, giving the centrum an ovoid articular view. These characteristics led to the initial identification of *Mustelus*, which is more likely than the predicted classification of *Galeorhinus*.

UCMP 148046 is a long, fluted cylinder, with no evidence for pores on the surface. This centrum is poorly preserved, so pores may have been obliterated during fossilization. This centrum was identified as *Sphyrna*, but was classified as *Mustelus*. This centrum does have strongly concave lateral walls that recurve at the rims. The dorso–ventral height is larger than medio–lateral breadth. The proper identification of this centrum is unclear.

UCMP 148048 is a small, cylinder–shaped centrum with strongly concave lateral walls. This centrum lacks any pores on the lateral walls or in the interforaminal areas. The centrum is shorter than most triakids, but similar to *Galeorhinus*. These characteristics led to an initial identification of *Galeorhinus*, though was predicted to be *Galeocerdo*. While these two genera do share some similarities in overall morphology, the small size of this centrum and lack of pores makes the prediction of *Galeocerdo* unlikely.

UCMP 148049 is a unique specimen. It is a long, fluted cylinder, though the lateral walls are only slightly concave. These walls recurve at the rims, giving it a shape that approaches an hourglass. This centrum has small, encircling pores. This centrum closely resembles the centra of *Sphyrna tiburo*, and was therefore identified as a *Sphyrna* centrum. USCMP 148049 was predicted as *Triakis* during the analysis, which it clearly is not. The long, narrow shape would be misleading in an analysis, especially when recurve at the rims and pore information are not represented in the data matrix.

The final centrum to be misclassified in this analysis was UCMP 148056. This centrum is a long, fluted cylinder. The medio–lateral breadth is greater than dorso–ventral height. Overall, it is a narrow, delicate specimen. The centrum was initially identified as *Mustelus*, but was predicted to be a *Galeorhinus* centrum. *Galeorhinus* centra tend to be shorter and stockier in appearance than is observed in this centrum. *Mustelus* is a more likely classification.

PHYLOGENETIC ANALYSIS

To test the hypothesis that the centrum characters discussed earlier reflect phylogeny, a data matrix of twenty–three unweighted characters was scored and subjected to a maximum parsimony analysis. Included in the data matrix were all genera discussed in the Systematic Description (with the exception of the two outgroups), and also the two indeterminate taxa. Information on ingroup taxa was obtained through examination of specimens during collection visitations and those available by loan at the Michigan State University Museum. Outgroup characters were obtained either through examination of specimens available by loan or from Hasse (1879–1885), Ridewood (1921), Nakaya (1975), and Compagno (1988). The list of centrum characters can be found in Appendix D.

To assess the relationships within the ingroup, two closely related taxa were chosen as the outgroup (Maddison et al., 1984). The two outgroup taxa chosen for this analysis are *Scyliorhinus* and *Haploblepharus*, which are both basal members of the Order Carcharhiniformes.

The heuristic search algorithm with closest addition sequence was used with the PAUP* 4.0 program (Swofford, 2000). This search algorithm selects a representative sample among the possible most parsimonious trees. For comparative purposes, the branch–and–bound search algorithm was also used on the same data matrix. In every analysis, both search algorithms provided identical results. Too many taxa were being analyzed to use the exhaustive search algorithm. Two different analyses were run. In the first analysis, characters 4, 5, 15, 16, 18, and 19 were ordered while the rest were unordered. The six ordered characters were all multistate characters with states that potentially imply progression. In the second analysis, all characters were unordered. Both Strict and Adams consensus trees were obtained from the resulting most parsimonious trees. MacClade 4.03 (Maddison and Maddison, 2001) was used to further manipulate the topology of the trees.

After the data matrix with centrum characters was subjected to maximum parsimony analyses, a second data matrix of unweighted characters was constructed and subjected to a maximum parsimony analysis. This second matrix included one hundred and thirteen characters of morphological characters from complete specimens of Recent carcharhiniform sharks, modified from Compagno (1988). Taxa included in this analysis were nearly the same as those included in the analyses using centrum data, minus the two indeterminate carcharhiniform sharks, and minus *Haploblepharus*, due to lack of complete character information. The heuristic search algorithm with closest addition sequence was used with this data matrix, and all characters were unordered. Finally, the original twenty–three centrum characters were added to this matrix, for a new matrix totaling one hundred and thirty–six whole body plus centrum characters. The heuristic search algorithm with closest addition sequence was used with this data matrix also. Characters 4, 5, 15, 16, 18, and 19 were analyzed as both ordered and unordered. Both results were identical, and will only be discussed once.

Results

The first analysis using only centrum characters, with characters 4, 5, 15, 16, 18, and 19 ordered produced three equally parsimonious trees, each 70 steps long with a consistency index of 0.784. The Strict and Adams consensus trees have the same topology (Figure 19a).

The second analysis using only unordered centrum characters produced eight equally parsimonious trees, each 66 steps long with a consistency index of 0.600. The Strict and Adams consensus trees differ only by the position of *Rhizoprionodon.* In the Strict consensus tree (Figure 20a), Rhizoprionodon is part of an unresolved polytomy including the outgroup taxa, *Mustelus,* the clade containing *Triakis* and *Galeorhinus*, and the clade containing all other taxa. In the Adams consensus tree *Rhizoprionodon* is united in a clade with *Mustelus*. These consensus trees are similar to those created using ordered characters, with a few notable exceptions. The two sets of trees differ with the position of *Prionace*. In the analysis using ordered characters, *Prionace* is positioned as the sister–taxon to the clade containing *Hemipristis* and the clade containing *Galeocerdo, Sphyrna, Negaprion*, and *Carcharhinus.* In the analysis using unordered characters, *Prionace* is positioned as the sister–taxon only to the clade containing *Galeocerdo, Sphyrna, Negaprion*, and *Carcharhinus.* Also, *Hemipristis* and the two indeterminate taxa no longer form a monophyletic clade as they do in the previous analysis. Finally, in the analysis using unordered characters, *Triakis* and *Galeorhinus* form a monophyletic clade, unlike the analysis using ordered characters.

The third analysis using 113 morphological characters from complete specimens of carcharhiniform sharks produced two equally parsimonious trees, each 116 steps long. The Strict and Adams consensus trees had a consistency index of 0.750, and produced trees with identical topologies (Figure 21a). The consensus tree resembled the trees obtained using centrum characters in the placement of the triakids and *Hemipristis*. The

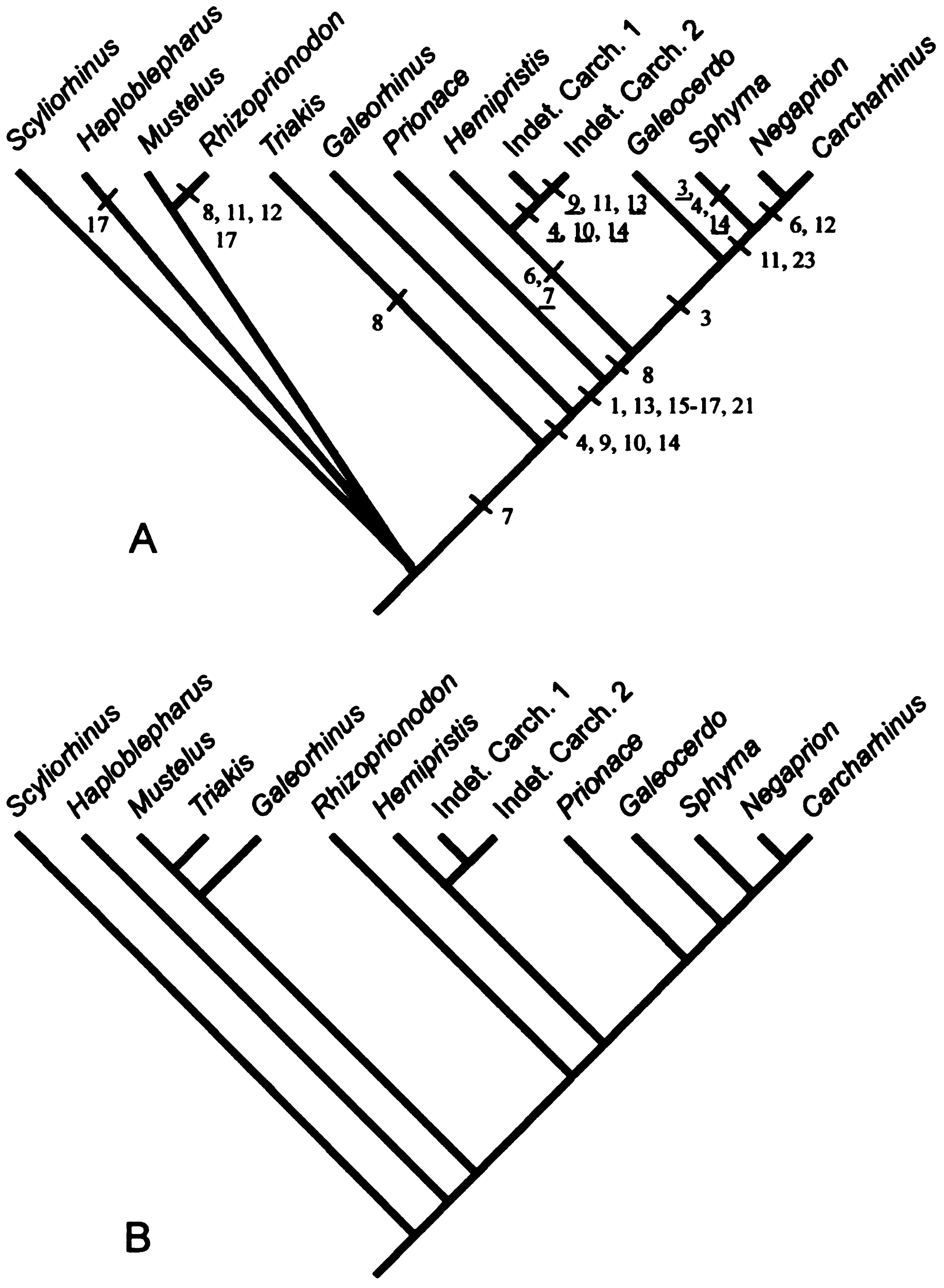


Figure 19. Cladograms showing relationships among Carcharhiniformes using centrum characters (with characters 4, 5, 15, 16, 18, and 19 ordered). **A.** Consensus tree of three equally parsimonious trees, showing character changes. Underlined numbers indicate reversal to primitive state. **B.** Manipulated consensus tree topology for Carcharhiniformes, resulting in 3 additional steps.

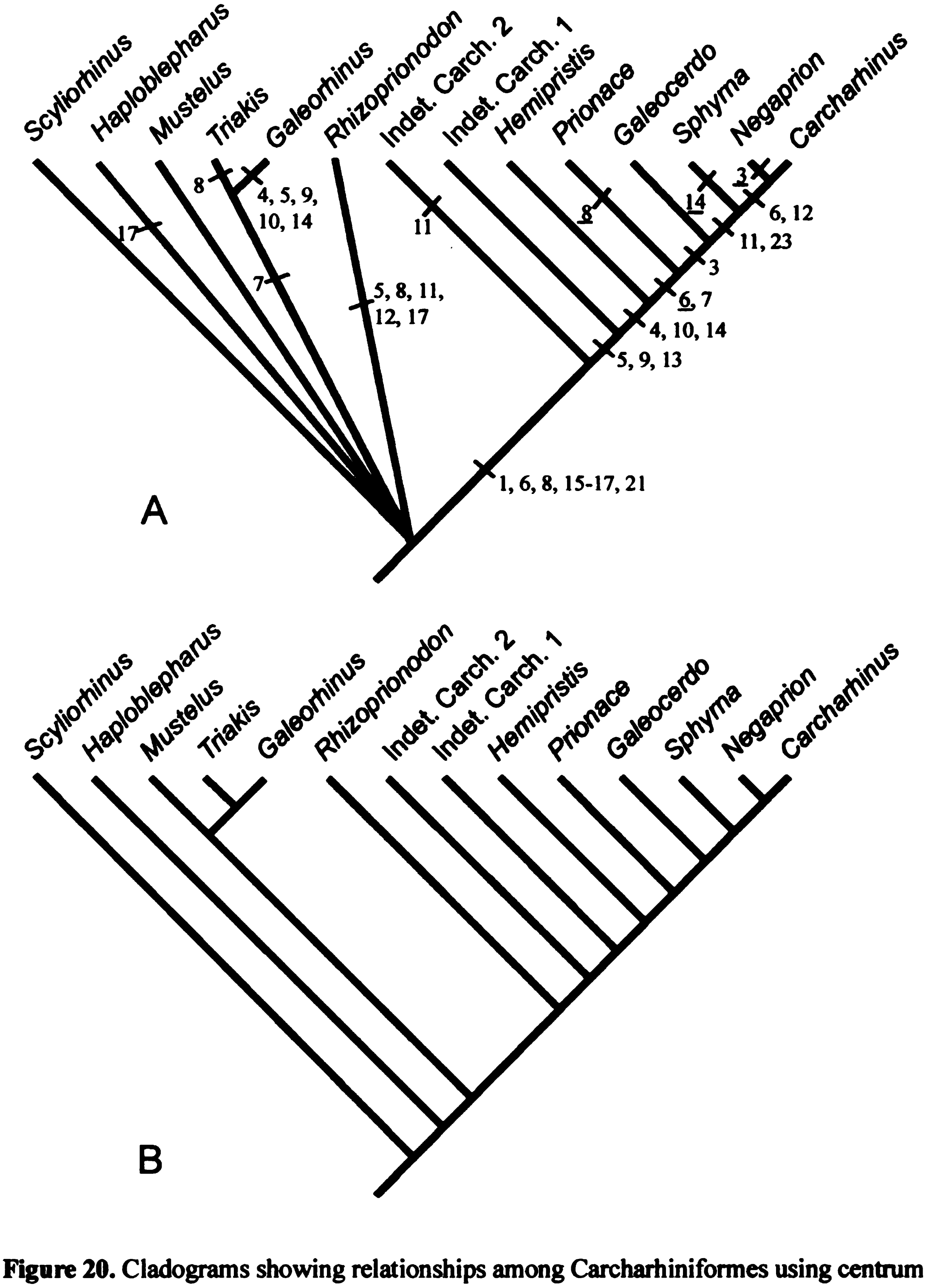


Figure 20. Cladograms showing relationships among Carcharhiniformes using centrum characters (with all characters unordered). **A.** Strict consensus tree of eight equally parsimonious trees, showing character changes. Underlined numbers indicate reversal to primitive state. **B.** Manipulated consensus tree topology for Carcharhiniformes, resulting in 4 additional steps.

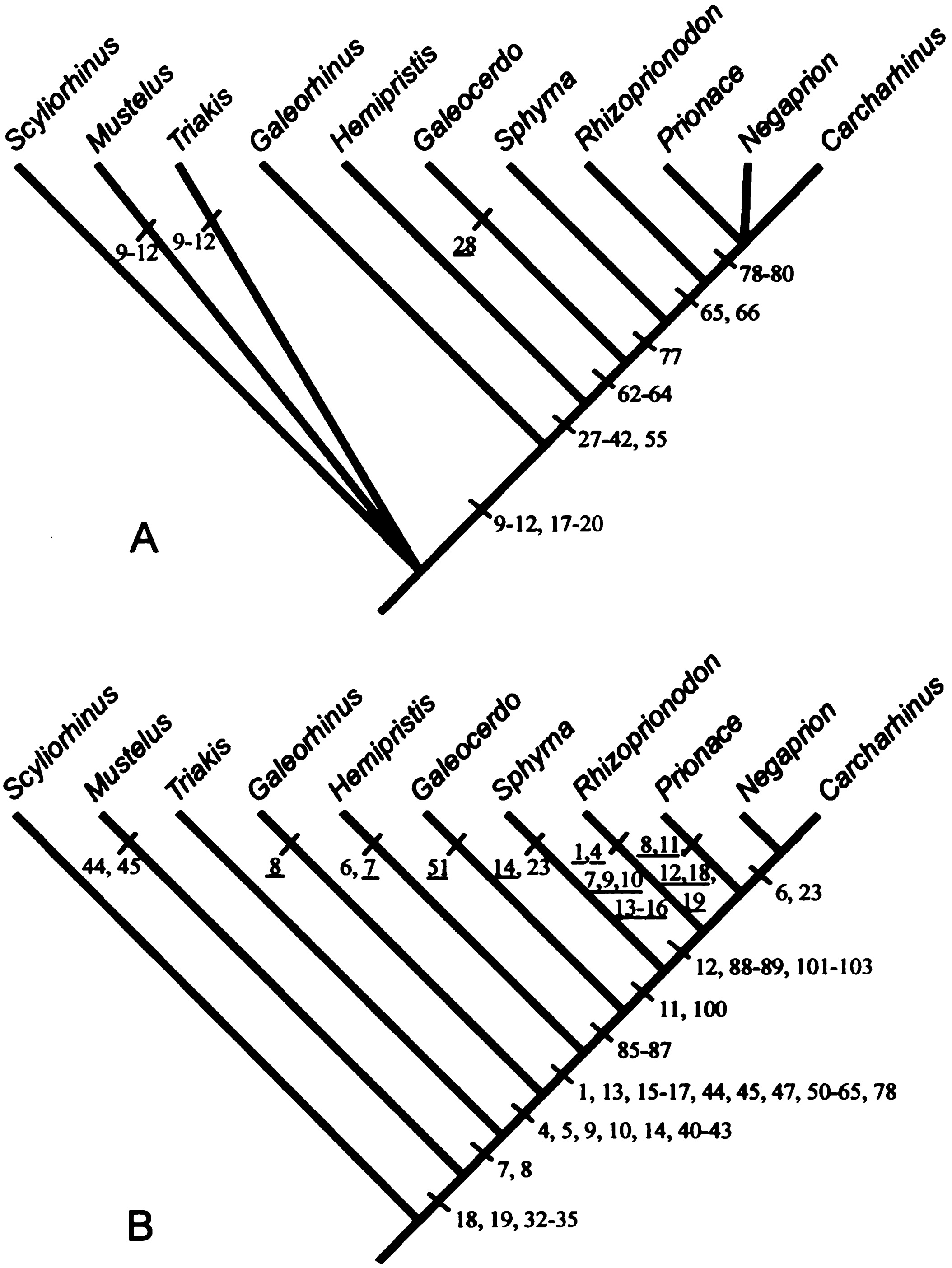


Figure 21. Cladograms showing relationships among Carcharhiniformes using complete morphological characters, showing character changes. Underlined numbers indicate reversal to primitive state. **A.** Consensus tree of two equally parsimonious trees, centrum characters not included. **B.** Single most parsimonious tree, combining complete morphological characters with centrum characters.

biggest differences were in the position of the various carcharhinid genera and *Sphyrna*. In the analysis using whole body morphology, *Prionace* forms an unresolved polytomy with *Negaprion* and *Carcharhinus*. *Sphyrna* is still positioned within the carcharhinids, as is *Rhizoprionodon*. *Galeocerdo* is the sister–taxon to all other carcharhinids and *Sphyrna* in this analysis.

The final analysis combining centrum characters with other morphological characters produced a single most parsimonious tree with 166 steps (Figure 21b). This tree is nearly identical to the tree using whole body characters minus the centrum characters, with the only difference being that the polytomies are now resolved.

Relationships of carcharhiniform sharks using centrum data

In the analysis using ordered characters (Figure 19a), the three equally most parsimonious trees vary little from one another. The topologies of the trees are nearly identical; the only variation in topology is the placement of *Rhizoprionodon* and *Mustelus*. *Rhizoprionodon* shares some plesiomorphic characters with triakids that are not present in other carcharhinids, including the fluted cylinder shape (character 1), absence of pores (character 15, 16) and bulbous basidorsal and basiventral cartilage shape in cross–sectional view (character 21). *Rhizoprionodon* share some apomorphic characters with other carcharhinids, including dorsal and ventral foramina that do not extend into rims (character 8), the ratio of dorsal interforaminal wall width/width at apices of the double cone (character 12), interior angle of the intermedialia (character 17), and presence of thin diagonal lamellae (character 19). In the consensus trees, *Rhizoprionodon* is the sistergroup of *Mustelus*, though other morphological (e.g., Compagno, 1988) and molecular (e.g. Lavery, 1992) data do not support this relationship. *Mustelus* is normally considered to be a less derived member of Triakidae, while *Rhizoprionodon* is united with the Carcharhinidae, suggesting convergence of centrum morphology among these taxa.

Genera that are typically united under the Triakidae (*Mustelus, Triakis,* and *Galeorhinus*) do not form a single clade in the consensus trees, and are therefore paraphyletic in this analysis. Maisey (1984) likewise reports the triakids to be paraphyletic. The relative placement of these genera in the trees compared to the other carcharhiniform sharks is consistent with previous hypotheses (e.g., Maisey, 1984; Compagno, 1988).

The family Carcharhinidae, as usually defined (e.g., Compagno, 1988), is polyphyletic because *Sphyrna* is embedded in the clade that is normally classified as Carcharhinidae, and is the sistergroup to the clade containing *Carcharhinus* and *Negaprion*. Compagno (1988) suggested a reclassification of the Carcharhinidae where the hammerheads (*Sphyrna* and *Eusphyra*) were assigned to the tribe Sphyrnini within the Carcharhinidae. Naylor (1992) conducted a distance Wagner analysis using protein variations among carcharhiniform sharks, the results of which support the suggestion of Compagno (1988) to combine the sphyrnids with the carcharhinids (Figure 22c), though their exact relationship has yet to be determined.

Prionace is usually considered a derived carcharhinid (e.g., Naylor, 1992), but is excluded from the clade that contains other carcharhinids when only centrum characters were used in the analysis. As discussed previously, centra of *Prionace* are distinct, and lack many of the derived characters present in other carcharhinids. *Prionace* retains many

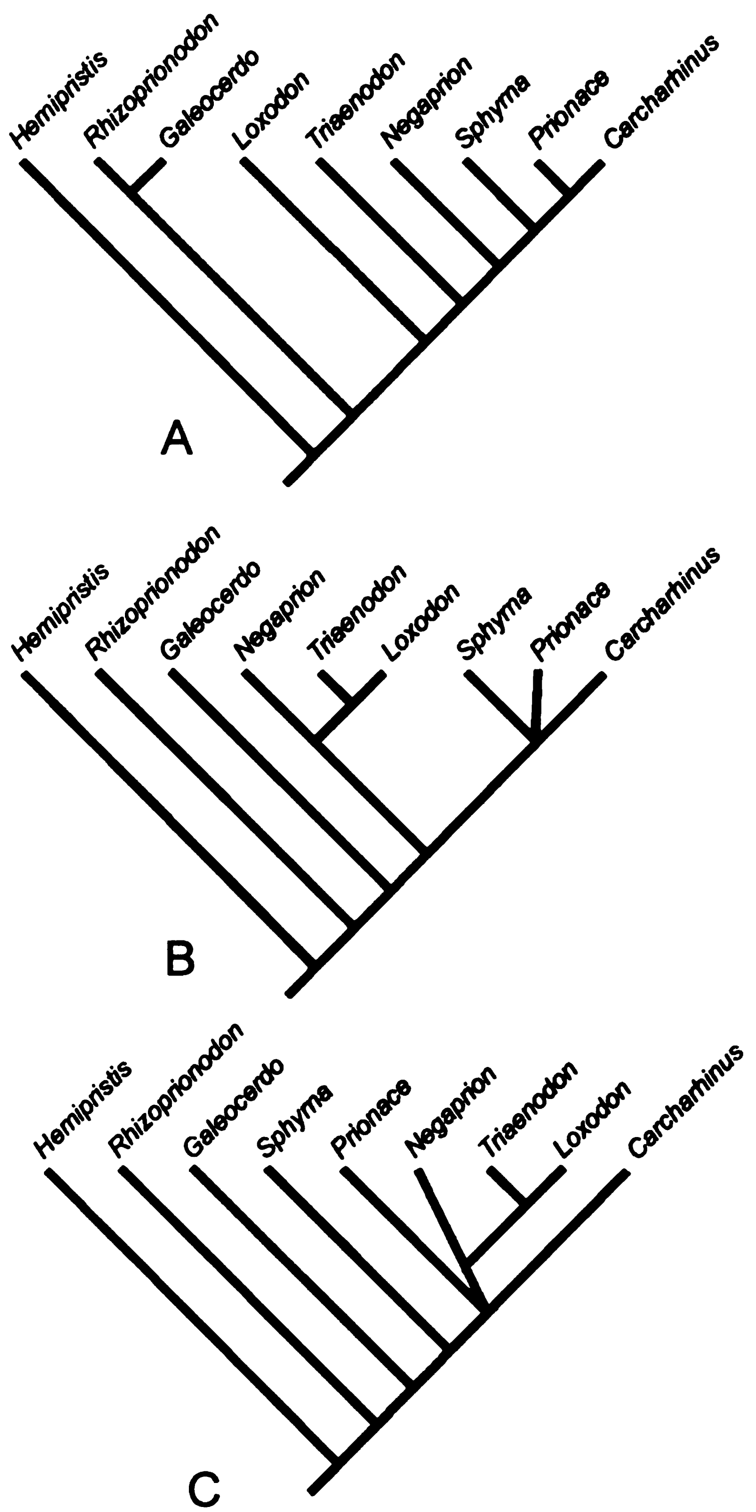


Figure 22. Cladograms showing relationships among Carcharhiniformes using molecular data. **A.** Majority rule consensus tree 1. **B.** Majority rule consensus tree 2. **C.** Distance Wagner tree. Modified from Naylor, 1992.

plesiomorphic centrum characters, including dorsal and ventral foramina that extend into the rims (character 8), dorsal foramina width/dorsal interforaminal wall width ratio less greater than 1.0 (character 11), dorsal interforaminal wall width/width at apices of double cone ratio less than 0.28 (character 12), and lack of diagonal calcified lamellae (characters 18, 19). The last two characters dealing with diagonal calcified lamellae were coded as absent because no lamellae were present in any modern *Prionace* centra. Some of the fossil centra tentatively identified as *Prionace* have diagonal calcifications, but due to uncertainties in the identification, were not included in the analysis. The two unknown taxa, Carcharhiniformes indeterminate A and B, are united with *Hemipristis* in the analyses, suggesting that they may be either members of the family Hemigaleidae or sister–taxa to that family. These indeterminate taxa are less derived than most carcharhinids based on centra characters.

The relationships of *Galeocerdo*, *Negaprion,* and *Carcharhinus* were consistent with other hypotheses (Compagno, 1988; Naylor, 1992) (Figure 22).

The consensus trees were manipulated using MacClade to explore how many additional steps were required to alter the tree topology to one that was more consistent with other morphological and molecular data. *Rhizoprionodon* was separated from the *Mustelus*, and *Mustelus, Triakis,* and *Galeorhinus* were united in a single, monophyletic clade. This manipulation required two additional steps. Placing *Prionace* as the sistergroup to the clade containing *Galeocerdo, Sphyrna, Negaprion* and *Carcharhinus* added one additional step to the tree (Figure 19b). Finally, moving *Sphyrna* outside the clade containing *Galeocerdo, Negaprion*, and *Carcharhinus* required two additional steps, but was not shown in the figure, as it is not consistent with more recent hypotheses (e.g., Compagno, 1988; Naylor, 1992).

The analysis using unordered centrum characters produced eight equally most parsimonious trees, and their consensus trees were very similar to those discussed above. The Strict and Adam's consensus trees differed only in the position of *Rhizoprionodon.* In the Adam's consensus tree, *Rhizoprionodon* was grouped with *Mustelus,* while it was isolated from *Mustelus* and included in a polytomy in the Strict consensus tree. The unordered characters produced a few other, minor differences from the analysis using ordered characters. In this second analysis, *Triakis* and *Galeorhinus* were united. *Hemipristis* was no longer united with the two indeterminate carcharhiniform sharks. The most notable difference was the placement of *Prionace* in this analysis. Instead of being placed as the first outgroup to the clade containing *Hemipristis* and the indeterminate carcharhiniform sharks, *Prionace* was placed within the clade containing *Galeocerdo, Sphyrna, Negaprion*, and *Carcharhinus*, more consistent with the hypotheses of Compagno (1988) and Naylor (1992). Because the resulting trees from the two analyses using centrum characters are so similar, it is difficult to indicate whether ordered or unordered characters performed better.

These consensus trees were manipulated in the same manner as the previous analysis. Removing the polytomy containing the outgroups *Scyliorhinus* and *Haploblepharus* required three additional steps. Placing *Mustelus* in the clade containing *Triakis* and *Galeorhinus* required no additional steps. Removing *Rhizoprionodon* from the polytomy required one additional step (Figure 20b). Placing *Sphyrna* outside the carcharhinids added two steps but was not shown in the figure, as it is not consistent with more recent hypotheses (e.g., Compagno, 1988; Naylor, 1992).

Relationships of carcharhiniform sharks using all available morphological characters

The results of the analysis using whole specimen carcharhiniform sharks, minus centrum characters (Figure 21a), produced two equally parsimonious trees that are very similar to one another. The only difference between the two trees is with the placement of *Mustelus*. In the first tree, *Mustelus* is part of an unresolved polytomy with *Scyliorhinus, Triakis*, and the clade containing the remaining taxa. In the second tree, the polytomy contains *Scyliorhinus*, *Triakis*, and the clade containing the remaining taxa, with *Mustelus* as the sistergroup to all taxa minus *Scyliorhinus* and *Triakis*.

The Strict and Adams consensus trees are identical to one another, and are also identical to the first tree discussed above (Figure 21a). This tree topology is similar to the topologies of trees using centrum characters in many ways. The three genera typically grouped together as Triakidae (*Mustelus, Triakis*, and *Galeorhinus*) do not form a distinct clade, making Triakidae paraphyletic. *Hemipristis* is the sistergroup to all of the carcharhinids and *Sphyrna*. *Rhizoprionodon* and *Prionace* are now included with the other carcharhinids, and *Sphyrna* is the sister group to the clade containing all of the carcharhinids except *Galeocerdo*. Of interest is the crown polytomy that includes *Prionace, Negaprion*, and *Carcharhinus*, indicating less clarity in the relationships of these taxa based on the whole specimen characters than analyses including centrum characters, but consistent with the hypothesis of Naylor (1992), who also hypothesized that these three taxa form an unresolved polytomy.

Tree topology was manipulated using MacClade for exploratory purposes. Grouping *Triakis* and *Mustelus* together required no additional steps. Adding *Galeorhinus* to the other triakids required four additional steps. Finally, moving *Sphyrna* outside the other carcharhinids (outside *Galeocerdo*) added one step to the total length of the tree.

The analysis that included the combination of centrum characters with all morphological characters resulted in a very distinct, perfectly pectinate tree (Figure 21b). As in previous analyses, the three genera typically normally grouped together as Triakidae (*Mustelus, Triakis, Galeorhinus*) do not form a distinct clade, making Triakidae paraphyletic. *Hemipristis*, being the only representative of the Hemigaleidae, is not grouped with any other taxa. This analysis once again suggests that Carcharhinidae, as normally defined, is paraphyletic. *Sphyrna* was included within the cluster of genera normally attributed to Carcharhinidae, supporting the suggestion of Compagno (1988) and Naylor (1992) to unite the Carcharhinidae and Sphyrnidae into a single family. The inclusion of the other morphological characters in the analysis produced a more customary placement for *Rhizoprionodon*, as it was once again included within the clade that includes Carcharhinidae and *Sphyrna*. The previous *Prionace, Negaprion*, and *Carcharhinus* polytomy was resolved when centrum characters were included in the data matrix.

The tree was manipulated using MacClade to explore how many additional steps were required to group the three triakid genera together. One additional step was required to group *Mustelus* and *Triakis*, but seven additional steps were required to also include *Galeorhinus*. *Galeorhinus* is generally considered to be the most derived triakid of the three included in the analysis (Compagno, 1988), and has several centrum apomorphies that distinguish it from other triakid genera. These apomorphies include a medio–lateral breadth approximately equal to dorso–ventral height (character 4), a centrum length/diameter ratio between 0.6 and 0.95 (character 5), dorsal foramina length/diameter ratio less than 0.57 (character 9), dorsal foramina length/dorsal foramina width ratio less than 3.0 (character 10), and ventral foramina length/ventral foramina width ratio less than 2.5 (character 14). Sphyrna was placed as the sistergroup to the carcharhinids, a move that required three additional steps.

CONCLUSIONS

Identification of carcharhiniform vertebral centra

Vertebral centra from the ten genera discussed in this study have distinct morphologies that allow them to be identified to the generic level. In most cases, examination of external morphology alone provides enough information for identification. When examination alone is not sufficient, measurements can be taken and applied to a discriminant analysis to predict identification. Discriminant analysis is useful for predicting the group membership in naturally occurring groups for cases of unknown membership (Klecka, 1980; Tabachnick and Fidell, 1983). The present study corroborates that of Kozuch and Fitzgerald (1989) who successfully used vertebral centra to identify sharks to the specific level at archaeological sites.

The morphology of the centra was not, however, distinct enough to identify specimens to genus in every instance. The centra of *Negaprion* and *Carcharhinus* have nearly identical morphologies. Most centra that fit the description of these genera are labeled as *Carcharhinus* simply because of the high diversity and common occurrence of this genus. Without teeth to aid in identification (e.g. UF 3245.1–3245.5), the identification of a centrum as *Negaprion* or *Carcharhinus* cannot be entirely certain. Because only one specimen of *Negaprion* with two centra was sampled in the study, a larger sample size may reveal additional differences useful for distinguishing the two genera.

Diplospondylous caudal centra are also very difficult to identify. These centra are proportionately much shorter than MP or DP centra, and tend to converge towards a cylindrical shape and lose morphological complexity as they become smaller among all carcharhiniform taxa. The pore distribution is still distinct in these centra, but is not enough for identification of the centra without other characters.

The six fossil centra tentatively identified as *Prionace* are significant because this genus is not currently known from Neogene deposits in North America. Currently, this genus is only known in the fossil record from the Pliocene of Italy (Landini, 1977). If these fossil centra are indeed from *Prionace*, it would indicate a significant geographic range extension. *Prionace* is found in oceans worldwide today (Compagno, 1984), and their presence in the Neogene of North American should not come as a surprise. Because *Prionace glauca* is a pelagic species, they are not as likely to be recovered as fossils. Unfortunately, *Prionace* centra were available from only one individual for the present study, and more comparative material is needed before any conclusions can be drawn.

Taxonomic value of shark vertebral centra

Carcharhiniform vertebral centra are also useful in a phylogenetic context. The results of the first two cladistic analyses based on centrum characters alone (Figures 19, 20) were very similar to published accounts of carcharhiniform phylogeny (Figure 22). A few taxa had positions within the cladograms that were contrary to previously published hypotheses, but in all of these cases, when the trees were manipulated to resemble the other hypotheses, the resulting trees were only a few steps longer.

Despite the paraphyletic nature of Triakidae, their relationship to the other carcharhiniform sharks was similar to the hypotheses of Maisey (1984), Compagno (1977), and Compagno (1988). Triakids are considered to be the sistergroup of the clade containing Hemigaleidae, Carcharhinidae, and Sphyrnidae. The paraphyletic nature of the three triakid genera studied in this analysis may not be problematic, as it required very few additional steps to combine them into a monophyletic clade (2 steps in the analysis using ordered centrum characters, and no additional steps in the analysis with all centrum characters unordered).

Rhizoprionodon is considered a carcharhinid (Compagno, 1988), but has usually been grouped with *Mustelus* or as part of an unresolved polytomy with the outgroups, triakids, and the clade containing the remaining taxa. This relationship was not entirely a surprise, however, as *Rhizoprionodon* has centra very similar to triakids in a number of characters, as discussed above. The habitat and distribution of *Rhizoprionodon* is not significantly different from that of other carcharhinids (Compagno, 1984), so it is unlikely that the vertebral differences from other carcharhinids are the result of environmental effects. It is, however, unclear whether the differences are the retention of plesiomorphic characters or reversals.

The usefulness of the diagonal calcifications as characters in a phylogenetic analysis needs to be further examined. While some authors have discussed apparent trends in these calcifications (e.g. White, 1938; Nakaya, 1975) (Figure 5), it is apparent from this study that the diagonal calcifications vary within a single genus or even an individual.

A separate analysis of characters derived from whole specimens, minus centrum data, was conducted to compare with the analyses based on centrum data alone. The resulting consensus tree (Figure 21a) had *Rhizoprionodon* and *Prionace* placed in a manner consistent with other hypotheses (e.g. Naylor, 1992). Triakidae was once again paraphyletic. The consensus tree resulted in two unresolved polytomies. The first was at the base of the tree that included *Scyliorhinus, Triakis, Mustelus*, and the clade containing the remaining taxa. The second polytomy included the three most derived taxa, *Prionace, Negaprion*, and *Carcharhinus*. When centrum data were added to the matrix containing characters from complete specimens, the resulting tree changed very little. The addition did result in clarity, however, as the polytomies became resolved in the final solution.

Compagno (1988) and Naylor (1992) suggest a re–classification of the hammerhead sharks (genus *Sphyrna*) as the tribe Sphyrnini within the Carcharhinidae based on both morphological and molecular data. The hammerheads have traditionally been assigned to their own family (Sphyrnidae), but the results of the phylogenetic analyses presented here create a polyphyletic Carcharhinidae. Based on the addition of centrum data, I suggest the cladistic re–classification of the hammerheads be adopted.

This re–classification would not affect the discriminant analyses using GENUS as the grouping variable, but would reduce the number of groups from three to two in the analyses using FAMILY as the grouping variable.

Vertebral centra do carry a phylogenetic signal. This hypothesis is supported strongly by the results of the several phylogenetic analyses performed above. In the two analyses using only centrum characters (Figures 19, 20) the topologies of the trees are very similar to other published hypotheses (e.g. Compagno, 1988; Naylor, 1992), (Figure 22), including the inclusion of *Sphyrna* within the clade containing carcharhinid genera. The hypothesis that vertebral centra carry a phylogenetic signal is further supported by the added clarity centrum data supplied to the analysis using whole body morphology (Figures 21a, b). In the analysis using whole body morphology without centrum data, several unresolved polytomies appeared. By adding centrum data, these polytomies became resolved, and resulted in a single most parsimonious tree.

While Hasse (1879–1885) and Applegate (1967) tried to create a series of classifications based on the cross sectional pattern of vertebral centra, no evidence was found for a distinct morphotype that could readily identify a particular genus or family in this study. Hasse (1879–1885) and Applegate (1967) may have been too optimistic about the value of the calcification patterns, but their work, along with Ridewood (1921), has laid an important foundation for studying shark centra. When distinct elements within the centra are examined separately (similar to Compagno, 1988), and coded as individual characters, the use of centrum morphology becomes more apparent. The use of centrum morphology becomes even more apparent when coupled with all possible shark morphological characters.

It is obvious that more Recent comparative specimens are needed for future analyses. The results presented in this study only include ten genera from four families, a small fraction of the nearly fifty genera of carcharhiniform sharks. In addition to incorporating additional taxa, centra from more individuals and from different regions are needed to insure an appropriately large sample size is available. Additionally, a more comprehensive selection of outgroup taxa, perhaps including basal lamniform sharks, would benefit future analyses.

Future work

Many possible areas for future research logically follow the research presented here. Fossil shark teeth have been studied extensively, but associated centra are often overlooked. Purdy et al. (2001) studied the shark fauna of the Lee Creek Mine. They did identify the centra from three different genera of carcharhiniform sharks, but there are many more left unidentified. Twelve carcharhiniform genera from the Lee Creek Mine were identified based on teeth alone. Additional centra may be identified to genus upon a more thorough examination of these centra, thus increasing the known diversity in the fossil record.

Three regions have been identified in the vertebral column of sharks, the monospondylous precaudal zone, diplospondylous precaudal zone, and the diplospondylous caudal zone (Compagno, 1970). The three identified regions have never been studied in a quantitative framework, and the nature of the variation between and within the zones is poorly understood. In addition to variation of centrum proportions, the internal calcification patterns also vary with position. The proportional variations within the column of a single individual can be better understood using geometric landmark morphometrics. X–radiographs of centra from the same individual will allow the nature of variation in calcification along the column to be studied. The minor variations between adjacent centra will be revealed as well as broader patterns along the entire column. These data will be compared to other sharks of the same species to compare consistency of the positional variations.

Similar studies quantifying shape change using geometric morphometrics can be conducted on a single species at different growth stages. Calcification of the vertebral centra increases throughout the lifetime of sharks, though the nature of this increase is poorly understood. A better understanding of the changing calcification patterns will improve the use of fossil centra for phylogenetic analysis.

The data gathered may also be important for future studies to interpret the relationship between centrum morphology and swimming characteristics in extant taxa. Bucholtz (1998, 2001) has identified a correlation in regional variation of centrum morphology and swimming mode in cetaceans. Massare and Sharkey (2003) and Kajiura et al. (2003) have conducted some preliminary work on the role of shark vertebral centra in swimming styles. Massare and Sharkey (2003) examined the variation in length, width, and height of vertebral centra with their position in the vertebral column of five sharks (four carcharhiniforms and one orectolobiform). They found considerable variation in the pattern of centrum shape, without identifying what the differences imply for swimming styles. Kajiura et al. (2003) show that there is no relationship between the number of vertebrae and the ability to bend the body laterally in juvenile *Sphyrna tiburo, S. lewini,* and *Carcharhinus plumbeus*. Because carcharhiniform sharks increasingly calcify their vertebral centra, the relationship between number of vertebrae and flexibility may be different for adult sharks. Vertebral proportions, regional variations, and degree and pattern of calcification, joined with counts of total vertebral number, can be used to evaluate the vertebral contribution to body flexibility and its role in swimming styles for carcharhiniform sharks.

This research can serve as a model for future studies among other clades. Fossil shark centra are regularly preserved from other groups, including Lamniformes, the sistergroup to Carcharhiniformes. The research presented here can serve to establish criteria and a methodological approach for including centrum morphology in future morphofunctional analyses of lamniforms and other chondrichthyans.

The results of this study support the hypothesis that carcharhiniform vertebral centra are morphologically distinct, identifiable, and useful in interpretation of phylogenetic relationships. Because of the well-documented difficulties with identifying isolated fossil shark teeth, shark vertebral centra should be utilized whenever they are available. The combination of fossil shark teeth and vertebral centra will provide a more rigorous means for studying fossil sharks than teeth alone.

Appendix A

AMNH - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
AMNH 93843.29	*Sphyrna tiburo*	13.68	13.96	11.1	12.82	10.96	7.5	1.53
AMNH 93843.34	*Sphyrna tiburo*	15.84	15.63	13.03	13.93	12.64	8.76	1.66
AMNH 93843.37	*Sphyrna tiburo*	15.98	16.1	14.04	14.63	13.79	8.98	1.62
AMNH 93846.34	*Carcharhinus brevipinna*	7.24	7.14	5.21	6.04	6.74	3.51	1.57
AMNH 93846.46	*Carcharhinus brevipinna*	7.85	8.07	6.28	6.44	7.4	3.95	1.21
AMNH 93846.48	*Carcharhinus brevipinna*	7.84	8.03	6.54	6.63	7.62	3.86	1.4
AMNH 93846.57	*Carcharhinus brevipinna*	9.2	8.44	8.15	5.99	7.55	4.05	1.46
AMNH 99048.26	*Galeocerdo cuvieri*	13.72	13.78	8.99	11.07	13.15	5.97	3.71
AMNH 99048.30	*Galeocerdo cuvieri*	13.54	13.79	9.03	11.69	13.66	5.86	3.75
AMNH 99048.34	*Galeocerdo cuvieri*	14.07	13.73	9.58	12.38	13.81	6.27	4.05
AMNH 99048.38	*Galeocerdo cuvieri*	14.67	14.61	10.02	12.55	13.88	6.23	3.47
AMNH 99048.42	*Galeocerdo cuvieri*	14.78	14.53	9.98	12.91	14.12	6.7	3.77
AMNH 99048.46	*Galeocerdo cuvieri*	14.37	14.21	10.07	12.54	14.16	6.63	3.87
AMNH 99048.50	*Galeocerdo cuvieri*	14.46	14.74	10.03	12.71	14.44	6.58	3.9
AMNH 99048.53	*Galeocerdo cuvieri*	13.71	13.95	8.55	12.56	13.85	5.04	3.53
AMNH 99048.54	*Galeocerdo cuvieri*	13.84	14.06	8.55	12.59	13.88	4.66	3.53
AMNH 99048.58	*Galeocerdo cuvieri*	13.56	13.48	8.84	12.34	13.63	5.19	3.57
AMNH 99058.37	*Sphyrna zygaena*	19.36	19.18	11.88	17.63	19.28	7.49	3.93
AMNH 99058.42	*Sphyrna zygaena*	19.76	19.81	13	18.09	20.33	7.95	3.89
AMNH 99058.45	*Sphyrna zygaena*	20.06	19.74	13.11	17.83	20.89	8.25	4.13
AMNH 99058.52	*Sphyrna zygaena*	20.4	20.37	14.33	17.73	21.68	9.85	4.31
AMNH 99058.55	*Sphyrna zygaena*	19.75	20.13	12.48	17.92	20.9	7.53	4.59
AMNH 99058.56	*Sphyrna zygaena*	19.72	20.13	13.39	17.99	20.55	8.11	4.4
AMNH 99064.53	*Sphyrna lewinii*	26.51	26.79	16.87	25.11	29.04	12.49	4.64
AMNH 99064.60	*Sphyrna lewinii*	28.51	28.66	18.49	26.15	30.15	14.31	5.05
AMNH 99064.63	*Sphyrna lewinii*	29.05	29.29	21.45	25.89	31.33	16.03	5.07
AMNH 99064.64	*Sphyrna lewinii*	29.37	29.32	22.68	25.78	30.55	17.21	4.56
AMNH 99064.65	*Sphyrna lewinii*	29.36	29.31	22.1	25.77	30.07	17.21	5.14
AMNH 99064.74	*Sphyrna lewinii*	26.96	27.02	16.34	25.25	27.36	11.65	3.32
AMNH 218150.31	*Carcharhinus acronotus*	11.36	11.37	7.7	9.5	10.46	6.18	2.76
AMNH 218150.39	*Carcharhinus acronotus*	12.45	12.42	10.41	9.73	10.81	8.05	2.92
AMNH 218150.46	*Carcharhinus acronotus*	13.45	13.4	11.72	10.02	11.85	9.07	3.13

Appendix A

AMNH - Recent Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
AMNH 93843.29	4.64	9.17	2.25	1.79
AMNH 93843.34	4.73	11.03	2.15	1.88
AMNH 93843.37	4.88	10.99	1.89	1.6
AMNH 93846.34	2.25	3.26	2.67	2.95
AMNH 93846.46	1.95	4.12	1.48	1.76
AMNH 93846.48	2.63	4.65	2.03	1.6
AMNH 93846.57	2.3	4.62	1.23	1.31
AMNH 99048.26	2.71	5.62	3.51	4.12
AMNH 99048.30	2.52	6.13	3.87	4.47
AMNH 99048.34	2.51	6.79	4.08	4.75
AMNH 99048.38	2.78	6.51	3.7	4.6
AMNH 99048.42	3.25	6.36	4.12	4.48
AMNH 99048.46	3.34	6.61	3.55	4.78
AMNH 99048.50	3.23	6.67	3.79	4.95
AMNH 99048.53	3.38	5.09	3.4	4.5
AMNH 99048.54	3.38	5.09	3.5	4.45
AMNH 99048.58	3.37	4.99	3.35	3.84
AMNH 99058.37	4.28	8.56	3.57	3.51
AMNH 99058.42	4.79	8.59	3.96	2.99
AMNH 99058.45	5.48	8.65	3.88	2.69
AMNH 99058.52	5.09	9.96	3.8	2.17
AMNH 99058.55	4.62	8.21	3.7	1.56
AMNH 99058.56	4.53	8.22	3.7	1.97
AMNH 99064.53	8.52	12.58	4.6	2.97
AMNH 99064.60	8.56	14.46	4.5	2.81
AMNH 99064.63	8.2	17.36	4.47	3.26
AMNH 99064.64	8.38	18.78	4.47	3.26
AMNH 99064.65	8.24	18.85	4.42	3.27
AMNH 99064.74	8.15	12.55	4.59	5.3
AMNH 218150.31	3	6.57	3.24	3.28
AMNH 218150.39	5.08	8.08	2.94	2.95
AMNH 218150.46	4.33	9.87	2.57	2.63

CAS - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
CAS 25822.01	*Galeorhinus zyopterus*	8.1	7.7	6.7	6.55	7.2	5.6	2.55	1.85
CAS 25822.02	*Galeorhinus zyopterus*	8.35	8.15	7.85	6.2	7.1	6.1	2.75	1.2
CAS 25822.03	*Galeorhinus zyopterus*	8.5	8.05	7.85	6.35	7.15	5.65	2.45	1.4
CAS 25822.05	*Galeorhinus zyopterus*	7.65	7.6	6.35	6.3	7.05	4.65	2	1.9
CAS 25822.09	*Galeorhinus zyopterus*	7.9	7.9	6.02	6.9	7.05	4.9	2.4	1.35
CAS 25822.20	*Galeorhinus zyopterus*	7.6	7.6	5.6	6.95	7	4.35	2.4	1.3
CAS 25822.25	*Galeorhinus zyopterus*	7.65	7.5	6.85	6.2	7	5.1	2.2	1.5
CAS 25822.28	*Galeorhinus zyopterus*	7.55	7.55	6.4	6.15	6.9	4.55	1.7	1.55
CAS 25822.41	*Galeorhinus zyopterus*	7.72	7.71	5.78	6.77	6.85	4.9	2.71	1.31
CAS 25822.46	*Galeorhinus zyopterus*	7.93	7.91	6.9	6.5	6.99	5.89	2.56	1.18
CAS 25825.13	*Triakis semifasciata*	14.31	14.26	15.69	10.21	11.76	12.99	3.91	2.21
CAS 25825.14	*Triakis semifasciata*	13.23	13.1	12.97	10.49	11.58	10.14	2.81	2.28
CAS 25825.15	*Triakis semifasciata*	12.9	12.76	11.94	10.86	11.43	8.95	2.65	2.51
CAS 25825.16	*Triakis semifasciata*	12.61	12.42	11.07	10.03	10.97	8.5	2.44	2.68
CAS 25825.17	*Triakis semifasciata*	11.78	11.54	11.48	8.38	9.75	8.02	2.18	1.8
CAS 25825.18	*Triakis semifasciata*	12.06	12.33	12.51	8.99	9.99	8.66	2.32	1.73
CAS 25825.19	*Triakis semifasciata*	13.02	12.93	11.51	10.84	11.07	8.74	2.44	2.65
CAS 25825.20	*Triakis semifasciata*	13.1	12.95	12.4	10.45	11.5	9.75	2.95	2.2
CAS 25825.21	*Triakis semifasciata*	11.15	10.55	11.05	7.8	8.75	7.65	1.9	1.9
CAS 25825.36	*Triakis semifasciata*	12.35	11.85	10.4	9.4	10.35	7.55	2.55	1.95
CAS 53006.28	*Mustelus californicus*	11.68	11.94	12.80	8.29	9.30	11.37	1.38	3.74
CAS 53006.29	*Mustelus californicus*	12.14	11.52	12.72	8.56	9.60	10.83	1.51	3.92
CAS 65084.2	*Galeocerdo cuvieri*	43.8	43.31	29.36	38.78	43.54	21.33	8.73	9.05
CAS 65084.3	*Galeocerdo cuvieri*	44.3	44.14	28.94	37.73	43.51	20.98	8.76	9.3

CAS - Recent Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
CAS 25822.01	4.7	2.15	1.6
CAS 25822.02	6.6	2.35	1.25
CAS 25822.03	5.75	1.95	1.45
CAS 25822.05	4.55	2.2	1.6
CAS 25822.09	4.8	3.1	1.5
CAS 25822.20	4.25	3.3	1.85
CAS 25822.25	5.15	2.25	1.25
CAS 25822.28	4.85	1.9	1.45
CAS 25822.41	4.76	3.2	1.48
CAS 25822.46	5.79	3.06	1.25
CAS 25825.13	11.83	2.5	2.52
CAS 25825.14	10.05	4.5	2.61
CAS 25825.15	9.23	4.27	3.5
CAS 25825.16	8.93	2.88	2.13
CAS 25825.17	8.18	3.03	1.87
CAS 25825.18	9.77	2.94	1.65
CAS 25825.19	8.62	3.64	4.82
CAS 25825.20	9.3	4.4	3.15
CAS 25825.21	8.2	2.75	1.4
CAS 25825.36	7.6	3.4	2.15
CAS 53006.28	10.21	1.83	3.03
CAS 53006.29	10.67	2.06	2.74
CAS 65084.2	20.37	10.99	16.05
CAS 65084.3	21.34	8.37	11.1

G. Hubbell Collection - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
G. Hubbell Collection 1	*Galeorhinus galeus*	15.48	15.26	11.07	13.1	13.09	8.73	4.55
G. Hubbell Collection 1	*Mustelus canis*	11.6	11.43	11.28	9.66	9.6	8.96	3.16
G. Hubbell Collection 2	no data	11.56	11.55	11.33	9.77	10.17	9.33	2.87
G. Hubbell Collection 3		11.64	11.61	10.12	10.41	9.58	8.77	2.56
G. Hubbell Collection 1	*Carcharhinus altimus*	25.04	24.51	12.32	24.05	23.87	8.26	6.85
G. Hubbell Collection 2	no data	25.04	24.82	13.02	23.83	24.38	8.51	6.47
G. Hubbell Collection 1	*Carcharhinus falciformis*	31.6	30.72	20.52	27.39	31.41	15.22	5.24
G. Hubbell Collection 2	male, 8'8", 269 lbs	29.96	29.72	18.09	28.32	30.5	13.26	5.37
G. Hubbell Collection 3		29.26	29	16.43	27.82	29.79	11.69	5.07
G. Hubbell Collection 4		29.29	28.99	15.75	28.08	29.7	11.01	5.17
G. Hubbell Collection 1	*Carcharhinus falciformis*	32.07	31.54	19.27	30.45	32.73	14.4	5.54
G. Hubbell Collection 2	9'1", 176 lbs	31.11	31.07	13.46	30.16	29.55	9.08	6.55
G. Hubbell Collection 4		31.27	31.2	13.3	29.92	28.74	9.11	6.01
G. Hubbell Collection 1	*Carcharhinus leucas*	31.51	31.5	14.36	31.77	31.01	9.36	5.56
G. Hubbell Collection 2	female, 8'9", 355 lbs	31.93	31.86	14.51	31.6	31.9	8.8	5.76
G. Hubbell Collection 3		32.78	32.57	14.29	32.63	32.7	9.69	5.42
G. Hubbell Collection 4		31.65	31.64	13.8	31.39	31.75	9.13	5.78
G. Hubbell Collection 5		32.13	31.64	13.91	31.58	31.94	9.21	5.83
G. Hubbell Collection 1	*Carcharhinus leucas*	32.2	31.69	14.83	31.62	31.79	10.37	5.68
G. Hubbell Collection 2	female, 8'9", 380 lbs	31.73	31.7	15.24	31.31	32.03	10.31	5.29
G. Hubbell Collection 3		32.85	32.82	14.01	32.58	32.46	9.4	5.78
G. Hubbell Collection 1	*Carcharhinus leucas*	27.14	27.08	12.45	26.88	26.67	7.69	4.59
G. Hubbell Collection 2	female, 7'9", 280 lbs	28.18	28.03	12.34	27.92	27.47	7.81	4.5
G. Hubbell Collection 1	*Carcharhinus limbatus*	17.9	17.83	9.92	16.61	17.71	6.79	3.01
G. Hubbell Collection 2	female, 5'6", 75 lbs	18.44	18.32	11.47	16.88	18.98	9.36	3.29
G. Hubbell Collection 3		19.08	18.68	12.25	17.25	19.18	10.22	3.29
G. Hubbell Collection 1	*Carcharhinus limbatus*	20.25	20	9.85	19.83	19.3	6.79	3.66
G. Hubbell Collection 2	female, 5'9", 90 lbs	19.97	19.82	9.64	19.48	19.22	6.5	3.69
G. Hubbell Collection 3		19.85	19.7	10.25	18.99	19.25	6.93	3.77
G. Hubbell Collection 1	*Carcharhinus perezi*	19.89	19.65	9.64	19.54	19.73	6.06	4.06
G. Hubbell Collection 2	female, 6'5", 120 lbs	19.86	19.83	9.5	19.6	19.66	5.74	4.17
G. Hubbell Collection 3		19.83	19.68	9.51	19.42	19.61	5.86	4.16
G. Hubbell Collection 1	*Carcharhinus perezi*	22.78	22.2	11.51	22.4	22.62	4.56	4.69
G. Hubbell Collection 2	female, 7', 147 lbs	21.12	21.11	14.33	21.2	21.92	11.33	4.51

G. Hubbell Collection - Recent Shark Centra Measurements

Specimen #	Identification	D Wall W	V Foram L	V Foram W	V Wall W
G. Hubbell Collection 1	*Galeorhinus galeus*	3.13	8.65	4.61	7.36
G. Hubbell Collection 1	*Mustelus canis*	1.8	10.26	3.34	3.53
G. Hubbell Collection 2	no data	2.13	10.26	2.65	3.67
G. Hubbell Collection 3		2.23	8.92	3.37	3.72
G. Hubbell Collection 1	*Carcharhinus altimus*	8.14	7.62	9.66	9.66
G. Hubbell Collection 2	no data	8.46	8.13	8.7	8.89
G. Hubbell Collection 1	*Carcharhinus falciformis*	6.06	16.17	5.04	9.56
G. Hubbell Collection 2	male, 8'8", 269 lbs	5.64	13.49	5.34	11.08
G. Hubbell Collection 3		5.68	12.26	4.67	12.44
G. Hubbell Collection 4		5.51	11.25	5.18	12.73
G. Hubbell Collection 1	*Carcharhinus falciformis*	6.04	15.11	4.97	12.73
G. Hubbell Collection 2	9'1", 176 lbs	6.41	9.29	4.75	11.11
G. Hubbell Collection 4		5.83	9.14	4.95	15.94
G. Hubbell Collection 1	*Carcharhinus leucas*	7.35	10.12	6.27	18.08
G. Hubbell Collection 2	female, 8'9", 355 lbs	7.29	9.89	6.2	19.73
G. Hubbell Collection 3		8.13	9.94	6.5	21.26
G. Hubbell Collection 4		7.32	9.56	6.46	19.62
G. Hubbell Collection 5		7.46	9.68	6.32	19.54
G. Hubbell Collection 1	*Carcharhinus leucas*	6.91	10.77	6.49	16.12
G. Hubbell Collection 2	female, 8'9", 380 lbs	7.33	10.98	6.59	14.76
G. Hubbell Collection 3		7.62	10.18	5.99	20.72
G. Hubbell Collection 1	*Carcharhinus leucas*	5.91	8.1	5.45	14.15
G. Hubbell Collection 2	female, 7'9", 280 lbs	7.01	8.4	5.25	16.33
G. Hubbell Collection 1	*Carcharhinus limbatus*	5.69	7.48	2.78	8.6
G. Hubbell Collection 2	female, 5'6", 75 lbs	6.13	8.46	3.29	6.38
G. Hubbell Collection 3		5.76	9.26	3.26	6.22
G. Hubbell Collection 1	*Carcharhinus limbatus*	5.77	7.05	3.19	10.42
G. Hubbell Collection 2	female, 5'9", 90 lbs	6.03	6.72	3.23	10.5
G. Hubbell Collection 3		5.71	7.5	3.2	9.66
G. Hubbell Collection 1	*Carcharhinus perezi*	4.96	6.56	4.68	7.99
G. Hubbell Collection 2	female, 6'5", 120 lbs	4.82	6.15	4.55	8.27
G. Hubbell Collection 3		4.95	6.06	4.57	8.24
G. Hubbell Collection 1	*Carcharhinus perezi*	4.97	8.62	4.38	12.15
G. Hubbell Collection 2	female, 7', 147 lbs	4.75	11.01	4.51	5.58

G. Hubbell Collection - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
G. Hubbell Collection 3		22.07	21.87	11.96	22.24	22.44	8.5	4.57
G. Hubbell Collection 4		21.46	21.32	14.05	21.21	22.11	11.05	4.56
G. Hubbell Collection 1	*Carcharhinus perezi*	18.53	18.37	8.79	18.06	18.02	5.6	3.96
G. Hubbell Collection 2	male, 5'11"	18.24	18.23	8.98	17.71	17.73	5.76	3.89
G. Hubbell Collection 3		18.39	18.23	8.8	17.99	18.01	5.41	4.03
G. Hubbell Collection 4		18.35	18.11	8.79	17.72	17.94	5.57	3.92
G. Hubbell Collection 1	*Carcharhinus plumbeus*	21.37	21.33	10.6	20.92	20.83	7.39	4.71
G. Hubbell Collection 2	male, 6'7"	19.77	19.49	11.69	19.13	19.36	8.62	4.42
G. Hubbell Collection 3		21.19	21.12	12.88	20.41	20.58	11.04	4.06
G. Hubbell Collection 4		21.6	21.48	12.62	20.76	20.73	10.53	4.43
G. Hubbell Collection 5		21.51	20.2	13.19	21.05	20.25	10.2	4.33
G. Hubbell Collection 1	*Carcharhinus signatus*	24.36	24.11	12.37	22.63	23.75	9.69	4.94
G. Hubbell Collection 2	male, 6'10.5", 114 lbs	24.89	24.53	13.61	22.48	23.85	10.81	4.93
G. Hubbell Collection 3		24.11	24.21	11.69	22.75	23.63	8.6	5.12
G. Hubbell Collection 4		24.02	24.01	11.21	22.72	22.86	8.08	4.76
G. Hubbell Collection 1	*Negaprion brevirostris*	21.86	21.69	12.13	20.89	21.49	8.11	3.79
G. Hubbell Collection 2	no data	22.08	20.47	11.12	19.36	21.94	8.37	3.78
G. Hubbell Collection 1	*Rhizoprionodon terraenovae*	9.47	9.4	6.78	7.44	9.35	4.9	1.46
G. Hubbell Collection 2	no data	8.78	8.73	7.87	6.81	8.89	6.74	1.59
G. Hubbell Collection 5		10.74	10.66	9.78	7.89	9.85	6.59	1.95
G. Hubbell Collection 1	*Prionace glauca*	27.69	27.68	11.17	23.39	24.61	9.48	6.45
G. Hubbell Collection 2	male, 9'6"	27.78	27.67	10.79	22.81	24.29	8.75	6.54
G. Hubbell Collection 3		27.34	27.17	12.41	25.3	25.49	10.55	6.26
G. Hubbell Collection 4		27.79	27.84	11.98	22.94	25.51	9.92	6.76
G. Hubbell Collection 5		25.9	25.44	10.58	22.33	22.59	6.68	5.94
G. Hubbell Collection 1	*Sphyrna mokarran*	34.26	34.21	20.9	33.34	35.82	13.9	6.38

G. Hubbell Collection - Recent Shark Centra Measurements

Specimen #	Identification	D Wall W	V Foram L	V Foram W	V Wall W
G. Hubbell Collection 3		4.77	9.19	4.56	10
G. Hubbell Collection 4		4.68	11.28	4.84	5.73
G. Hubbell Collection 1	*Carcharhinus perezi*	4.92	5.53	4.35	7.16
G. Hubbell Collection 2	male, 5'11"	4.91	5.78	4.06	6.96
G. Hubbell Collection 3		5.08	5.5	4.15	6.82
G. Hubbell Collection 4		4.99	5.42	4.13	7.1
G. Hubbell Collection 1	*Carcharhinus plumbeus*	6.79	7.78	4.05	10.17
G. Hubbell Collection 2	male, 6'7"	3.72	8.63	3.21	5.39
G. Hubbell Collection 3		4.57	9.45	3.85	6.49
G. Hubbell Collection 4		4.88	9.12	3.41	6.15
G. Hubbell Collection 5		3.93	10.52	3.26	5.82
G. Hubbell Collection 1	*Carcharhinus signatus*	2.9	9.45	4.88	5.56
G. Hubbell Collection 2	male, 6'10.5", 114 lbs	3.12	10.57	4.93	5.39
G. Hubbell Collection 3		3.53	8.56	5.03	5.42
G. Hubbell Collection 4		3.86	8.58	4.8	5.45
G. Hubbell Collection 1	*Negaprion brevirostris*	6.14	8.03	4.19	9.19
G. Hubbell Collection 2	no data	5.96	8.77	3.89	7.33
G. Hubbell Collection 1	*Rhizoprionodon terraenovae*	2.96	5.14	1.14	2.98
G. Hubbell Collection 2	no data	2.74	5.93	1.82	3.01
G. Hubbell Collection 5		2.79	7.93	2.07	3.67
G. Hubbell Collection 1	*Prionace glauca*	4.46	9.27	6.93	8.09
G. Hubbell Collection 2	male, 9'6"	4.15	8.07	5.63	9.7
G. Hubbell Collection 3		5.75	10.44	5.61	5.52
G. Hubbell Collection 4		4.68	8.61	6.73	6.32
G. Hubbell Collection 5		4.22	8.86	5.33	4.78
G. Hubbell Collection 1	*Sphyrna mokarran*	6.94	15.43	5.94	9.79

L. Whitenack Donation - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
L. Whitenack Donation 1	*Carcharhinus limbatus*	9.18	8.95	4.01	8.55	8.72	2.79	1.59
L. Whitenack Donation 2	*Carcharhinus limbatus*	8.8	8.83	4.35	8.45	8.61	2.32	1.59
L. Whitenack Donation 3	*Carcharhinus limbatus*	8.8	8.89	4.8	8.48	8.58	2.49	1.45
L. Whitenack Donation 4	*Carcharhinus limbatus*	8.77	8.74	4.31	8.49	8.51	2.43	1.51
L. Whitenack Donation 5	*Carcharhinus limbatus*	8.67	8.62	4.46	8.24	8.46	2.46	1.53
L. Whitenack Donation 6	*Carcharhinus limbatus*	8.62	8.64	4.18	8.32	8.32	2.26	1.61
L. Whitenack Donation 7	*Carcharhinus limbatus*	8.55	8.49	4.36	8.2	8.34	2.4	1.62
L. Whitenack Donation 8	*Carcharhinus limbatus*	8.5	8.56	4.27	8.17	8.2	2.57	1.53
L. Whitenack Donation 9	*Carcharhinus limbatus*	8.49	8.5	4.27	8.16	8.17	2.44	1.53
L. Whitenack Donation 10	*Carcharhinus limbatus*	8.5	8.51	4.24	8.15	8.13	2.44	1.39
L. Whitenack Donation 11	*Carcharhinus limbatus*	8.53	8.49	4.23	8.23	8.22	2.4	1.71
L. Whitenack Donation 12	*Carcharhinus limbatus*	8.43	8.42	4.01	8.18	8.15	2.35	1.64
L. Whitenack Donation 13	*Carcharhinus limbatus*	8.42	8.28	3.96	8.15	8.08	2.34	1.58
L. Whitenack Donation 14	*Carcharhinus limbatus*	8.23	8.29	3.74	8.05	7.98	2.44	1.59
L. Whitenack Donation 15	*Carcharhinus limbatus*	8.33	8.26	3.97	8.09	8.08	2.43	1.58
L. Whitenack Donation 1	*C. limbatus,* juvenile	6.11	5.93	3.2	5.8	5.88	1.45	1.23
L. Whitenack Donation 2	*C. limbatus,* juvenile	5.84	5.91	3.2	5.73	5.64	1.73	1.33
L. Whitenack Donation 3	*C. limbatus,* juvenile	5.88	5.89	2.88	5.76	5.65	1.31	1.24
L. Whitenack Donation 4	*C. limbatus,* juvenile	5.82	5.79	3.01	5.49	5.61	1.58	1.18
L. Whitenack Donation 5	*C. limbatus,* juvenile	5.73	5.78	2.97	5.62	5.58	1.38	1.4
L. Whitenack Donation 6	*C. limbatus,* juvenile	5.77	5.76	2.97	5.65	5.57	1.39	1.4
L. Whitenack Donation 7	*C. limbatus,* juvenile	5.74	5.77	2.9	5.59	5.62	1.43	1.24
L. Whitenack Donation 8	*C. limbatus,* juvenile	5.71	5.71	2.88	5.58	5.58	1.69	1.39
L. Whitenack Donation 9	*C. limbatus,* juvenile	5.67	5.7	2.69	5.58	5.58	1.66	1.29
L. Whitenack Donation 10	*C. limbatus,* juvenile	5.67	5.65	2.74	5.57	5.54	1.62	1.44
L. Whitenack Donation 11	*C. limbatus,* juvenile	5.6	5.62	2.77	5.51	5.61	1.8	1.32
L. Whitenack Donation 12	*C. limbatus,* juvenile	5.6	5.52	2.97	5.45	5.54	1.81	1.37
L. Whitenack Donation 1	*Sphyrna mokarran*	9.81	9.65	5.36	9.11	10.14	3.15	1.79
L. Whitenack Donation 3	*Sphyrna mokarran*	9.73	9.74	5.35	9.24	10.11	2.76	1.87
L. Whitenack Donation 4	*Sphyrna mokarran*	9.72	9.59	5.31	9.11	10.07	3.06	2.23

L. Whitenack Donation - Recent Shark Centra Measurements

Specimen #	Identification	D Wall W	V Foram L	V Foram W	V Wall W
L. Whitenack Donation 1	*Carcharhinus limbatus*	3.27	2.33	1.48	1.58
L. Whitenack Donation 2	*Carcharhinus limbatus*	3.27	2.38	1.73	1.7
L. Whitenack Donation 3	*Carcharhinus limbatus*	2.98	2.46	1.55	1.86
L. Whitenack Donation 4	*Carcharhinus limbatus*	2.97	2.32	1.85	1.95
L. Whitenack Donation 5	*Carcharhinus limbatus*	2.87	2.43	1.67	1.74
L. Whitenack Donation 6	*Carcharhinus limbatus*	2.93	2.36	1.72	1.78
L. Whitenack Donation 7	*Carcharhinus limbatus*	2.72	2.44	1.67	1.87
L. Whitenack Donation 8	*Carcharhinus limbatus*	2.89	2.24	1.64	1.87
L. Whitenack Donation 9	*Carcharhinus limbatus*	2.79	2.37	1.63	1.84
L. Whitenack Donation 10	*Carcharhinus limbatus*	2.95	2.33	1.68	1.88
L. Whitenack Donation 11	*Carcharhinus limbatus*	2.86	2.33	1.73	1.8
L. Whitenack Donation 12	*Carcharhinus limbatus*	3.3	2.33	1.68	1.83
L. Whitenack Donation 13	*Carcharhinus limbatus*	2.89	2.26	1.67	1.75
L. Whitenack Donation 14	*Carcharhinus limbatus*	2.91	2.25	1.71	1.81
L. Whitenack Donation 15	*Carcharhinus limbatus*	2.66	2.21	1.71	1.66
L. Whitenack Donation 1	*C. limbatus*, juvenile	2.6	1.54	1.24	1.32
L. Whitenack Donation 2	*C. limbatus*, juvenile	2.06	1.52	0.94	1.38
L. Whitenack Donation 3	*C. limbatus*, juvenile	2.03	1.49	0.98	1.52
L. Whitenack Donation 4	*C. limbatus*, juvenile	2.5	1.49	0.91	1.45
L. Whitenack Donation 5	*C. limbatus*, juvenile	2.31	1.4	0.93	1.42
L. Whitenack Donation 6	*C. limbatus*, juvenile	2.17	1.37	0.92	1.48
L. Whitenack Donation 7	*C. limbatus*, juvenile	1.88	1.4	1.12	1.34
L. Whitenack Donation 8	*C. limbatus*, juvenile	1.98	1.31	1.12	1.43
L. Whitenack Donation 9	*C. limbatus*, juvenile	2.17	1.25	1.02	1.41
L. Whitenack Donation 10	*C. limbatus*, juvenile	2.13	1.34	1.14	1.39
L. Whitenack Donation 11	*C. limbatus*, juvenile	2.25	1.32	1.11	1.27
L. Whitenack Donation 12	*C. limbatus*, juvenile	2.15	1.25	1.02	1.23
L. Whitenack Donation 1	*Sphyrna mokarran*	3.02	3.3	2.25	2.01
L. Whitenack Donation 3	*Sphyrna mokarran*	2.86	3.13	2.3	1.65
L. Whitenack Donation 4	*Sphyrna mokarran*	3.04	3.13	2.2	1.75

L. Whitenack Donation - Recent Shark Centra Measurements

Specimen #	Identification	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
L. Whitenack Donation 5	*Sphyrna mokarran*	9.61	9.6	5.08	9.08	9.99	2.8	1.84
L. Whitenack Donation 6	*Sphyrna mokarran*	9.46	9.42	4.97	8.72	9.89	2.7	2.2
L. Whitenack Donation 7	*Sphyrna mokarran*	9.54	9.47	4.88	8.99	9.98	3.25	2.01
L. Whitenack Donation 8	*Sphyrna mokarran*	9.43	9.49	4.99	8.86	10.04	2.36	2.25

L. Whitenack Donation - Recent Shark Centra Measurements

Specimen #	Identification	D Wall W	V Foram L	V Foram W	V Wall W
L. Whitenack Donation 5	*Sphyrna mokarran*	3.03	3.25	2.4	1.7
L. Whitenack Donation 6	*Sphyrna mokarran*	3.08	2.83	2.33	1.7
L. Whitenack Donation 7	*Sphyrna mokarran*	2.98	3.24	2.58	1.48
L. Whitenack Donation 8	*Sphyrna mokarran*	3.5	3.15	2.44	1.26

UCMP - Recent Shark Centra Measurements

UCMP 136058.3	*Trakis semifasciata*	8.6	8.58	9.01	6.78	7.75	7.02	2.51	1.32
UCMP 136058.4	*Trakis semifasciata*	8.87	8.65	9.5	6.85	7.44	7.65	2.37	1.28
UCMP 136058.5	*Trakis semifasciata*	9.27	8.89	9.69	6.89	8.01	7.7	3.14	1.13

UCMP - Recent Shark Centra Measurements

UCMP 136058.3	6.78	3.22	1.43
UCMP 136058.4	7.18	2.13	1.57
UCMP 136058.5	7.23	2.34	1.53

ANSP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
ANSP 308.1	Tert, DE	23.8	23.54	11.54	20.12	23.91	7.77	5.96	4.62
ANSP 308.2	Tert, DE	23.34	23.68	11.81	19.17	22.42	8.19	6.37	5.19
ANSP 308.3	Tert, DE	23.95	23.53	12.02	20.26	23.44	8.45	6.35	4.4
ANSP 308.5	Tert, DE	18.33	18.13	9.41	17.25	17.29	6.83	4.16	4.67
ANSP 3331	Tert, CO	7.78	7.83	5.38	7.34	8.06	4.1	2.43	0.9
ANSP 6480	Unknown	30.83	30.72	15.98	30.37	32.71	11.31	6.76	6.28
ANSP 7054	Tert, England	39.29	39.14	18.27	38.99	39.47	12.63	6.55	9.05
ANSP 7055	Mioc, NJ	32.88	32.33	12.59	33.17	32.15	5.4	6.42	5.27
ANSP 7056	Mioc, NJ	34.49	34.46	13.27	34.93	35.27	8.22	6.41	7.72
ANSP 7057	Mioc, NJ			13.42					
ANSP 7058	Mioc, NJ			13.68		34.76	8.09	5.94	7.4
ANSP 7059	Mioc, NJ			11.94					
ANSP 7060	Mioc, NJ	34.84	34.49	14.02	34.82		6.19	6.13	5.03
ANSP 7061	Mioc, NJ	32.63	33.69	14.11	33.77	35.18	8.1	6	7.88
ANSP 8040	Eoc, AL	25.65	25.61	13.82	25.08	24.92	9.99	6.05	5.84
ANSP 8131	Tert, VA	20.89	20.79	11.41	20.64	19.36	7.92	4.51	4.91
ANSP 14698	Tert, England	21.64	21.2	11.62	19.87	18.77	8.57	4.21	4.58
ANSP 15415.02	Tert, NJ	22.28	21.69	12.01	20.94	20.61	8.77	3.84	5.24
ANSP 15415.03	Tert, NJ	23.83	23.78	12.61	22.02	21.61	9.99	4.61	6.48
ANSP 15415.05	Tert, NJ	17.57	17.16	9.86	16.92	16.7	6.95	4.92	5.54
ANSP 15415.06	Tert, NJ	13.82	13.71	8.86	12.81	13.65	5.66	3.26	2.66
ANSP 15415.07	Tert, NJ	14.28	14.1	9.32	13.03	12.65	6.6	3.75	2.52
ANSP 15415.08	Tert, NJ	13.81	13.72	8.88	12.85	13.73	6.12	2.87	2.97
ANSP 15433	Mioc, MD	25.79	26.33	11.24	24.03	22.48	7.27	6.28	4.47
ANSP 20148.1	Pleist, FL	25.76	25.72	12.51	25.46	27.3	8.22	4.16	8.19
ANSP AF 1	Mioc, FL	24.66	24.03	21.75	19.84	14.15	11.56		
ANSP AF 2	Mioc, FL	25.95	24.54	16.87	21.84	19.3	13.61	4.28	4.56
ANSP AF 3	Mioc, FL	17.09	16.74	16.73	12.08	14.29	13.76	4.47	1.41
ANSP AF 4	Mioc, FL	14.81	14.5	10.76	11.35	10.94	8.07	3.19	2.2
ANSP AF 6	Mioc, FL	11.37	11.24	8.67	8.99	9.25	6.12	2.16	1.72

ANSP - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
ANSP 308.1	8.09	5.88	6.75
ANSP 308.2	9.06	5.12	5.43
ANSP 308.3	8.83	5.98	5.57
ANSP 308.5	6.95	4.4	7.33
ANSP 3331	4.02	2.37	1.16
ANSP 6480	11.68	5.34	9.58
ANSP 7054	12.96	7.88	11.87
ANSP 7055	6.63	5.79	7.36
ANSP 7056	8.6	6.42	9.09
ANSP 7057	8.45	4.97	9.08
ANSP 7058	8.4	6.03	9.58
ANSP 7059			
ANSP 7060	9.1	5.88	9.76
ANSP 7061	9.84	5.81	9.44
ANSP 8040	10.21	4.75	6.63
ANSP 8131	7.42	3.96	7.31
ANSP 14698	7.01	4.07	5.47
ANSP 15415.02	8.14	4.13	6.36
ANSP 15415.03	9.57	4.01	8.95
ANSP 15415.05	7.01	4.93	5.97
ANSP 15415.06	6.64	2.73	3.34
ANSP 15415.07	7.67	3.55	3.9
ANSP 15415.08	6.55	2.64	3.35
ANSP 15433	6.95	5.87	7.91
ANSP 20148.1	8.5	4.36	14.3
ANSP AF 1	15.22	6.07	5.07
ANSP AF 2	11.82		
ANSP AF 3	13.83	4.98	3.89
ANSP AF 4	8.1	3.91	3.71
ANSP AF 6	6.79	2.44	3.42

ANSP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
ANSP AF 7	Mioc, FL	12.38	12.37	10.11	10.62	10.74	6.58	2.69	2.35
ANSP AF 11	Mioc, FL	18.15	17.78	8.89	16.46	15.1	5.15	2.9	3.43
ANSP AF 13	Mioc, FL	11.87	11.44	5.98	10.77	10.27	2.83	2.32	2.51
ANSP BVA 1	Tert, VA	24.57	24.18	11.8	24.04	23.16	8.81	4.4	5.82
ANSP BVA 2	Tert, VA	25.38	24.89	11.51	25.01	22.36	8.56	5.45	6.04
ANSP BVA 3	Tert, VA	18.48	18.44	9.81	18.22	16.48	6.83	3.58	4.94
ANSP GM 3	Tert, FL	24.83	24.45	17.36	20.81	24.8	14.95	5.1	5.13
ANSP GM 5	Tert, FL	15.69	15.51	8.42	15.43	14.85	5.97	3.42	2.79
ANSP LCM 1	Plioc, NC	34.67	33.9	23.52	31.08	30.23	17.11	4.92	7.59
ANSP LCM 2	Plioc, NC	23.95	23.74	13.17	23.62	25.43	9.85	4.79	5.87
ANSP LCM 3	Plioc, NC	26.01	25.93	10.33	25.59	25.83	4.22	6.52	4.67
ANSP LCM 4	Plioc, NC	22.1	21.57	9.52	20.43	20.94	6.43	4.98	3.54
ANSP LCM 5	Plioc, NC	25.52	25.47	12.35	25.24	25.41	8.13	4.15	7.84
ANSP LCM 6	Plioc, NC	23.12	22.87	14.65	18.9	19.86	9.46	4.33	2.63
ANSP LCM 7	Plioc, NC	27.67	27.21	15.74	25.75	24.82	12.49	5.25	4.9
ANSP LCM 8	Plioc, NC	32.82	32.49	17.37	30.75	30.27	14.63	5.99	8.32
ANSP LCM 9	Plioc, NC	28.63	28.54	12.99	27.12	27.59	7.48	5.23	4.74
ANSP LCM10	Plioc, NC	21.74	21.45	14.22	19.93	21.05	10.5	5.22	4.92
ANSP LCM 12	Plioc, NC	24.79	23.43	12.84	21.8	22.04	8.46	4.57	5.95
ANSP LCM 13	Plioc, NC	25.12	25.1	15.54	23.01	26.97	12.45	5.4	2.29
ANSP LCM 14	Plioc, NC	24.38	24.16	11.22	23.07	21.18	7.21	3.99	4.47
ANSP LCM 15	Plioc, NC	21.64	21.54	12.75	21.29	19.76	9.47	5.34	2.25
ANSP LCM 16	Plioc, NC	18.3	17.92	15.4	17.74	15.24	12.46	2.57	3.84
ANSP LCM 17	Plioc, NC	24.11	24	16.96	20.03	21.3	12.93	4.32	4.97
ANSP LCM 18	Plioc, NC	22.24	22.11	10.42	22.46	20.09	5.01	9.17	7.07
ANSP LCM 19	Plioc, NC	15.13	15.09	13.76	12.79	12.78	11.55	2.99	2.16
ANSP LCM 20	Plioc, NC	16.6	16.34	12.88	14.08	14.33	9.78	2.9	3.05
ANSP LCM 21	Plioc, NC	22.32	21.45	11.06	21.2	19.11	8.18	4.4	6.32
ANSP LCM 22	Plioc, NC	18.95	18.79	13.07	17.13	15.69	10.36	2.52	5.41
ANSP LCM 23	Plioc, NC	18.92	18.87	7.17	18.04	16	5.65	3.65	3.44

ANSP - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
ANSP AF 7	7.99	2.58	3.11
ANSP AF 11	7.2	4.17	3.94
ANSP AF 13	3.47	2.86	4.44
ANSP BVA 1	8.86	2.67	16.24
ANSP BVA 2	9.01	5.94	6.93
ANSP BVA 3	7.53	3.22	9.95
ANSP GM 3	13.07	4.77	7.38
ANSP GM 5	5.95	3.04	4.18
ANSP LCM 1	16.42	7.06	8.38
ANSP LCM 2	8.18	3.91	7.6
ANSP LCM 3	4.29	5.75	5.28
ANSP LCM 4	6.63	4.69	5.4
ANSP LCM 5	8.86	4.7	12.92
ANSP LCM 6	9.85	3.81	5.55
ANSP LCM 7	13.33	6.06	8.92
ANSP LCM 8	13.65	5.7	17.02
ANSP LCM 9	6.41	6.58	6.52
ANSP LCM10	10.99	4.09	6.26
ANSP LCM 12	8.2	4.12	7.05
ANSP LCM 13	10.78	6.24	6.49
ANSP LCM 14	8.17	4.35	9.28
ANSP LCM 15	8.28	4.08	3.12
ANSP LCM 16	11.21	2.14	4.47
ANSP LCM 17	12.83	4.55	5.85
ANSP LCM 18	6.03	7.42	4.82
ANSP LCM 19	9.17	2.56	2.77
ANSP LCM 20	9.26	2.55	3.12
ANSP LCM 21	7.41	4.48	6.79
ANSP LCM 22	9.87	3.71	6.06
ANSP LCM 23	5.12	3.66	4.99

ANSP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
ANSP LCM 24	Plioc, NC	18.3	17.81	13.38	16.96	14.35	8.59	2.12	3.55
ANSP LCM 25	Plioc, NC	19.53	19.21	13.5	16.25	19.07	9.69	4.54	2.73
ANSP LCM 26	Plioc, NC	23.1	23	10.89	23.32	23.62	7.4	5.55	7.01
ANSP LCM 27	Plioc, NC	24.63	24.46	11.95	24.61	22.4	8.02	4.26	6.88
ANSP LCM 28	Plioc, NC	23.35	22.92	13.01	22.58	24.46	9.87	3.83	6.61
ANSP LCM 29	Plioc, NC	20.22	20.17	9.83	18.53	19.09	5.95	3.49	5.84
ANSP LCM 30	Plioc, NC	22.41	22.03	10.5	19.46	20	8.37	4.61	4.82
ANSP LCM 31	Plioc, NC	23.54	23.22	14.72	21.83	25.23	10.43	4.58	2.57
ANSP LCM 32	Plioc, NC	24.03	23.85	22.17	20.45	19.48	18.29	2.36	5.91
ANSP LCM 33	Plioc, NC	27.67	25.86	19.54	25.48	22.17	15.27	4.75	3.57
ANSP LCM 34	Plioc, NC	24.69	23.82	23.63	21.67	20.22	15.75	3	5.64
ANSP LCM 35	Plioc, NC	21.95	21.62	23.13	19.69	17.95	16.86	5.57	3.72
ANSP LCM 36	Plioc, NC	22.43	22	23.57	21.52	18.7	19.32	3.6	5.47
ANSP LCM 37	Plioc, NC	21.03	20.79	21.15	19.25	17.44	17.28	5.54	3.43
ANSP LCM 38	Plioc, NC	22.27	21.51	20.54	20.88	19.27	16.04	3	5.41
ANSP LCM 39	Plioc, NC	21.28	20.75	24.25	18.21	16.33	18.45	3.99	3.48
ANSP LCM 40	Plioc, NC	21.25	21.19	19.28	17.83	15.79	14.2	3.07	4.54
ANSP LCM 41	Plioc, NC	18.9	18.6	20.21	16.93	15.87	14.71	3.06	4.9
ANSP LCM 42	Plioc, NC	16.61	16.54	15.26	16.09	15.9	12.85	2.97	3.95
ANSP LCM 43	Plioc, NC	18.13	17.03	19.33	14.53	14.3	15.8	3.95	3.42
ANSP LCM 44	Plioc, NC	24.22	23.92	13.14	23.83	25.18	10.18	5.25	6.2
ANSP LCM 45	Plioc, NC	21.29	21.2	9.25	21.36	20.58	5.88	3.25	5.11
ANSP LCM 46	Plioc, NC	20.57	20.51	8.9	20.59	19.53	6.18	3.61	4
ANSP LCM 47	Plioc, NC	26.89	26.72	11.83	27.03	26.87	8.06	4.11	8.88
ANSP LCM 48	Plioc, NC	19.96	19.82	11.3	19.74	21.31	7.34	3.93	5.3
ANSP LCM 49	Plioc, NC	23.83	23.64	12.9	22.14	23.42	8.57	4.6	6.43
ANSP LCM 50	Plioc, NC	27.57	27.5	12.61	26.78	27.85	7.46	5.82	5.94
ANSP LCM 51	Plioc, NC	29.12	28.92	11.32	29.04	29.27	6.42	5.87	6.13
ANSP LCM 52	Plioc, NC	29.13	28.99	15.89	27.67	29.69	10.59	6.54	7.17
ANSP LCM 53	Plioc, NC	25.13	25.06	12.12	24.41	23.34	8.27	4.35	7.84

ANSP - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
ANSP LCM 24	9.4	2.47	5.07
ANSP LCM 25	9.82	4.3	4.92
ANSP LCM 26	8.14	5.01	10.23
ANSP LCM 27	8.56	4.31	8.67
ANSP LCM 28	10.31	4.92	6.63
ANSP LCM 29	6.42	4.3	6.83
ANSP LCM 30	8.98	4.99	6.45
ANSP LCM 31	9.2	7.14	6.84
ANSP LCM 32	18.73	3.54	5.77
ANSP LCM 33	15.74	4.71	4.65
ANSP LCM 34	19.24	3.66	7.56
ANSP LCM 35	17.41	3.52	4.74
ANSP LCM 36	19.05	3.71	5.37
ANSP LCM 37	16.3	3.7	4.59
ANSP LCM 38	15.51	3.72	8.08
ANSP LCM 39	18.9	2.76	4.56
ANSP LCM 40	12.98	3.41	6.36
ANSP LCM 41	15.83	3.65	4.89
ANSP LCM 42	10.24	2.79	5.19
ANSP LCM 43	15.88	2.5	4.56
ANSP LCM 44	8.93	4.72	5.87
ANSP LCM 45	4.97	3.43	7.14
ANSP LCM 46	5.54	2.54	7.27
ANSP LCM 47	8.85	4.63	14.02
ANSP LCM 48	7.55	3.46	6.13
ANSP LCM 49	8.86	4.76	10.58
ANSP LCM 50	7.91	4.63	7.92
ANSP LCM 51	5.93	6.64	6.7
ANSP LCM 52	10.26	5.14	7.96
ANSP LCM 53	9.01	4.16	8.22

ANSP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
ANSP LCM 54	Plioc, NC	25.77	25.58	11.08	25.84	24.98	7.68	4.67	7.79
ANSP LCM 55	Plioc, NC	24.66	24.66	12.27	24.55	25.75	8.63	4.09	6.85
ANSP LCM 56	Plioc, NC	21.84	21.79	12.33	20.98	22.37	8.68	4.17	4.07
ANSP LCM 57	Plioc, NC	24.44	24.4	10.39	23.76	20.43	9.82	5.8	4.4
ANSP LCM 58	Plioc, NC	21.26	21.14	10.21	21.33	19.66	6.46	5.19	5.71
ANSP LCM 59	Plioc, NC	13.35	13.04	9.29	11.84	11.71	6.93	2.83	2.06
ANSP LCM 60	Plioc, NC	18.36	18.33	11.18	17.45	17.6	7.73	5.27	4.25
ANSP LCM 61	Plioc, NC	16.75	16.25	12.83	15.31	14.85	9.53	2.72	2.71
ANSP LCM 63	Plioc, NC	17.64	17.42	9.06	16.32	16.75	6.36	3.39	4.64
ANSP LCM 64	Plioc, NC	18.51	18.13	8.6	15.58	18.56	4.98	5.27	2.68
ANSP LCM 65	Plioc, NC	16.98	16.67	9.62	14.99	16.44	6.24	3.52	3.83
ANSP LCM 66	Plioc, NC	16.54	15.99	9	13.77	15.04	6.39	3.7	2.35
ANSP LCM 67	Plioc, NC	19.12	18.94	9.18	18.12	20.24	5.58	4.25	2.91
ANSP LCM 68	Plioc, NC	19.01	18.49	14.58	18.53	17.92	11.81	4.1	2.97
ANSP LCM 69	Plioc, NC	33.01	31.46	25.47	31.82	27.12	20.61	5.73	6.31
ANSP LCM 70	Plioc, NC	20.93	20.54	22.86	14.31	16.89	15.18	4.71	2.51
ANSP LCM 71	Plioc, NC	20.7	19.47	18.64	14.43	15.39	16.21	4	1.67
ANSP LCM 72	Plioc, NC	29.35	29.03	12.51	27.44	27.86	7.63	4.49	8.44
ANSP LCM 73	Plioc, NC	15.38	15.36	7.67	14.69	14.77	4.78	2.93	2.84
ANSP LCM 75	Plioc, NC	13.07	12.99	7.75	11.69	12.04	4.91	2.14	3.37
ANSP LCM 76	Plioc, NC	16.75	16.71	10.1	13.97	14.2	8.24	3.23	1.77
ANSP LCM 78	Plioc, NC	16.52	16.16	13.02	14.96	13.87	9.7	2.62	4
ANSP LCM 79	Plioc, NC	10.74	10.71	5.92	9.96	10.38	4.27	2.23	3.13
ANSP LCM 80	Plioc, NC	11.03	10.65	9.36	9.02	10.16	6.91	3.05	1.77
ANSP LCM 81	Plioc, NC	9.35	9.18	6.17	8.17	8.68	4.64	1.81	2.48
ANSP LCM 82	Plioc, NC	13.19	13	7.41	11.69	12.16	4.31	2.81	2.14
ANSP LCM 83	Plioc, NC	12.86	12.85	6.35	12.69	12.55	4.54	2.69	4.26
ANSP LCM 84	Plioc, NC	14.68	14.3	11.21	12.91	10.77	8.8	2.74	1.67
ANSP LCM 86	Plioc, NC	12.58	12.47	6.18	10.97	12.08	4.7	3.03	2.46
ANSP LCM 88	Plioc, NC	24.41	24.27	13.03	22.86	20.79	8.17	5.5	3.75

ANSP - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
ANSP LCM 54	7.71	5.1	10.68
ANSP LCM 55	9.1	4.24	12.34
ANSP LCM 56	8.84	3.02	6.32
ANSP LCM 57	9.89	5.5	4.5
ANSP LCM 58	6.35	5.31	7.2
ANSP LCM 59	5.5	2.38	2.98
ANSP LCM 60	8.7	4.25	5.58
ANSP LCM 61	9.27	2.65	4.63
ANSP LCM 63	5.45	3.73	5.85
ANSP LCM 64	5.5	3.79	4.48
ANSP LCM 65	5.93	3.15	4.28
ANSP LCM 66	7.33	3.68	5.51
ANSP LCM 67	5.46	4.09	5.65
ANSP LCM 68	11.16	4.42	3.82
ANSP LCM 69	21.02	5.68	7.85
ANSP LCM 70	15.06	4.72	3.05
ANSP LCM 71	16.18	4.25	3.04
ANSP LCM 72	8.07	5.01	7.41
ANSP LCM 73	4.62	2.72	3.76
ANSP LCM 75	5.27	2.74	3.87
ANSP LCM 76	8.55	3.25	3.21
ANSP LCM 78	8.18	2.1	4.07
ANSP LCM 79	4.24	2.16	4.79
ANSP LCM 80	7.63	2.91	3.8
ANSP LCM 81	4.71	1.68	2.99
ANSP LCM 82	4.78	3.08	4
ANSP LCM 83	4.77	2.3	4.92
ANSP LCM 84	6.75	2.87	2.64
ANSP LCM 86	4.75	3.12	3.49
ANSP LCM 88	9.96	4.87	6.41

ANSP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
ANSP LCM 89	Plioc, NC	28.19	28.08	18.51	27.18	27.78	13.61	5.7	4.87
ANSP LCM 90	Plioc, NC	27.7	26.72	12.37	25.41	23.98	8.35	6.02	5.05
ANSP LCM 91	Plioc, NC	23.96	23.92	8.98	23.55	24.54	4.37	7.76	2.78
ANSP LCM 92	Plioc, NC	25.58	24.53	15.07	22.95	24.5	12.47	4.07	5.05
ANSP LCM 93	Plioc, NC	19.27	18.65	10.82	18.75	19.8	7.5	3.9	3.86
ANSP LCM 94	Plioc, NC	29.05	28.89	11.94	28.5	22.66	9.05	6.82	5.27
ANSP LCM 96	Plioc, NC	29.67	29.34	11.74	29.22	26.77	7.11	7.47	5.54
ANSP LCM 97	Plioc, NC	26.86	26.06	10.97	24.72	26.28	6.8	5.46	5.17
ANSP LCM 102	Plioc, NC	22.69	21.29	24.77	18.81	17.1	19.32	3.65	3.52
ANSP LCM 103	Plioc, NC	23.31	19.75	23.05	19.54	17.86	19.85	3.06	4.52
ANSP LCM 104	Plioc, NC	40.74	39.42	16.5	38.51	40.28	14.4	7.51	8.07

ANSP - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
ANSP LCM 89	14.62	5.43	6.82
ANSP LCM 90	9.16	4.55	8.4
ANSP LCM 91	4.02	6.65	4.82
ANSP LCM 92	12.25	3.67	6.97
ANSP LCM 93	6.51	3.46	4.79
ANSP LCM 94	8.88	5.77	8.2
ANSP LCM 96	5.45	6.38	13.53
ANSP LCM 97	12.07	6.51	5.93
ANSP LCM 102	19.1	3.32	3.62
ANSP LCM 103	19.46	4.26	5.33
ANSP LCM 104	10.59	8.63	9.09

BMNH - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
BMNH 1309	Eoc, SC	25.58	25.37	14.15	23.66	24.52	9.9	5.65
BMNH 1965	Mioc, Malta	66.42	64.86	39.04	66.66	47.74	34.51	7.5
BMNH 4645.1	Eoc, AL	23.78	23.75	12.36	22.98	24.16	8.16	3.82
BMNH 4645.2	Eoc, AL	22.32	22.25	10.93	22.71	20.29	8.08	4.91
BMNH 4645.3	Eoc, AL	13.03	13.02	5.77	12.42	12.7	3.29	3.23
BMNH 4645.4	Eoc, AL	16.94	16.77	9.6	16.01	15.92	6.17	3.1
BMNH 4645.5	Eoc, AL	12.96	12.84	5.62	12.46	12.05	3.82	3.29
BMNH 5571.1	Tert, England	26.29	25.3	12.95	24.43	21.77	10.62	4.23
BMNH 5571.3	Tert, England	25.04	24.77	13.3	23.94	21.74	10.36	5.76
BMNH 5571.4	Tert, England	25.55	24.93	12.59	24.27	20.75	10.05	6.05
BMNH 5752.1	Eoc, AL	49.57	49.39	27.35	47.85	39.07	24.29	8.16
BMNH 13794	Mioc, Malta	49.82	49.59	24.34	47.95	34.86	21.17	7.14
BMNH 13795	Mioc, Malta	32.04	30.43	24.62	28.86	28.17	19.05	6.05
BMNH 13796	Mioc, Malta	49.43	49.08	23.87	48.84	35.72	17.14	9.08
BMNH 13797	Mioc, Malta	33.49	33.2	19.4	31.52	29.35	15.11	4.3
BMNH 13798.2	Mioc, Malta	15.15	14.72	6.13	15.52	11.81	3.69	5.01
BMNH 13799	Mioc, Malta	29.1	27.98	18.18	26.61	27.67	13.42	5.7
BMNH 35611a.1	Eoc, AL	20.71	20.68	12.99	19.71	20.3	9.17	4.6
BMNH 35611a.2	Eoc, AL	24.15	24.11	12.38	23.5	24.07	8.83	4.92
BMNH 35611a.3	Eoc, AL	14.4	14.06	6.96	14.01	12.9	4.89	3.56
BMNH 35611a.4	Eoc, AL	13.47	13.44	7.12	13.65	11.84	4.98	3.02
BMNH 35611a.5	Eoc, AL	19.3	19.29	11.65	18.55	18.05	8.71	4.42
BMNH 35611a.6	Eoc, AL	19	18.19	9.3	19.31	18.27	5.81	5.45
BMNH 35611a.7	Eoc, AL	11.75	11.48	5.02	11.05	11.24	3.1	3.34
BMNH 35611a.8	Eoc, AL	17.52	17.31	9.43	17.37	16.11	6.59	3.44

BMNH - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
BMNH 1309	3.23	10.45	5.98	5.85
BMNH 1965	9.49	34.69	7.52	6.44
BMNH 4645.1	8.15	8.7	4.46	13.74
BMNH 4645.2	5.66	7.3	4.29	7.69
BMNH 4645.3	1.57	3.99	4.27	3.69
BMNH 4645.4	4.09	6.23	3.65	6.3
BMNH 4645.5	2.26	3.66	2.59	3.1
BMNH 5571.1	3.94	8.9	7.94	5
BMNH 5571.3	1.89	10.53	7.03	5.32
BMNH 5571.4	3.45	10.27	6.03	10.1
BMNH 5752.1	5.1	20.67	6.22	9.92
BMNH 13794	5.07	18.62	3.63	20.69
BMNH 13795	5.61	17.29	4.48	6.62
BMNH 13796	5.19	17.16	8.78	8.71
BMNH 13797	7.26	13.73	3.6	9.83
BMNH 13798	3.97	3.36	6.38	4.38
BMNH 13799	4.8	12.99	6.08	6.26
BMNH 35611a.1	5.47	10.28	4.74	6.51
BMNH 35611a.2	4.97	9.55	5.47	11.19
BMNH 35611a.3	3.82	5.37	3.39	3.6
BMNH 35611a.4	2.82	4.87	3.42	4.38
BMNH 35611a.5	4.22	8.9	5.26	6.69
BMNH 35611a.6	6.42	4.49	6.87	6.33
BMNH 35611a.7	1.13	3.52	2.79	2.24
BMNH 35611a.8	4.4	7.22	4.05	5.06

CMMV - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
CMM V 815	Mioc, MD	41.88	40.75	16.8	37.65	36.98	10.95	11.88	3.83
CMMV 1013	Mioc, MD	32.6	31.46	14.95	31.19	30.88	10.47	5.21	8.99
CMMV 1131	Mioc, MD	43.21	42.38	19.41	42.16	40.35	12.81	8.4	6.86
CMMV 1133	Mioc, MD	35.15	34.26	16.42	33.14	33.53	10.34	4.4	9.22
CMMV 1139	Mioc, MD	39.33	38.64	33.97	29.56	32.26	28.1	6.28	2.9
CMMV 1575	Mioc, MD	40.28	40.16	19.75	38.71	40	13.55	7.14	9.34
CMMV 1577	Mioc, MD	32.43	32.68	16.28	33.14	31.82	13.02	7.52	5.56
CMMV 1578	Mioc, MD	18.92	18.81	7.77	18.63	19.54	4.74	4.12	5.36
CMMV 1581	Mioc, MD	14.13	14.09	7.03	13.28	13.76	5.1	2.93	2.63
CMMV 1582	Mioc, MD	19.73	19.58	9.51	19.73	17.5	6.83	3.54	5.87
CMMV 1652.01	Mioc, MD	36.06	35.69	15.8	36.11	34.14	10.33	6.15	7.77
CMMV 1652.02	Mioc, MD	35.21	35.08	15.13	35.68	33.54	10.8	6.11	6.05
CMMV 1652.03	Mioc, MD	34.35	34.62	15.27	35.42	34.15	10.07	6.33	8.59
CMMV 1652.04	Mioc, MD	35.12	34.83	16.16	36.15	33.3	10.19	6.82	8.97
CMMV 1652.05	Mioc, MD	35.03	34.94	15.93	35.96	34.19	10.49	7.05	9.1
CMMV 1652.06	Mioc, MD	35.06	34.8	15.23	35.67	34.13	10.12	6.41	7.97
CMMV 1652.07	Mioc, MD	35.3	34.94	15.59	35.91	34.33	10.38	6.73	8.45
CMMV 1652.08	Mioc, MD	35.27	35.17	14.78	35.51	33.14	10.1	6.2	6.77
CMMV 1652.09	Mioc, MD	35.3	34.89	15.17	35.77	34.1	9.69	6.4	8.64
CMMV 1652.10	Mioc, MD	35.38	34.55	15.2	35.76	33.97	9.9	6.5	8.62
CMMV 1784	Plioc, NC	31.06	30.88	18.57	30.22	31.27	14.57	6.15	7.36
CMMV 1887	Mioc, MD	48.35	48.22	21.66	45.82	45.28	15.95	7.87	9.64

CMMV - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
CMM V 815	11.91	12.13	7.6
CMMV 1013	11.57	4.88	13.99
CMMV 1131	13.52	9.2	11.2
CMMV 1133	11.1	6.61	11.21
CMMV 1139	29.51	4.9	6.03
CMMV 1575	11.45	8.47	12.13
CMMV 1577	10.99	5.4	7.21
CMMV 1578	4.85	4.15	5.45
CMMV 1581	4.85	2.83	4.2
CMMV 1582	6.67	3.06	7.18
CMMV 1652.01	10.73	5.16	13.02
CMMV 1652.02	10.18	5.75	17.01
CMMV 1652.03	10.95	6.27	9.67
CMMV 1652.04	10.61	5.95	11.08
CMMV 1652.05	10.85	5.92	10.58
CMMV 1652.06	10.56	5.16	12.75
CMMV 1652.07	9.72	5.6	10.74
CMMV 1652.08	9.96	6.38	13.8
CMMV 1652.09	10.56	5.66	11.16
CMMV 1652.10	11.1	5.4	11.93
CMMV 1784	14.19	6.96	10.21
CMMV 1887	13.68	7.99	17.13

UF - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W	D Wall W
UF 3245.1	Mioc, FL	2.28	22.03	10.29	21.79	23.5	6.34	4.66	6.27
UF 3245.2	Mioc, FL	22.01	22	10.12	21.42	23.44	6.3	4.67	6.1
UF 3245.3	Mioc, FL	22.47	22.22	10.1	21.87	23.8	5.98	4.68	6.76
UF 3245.4	Mioc, FL	16.85	16.76	7.78	16.54	17.45	4.62	4.82	2.51
UF 3245.5	Mioc, FL	16.52	16.23	7.74	16.08	16.92	4.92	4.17	2.72
UF 92276	Mioc, FL	24.41	24.37	11.33	25.29	23	7.43	4.21	7.48
UF 92277	Mioc, FL	13.12	13.02	7.12	11.55	12.07	5.77	3.44	1.79
UF 92280	Mioc, FL	11.66	11.48	6.03	11.2	12.62	3.79	2.28	2.14
UF 92281	Mioc, FL	44.9	43.79	22.68	42.01	42.5	16.65	8.06	8.45
UF 92282	Mioc, FL	14.84	12.71	6.41	13.4	13.7	4.61	2.87	1.16
UF 92289	Mioc, FL	12.86	12.76	10.1	10.79	13.38	8.27	2.47	1.31
UF 92295	Mioc, FL	3.98	3.9	2.79	3.6	3.39	1.5	1.16	1.77
UF 122234	Pleist, FL	15.49	15.1	17.93	12.77	9.64			
UF 122858	Pleist, FL	11.14	10.24	11.5	8.79	8.35			
UF 123154	Pleist, FL	15.39	15.06	18.54	12.97	11.46	16.26	2.52	3.14
UF 128906	Plioc, FL	43.2	42.89	21.27	40.44	36.74	16.08	6.51	5.2

UF - Fossil Shark Centra Measurements

Specimen #	V Foram L	V Foram W	V Wall W
UF 3245.1	6.92	4.86	7.84
UF 3245.2	6.82	4.99	7.96
UF 3245.3	6.58	5.01	7.75
UF 3245.4	4.66	5.42	4.7
UF 3245.5	4.46	5.04	4.31
UF 92276	8.44	4.38	10.88
UF 92277	2.74	5.82	3.5
UF 92280	3.84	2.05	3.66
UF 92281	16.79	6.94	10.62
UF 92282	3.43	2.81	4
UF 92289	7.79	2.58	3.69
UF 92295	1.15	0.96	2.11
UF 122234			
UF 122858			
UF 123154	15.76	3.09	4.33
UF 128906	18.11	6.38	19.11

USNM - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
USNM 464	Mioc, MC	34.28	33.89	14.16	34.21	35.73	7.63	7.92
USNM 24914.01	Mioc, MD	19.84	19.69	10.92	19.19	20.41	7.33	3.36
USNM 24914.02	Mioc, MD	19.99	19.63	10.72	19.21	20.49	7.09	3.3
USNM 24914.03	Mioc, MD	20.08	20.05	10.47	19.86	20.2	7.47	3.56
USNM 24914.04	Mioc, MD	20.27	20	10.55	19.99	20.01	6.94	3.45
USNM 24914.05	Mioc, MD	19.98	19.94	10.5	19.93	20.17	7.06	3.33
USNM 24914.06	Mioc, MD	20.13	20.01	10.48	20.08	20.01	6.9	3.24
USNM 24914.07	Mioc, MD	20.22	19.99	10.46	19.84	19.96	6.96	3.25
USNM 24914.08	Mioc, MD	20.24	20.22	10.46	20.11	19.86	6.96	3.29
USNM 24914.09	Mioc, MD	20.34	20.22	10.27	20.17	19.93	6.84	3.45
USNM 24914.10	Mioc, MD	20.29	20.29	10.38	20.05	19.61	6.83	3.2
USNM 24914.11	Mioc, MD	20.12	20.04	10.4	19.84	19.65	6.92	3.38
USNM 24914.12	Mioc, MD	20.08	20.06	10.29	19.86	19.69	7.08	3.24
USNM 24914.13	Mioc, MD	20.1	20.01	10.37	19.77	19.91	6.92	3.35
USNM 288014	Plioc, NC	19.24	18.39	19.41	14.6	17.43	13.89	2.16
USNM 288017	Plioc, NC	28.56	27.59	10.33	27.7	28.81	6.08	6.82
USNM 288020	Plioc, NC	31.21	30.99	13.36	31.03	32.45	7.38	8.06
USNM 288023	Plioc, NC	32.75	32.27	13.24	30.71	30.89	6.99	8.4
USNM 288026	Unknown	33.87	31.33	21.47	28.29	28.36	15.85	4.71
USNM 288027	Unknown	33.01	30.56	21.57	28.93	28.22	17.2	4.9
USNM 288037	Unknown	39.82	39.77	19.11	38.28	39.03	12.4	7.58
USNM 288039	Plioc, NC	42.24	41.93	18.61	41.34	41.87	9.68	9.98
USNM 288041	Unknown	39.88	38.32	29.91	28.07	30.47	23.51	6.94
USNM 288042	Plioc, NC	53.19	53.05	24.26	52.87	51.84	15.61	10.91
USNM 288043	Plioc, NC	45.51	45.2	32.9	38.8	37.48	25.94	7.11
USNM 288045	Plioc, NC	49.89	49.36	21.63	47.76	47.03	15.6	10.27
USNM 288049	Plioc, NC	43.78	43.56	37.65	31.81	33.06	29.54	8.42
USNM 288051	Plioc, NC	49.12	47.2	43.72	27.66	35.34	30.48	7.72
USNM 288055	Plioc, NC	41.88	41.83	35.75	32.66	32.67	29.37	8.05
USNM 288056.1	Plioc, NC	45.17	43.17	39.85	35.75	35.06	32.37	7.14

USNM - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
USNM-V-464	5.97	7.83	7.59	6.51
USNM 24914.01	6.2	7.8	3.42	12.03
USNM 24914.02	6.32	7.82	3.28	12.33
USNM 24914.03	5.98	7.48	2.91	12.93
USNM 24914.04	5.75	7.65	3.15	12.84
USNM 24914.05	6.14	7.4	3.16	12.7
USNM 24914.06	6.31	7.51	3.12	12.58
USNM 24914.07	6.33	7.33	3.1	12.57
USNM 24914.08	6.11	7.41	3.07	12.75
USNM 24914.09	5.95	7.16	3.13	13.15
USNM 24914.10	6.23	7.23	3.24	12.06
USNM 24914.11	6.07	7.63	3.57	11.87
USNM 24914.12	6.24	7.62	3.44	11.44
USNM 24914.13	6.26	7.81	3.51	10.91
USNM 288014	3.63	15.55	2.55	4.58
USNM-V-288017	5.98	5.22	6.25	5.87
USNM-V-288020	4.447	7.36	6.55	5.4
USNM-V-288023	4.98	7.54	8	5.67
USNM 288026	5.18	16.62	4.52	7.16
USNM 288027	4.97	17.71	4.62	7.41
USNM 288037	7.19	12.28	10.36	11.24
USNM-V-288039	7.65	13.05	12.31	10.2
USNM 288041	8.49	22.07	6.34	16.12
USNM-V-288042	8.81	15.96	13.7	14.31
USNM 288043	6.61	26.74	5.81	8.19
USNM-V-288045	9.8	16.48	10.84	16.24
USNM 288049	4.25	29.56	8.63	5
USNM 288051	7.91	31.35	7.16	8.21
USNM 288055	7.5	28.55	8.65	8.47
USNM 288056.1	6.62	31.46	8.39	6.94

USNM - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
USNM 288057	Plioc, NC	47.72	47.16	40.22	41.6	35.19	33.37	7.53
USNM 290319	Plioc, NC	35.5	36.14	16.4	36.36	35.53	9.9	8.11
USNM 369890	Mioc, MD	38.88	38.62	17.8	37.97	37.01	13.07	8.21
USNM 435324.01	Plioc, NC	10.82	10.62	7.49	10.15	10.38	5.48	2.6
USNM 459870	Plioc, NC	23.63	23.44	23.51	19.97	22.32	20.18	5.56
USNM 467529	Plioc, NC	46.56	46.25	20.1	46.25	42.95	11.03	12.54
USNM 467530	Plioc, NC	49.91	49.53	23.45	47.81	49.61	18.19	11.34
USNM 494463.01	Mioc, MD	33.32	33.31	16.71	33.4	34.84	11.54	6.89
USNM 494463.02	Mioc, MD	33.3	33.27	16.72	33.4	34.99	13.03	7.1
USNM 494463.03	Mioc, MD	33.52	33.37	16.13	33.08	33.19	12	6.42
USNM 494463.04	Mioc, MD	33.5	33.15	16.19	32.8	34.29	11.95	8.29
USNM 494463.05	Mioc, MD	34.73	34.04	17.8	33.9	34.55	12.41	6.45
USNM 494463.06	Mioc, MD	34.12	33.95	16	33.53	34.51	11.83	6.37
USNM 494463.07	Mioc, MD	34.06	33.71	17.68	32.55	33.57	12.88	6.25
USNM 494463.08	Mioc, MD	34.55	34.06	17.85	33.42	35.78	13.22	6.83
USNM 494463.09	Mioc, MD	33.97	34.09	17.51	32.93	34.41	12.8	5.99
USNM 494463.10	Mioc, MD	34.23	33.85	16.68	32.29	33.51	10.73	6.39
USNM 494463.11	Mioc, MD	34.31	33.82	16.33	31.74	33.7	11.48	6.34
USNM 494464	Plioc, NC	43.92	42.26	32.15	37.12	32.02	24.51	6.49
USNM 494465	Plioc, NC	49.12	48.05	3887	32.17	35.19	32.8	6.83
USNM 494466	Plioc, NC	57.8	57.47	48.24	51.41	55.68	37.93	10.73
USNM 494467	Plioc, NC	64.53	61.01	41.06	60.15	66.51	32.36	12.92

USNM - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
USNM 288057	5.2	33.59	7.9	6.87
USNM-V-290319	5.01	9.6	6.9	8.04
USNM 369890	7.03	13.43	8.69	11
USNM 435324.01	2.91	5.73	2.6	3.36
USNM 459870	2.27	19.87	6.15	4.28
USNM-V-467529	9.1	12.21	9.33	10.36
USNM-V-467530	7.34	16.85	13.19	15.63
USNM 494463.01	9.51	14.12	5.59	11.61
USNM 494463.02	9.5	14.54	5.13	12.9
USNM 494463.03	7.93	14.67	5.83	13.98
USNM 494463.04	8.08	14.6	5.36	14.75
USNM 494463.05	7.45	14.92	5.8	15.34
USNM 494463.06	7.8	14.58	6.68	15.23
USNM 494463.07	8.24	14.01	6.21	15.3
USNM 494463.08	7.95	14.23	6.67	16.44
USNM 494463.09	7.73	12.8	6.6	15.4
USNM 494463.10	7.83	12.91	6.54	15.37
USNM 494463.11	7.54	13.24	6.19	16
USNM 494464	6.23	24.64	7.79	6.77
USNM 494465	5.67	28.85	6.9	9.74
USNM 494466	7.13	35.91	11.83	25.05
USNM 494467	11.26	29.89	12.19	14.24

SDNHM - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
SDNHM 25782	Plioc, CA	22.38	21.77	11.98	20.87	20.81	8.33	4.52
SDNHM 28495	Mioc, CA	19.87	19.28	23.85	11.34	12.71	17.92	3.07
SDNHM 61933.01	Plioc, CA	6.79	6.79	4.87	6.06	5.82	4.05	1.53
SDNHM 61933.02	Plioc, CA	7.49	7.4	5.21	6.52	6.73	3.73	1.86
SDNHM 61933.03	Plioc, CA	7.27	7.21	5.4	6.24	6.77	4.44	2.3
SDNHM 61933.04	Plioc, CA	7.48	7.38	5.3	6.49	6.23	4.29	1.66
SDNHM 61933.06	Plioc, CA	9.17	9.08	5.43	8.74	7.64	3.87	1.88
SDNHM 61933.07	Plioc, CA	8.67	5.57	7.38	7.05	7.69	4.66	2.29
SDNHM 61933.08	Plioc, CA	10.33	10.24	6.46	8.77	10.1	4.93	2.41
SDNHM 61933.09	Plioc, CA	10.75	10.01	7.79	8.24	9.64	6.41	2.24
SDNHM 61933.10	Plioc, CA	11.8	11.68	8.12	9.4	9.3	6.27	2.39
SDNHM 61933.11	Plioc, CA	11.51	11.44	8.94	9.86	9.97	6.16	3.21
SDNHM 61933.12	Plioc, CA	10.95	10.87	11.86	8.06	9.08	9.13	2.56
SDNHM 61933.13	Plioc, CA	10.67	10.64	8.81	8.45	10.7	7.3	2.84
SDNHM 61933.14	Plioc, CA	11.44	11.32	10.77	8.06	8.59	8.07	2.72
SDNHM 61933.15	Plioc, CA	12.16	12.03	9.33	8.74	11.45	7.51	2.92
SDNHM 61933.16	Plioc, CA	14.06	13.99	13.19	10.99	12.39	10.25	2.97
SDNHM 61937.01	Plioc, CA	36.95	36.55	20.08	33.61	33.61	14.7	6.8
SDNHM 61937.02	Plioc, CA	24.23	24.11	10.45	23.15	20.61	7.41	4.18
SDNHM 63154	Plioc, CA	36.14	35.51	21.74	32.43	32.47	14.79	7.7
SDNHM 65993	Plioc, CA	21.01	20.55	12.88	18.17	18	9.2	4.08
SDNHM 65995	Plioc, CA	23.1	22.7	14.23	20.89	21.08	10.33	5.25
SDNHM 71142.01	Plioc, CA	16.39	15.62	18.74	9.14	11.54	16.03	2.77
SDNHM 71142.02	Plioc, CA	14.5	14.03	14.5	8.76	10.33	12.43	3.29
SDNHM 71142.03	Plioc, CA	13.97	13.7	13.79	9.54	11.24	12.07	3.1
SDNHM 71142.04	Plioc, CA	14	13.94	7.92	12.05	12.9	5.47	3.55
SDNHM 71142.05	Plioc, CA	14.17	14.15	14.2	9.49	11.4	12.07	3.16
SDNHM 71142.06	Plioc, CA	13.89	13.97	10.37	11.38	11.76	8.74	3.42
SDNHM 71142.08	Plioc, CA	10.58	10.12	13.46	6.95	7.99	11.62	3.52
SDNHM 71142.09	Plioc, CA	13.19	12.99	9.12	11.58	10.55	7.48	4.26

SDNHM - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
SDNHM 25782	4.56	9.41	4.68	4.76
SDNHM 28495	2.09	20.51	4.08	2.54
SDNHM 61933.01	1.19	3.71	1.45	1.7
SDNHM 61933.02	0.86	3.9	2.11	1.93
SDNHM 61933.03	0.71	4.35	2.24	1.77
SDNHM 61933.04	1.34	4.1	1.37	1.78
SDNHM 61933.06	0.99	3.71	1.57	2.43
SDNHM 61933.07	1.56	5.26	2.54	1.97
SDNHM 61933.08	1.38	4.9	2.19	3.28
SDNHM 61933.09	2.21	5.53	2.17	3.1
SDNHM 61933.10	2.14	5.76	2.67	2.37
SDNHM 61933.11	2.03	7.14	2.79	2.24
SDNHM 61933.12	1.32	9.35	2.53	2.32
SDNHM 61933.13	1.24	6.83	2.45	3.03
SDNHM 61933.14	0.61	9.02	2.28	2.59
SDNHM 61933.15	1.38	7.6	2.51	2.32
SDNHM 61933.16	2.66	9.7	321	6.05
SDNHM 61937.01	7.27	14.41	7.36	16.91
SDNHM 61937.02	1.66	5.21	6.02	8.07
SDNHM 63154	6.66	16.66	6.63	7.53
SDNHM 65993	4.19	9.47	3.99	4.89
SDNHM 65995	5.6	9.75	5.32	7.23
SDNHM 71142.01	1.88	16.89	3.04	2.39
SDNHM 71142.02	1.53	13.23	2.7	2.74
SDNHM 71142.03	2.26	12.35	2.88	3.02
SDNHM 71142.04	2.07	6.12	3.03	3.51
SDNHM 71142.05	2.06	11.01	3.05	2.82
SDNHM 71142.06	3.08	1.51	3.14	6.4
SDNHM 71142.08	0.79	10.37	3.59	0.89
SDNHM 71142.09	3.34	6.33	3.96	6.32

SDNHM - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
SDNHM 71142.10	Plioc, CA	15.14	11.79	12.71	7.81	9.19	10.2	2.48
SDNHM 71142.12	Plioc, CA	12.28	12.14	8.73	10.53	9.3	6.78	4.33
SDNHM 71142.13	Plioc, CA	10.23	10.08	7.61	8.12	8.24	6.15	2.85
SDNHM 71142.14	Plioc, CA	10.29	10.06	10.01	8.29	9.09	8.4	2.44
SDNHM 71142.16	Plioc, CA	9.4	8.68	7.62	7.07	6.66	6.19	2.79
SDNHM 71142.17	Plioc, CA	10.69	10.39	7.22	7.99	8.44	5.28	2.35
SDNHM 71142.19	Plioc, CA	10.62	8.82	10.89	7.41	7.9	8.98	2.86
SDNHM 71142.20	Plioc, CA	9.33	9.29	8.52	6.95	7.75	7.35	3.38
SDNHM 71142.21	Plioc, CA	11.05	10.71	7.14	9.19	9.9	5.43	2.51
SDNHM 71142.22	Plioc, CA	9.34	9.34	7.04	7.1	8.39	4.83	2.3
SDNHM 71142.23	Plioc, CA	9.37	9.07	5.12	7.67	8.2	4.26	2.22
SDNHM 71142.24	Plioc, CA	7.99	7.59	5.11	6.45	6.33	3.94	2.19
SDNHM 71142.25	Plioc, CA	7.51	7.48	4.43	6.48	6.65	3.16	1.79
SDNHM 71142.27	Plioc, CA	7.09	6.96	5.43	6.1	5.58	3.59	1.79
SDNHM 71142.28	Plioc, CA	5.1	5.08	3.91	4.5	5.03	2.77	1.52
SDNHM 71142.29	Plioc, CA	6.13	6.12	3.82	5.42	5	3.14	1.72
SDNHM 71143	Plioc, CA	38.39	38.05	31.34	33.29	40.15	25.62	6.87
SDNHM 75551	Plioc, CA	6.6	6.52	5.44	5.62	5.18	3.3	1.48

SDNHM - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
SDNHM 71142.10	1.48	11.51	2.55	1.53
SDNHM 71142.12	2.29	6.36	3.79	4.23
SDNHM 71142.13	0.89	5.84	2.48	2.54
SDNHM 71142.14	1.43	8.63	3.24	1.98
SDNHM 71142.16	0.39	6.3	2.35	1.09
SDNHM 71142.17	1.76	5.36	2.52	2.26
SDNHM 71142.19	0.9	8.02	2.57	1.39
SDNHM 71142.20	0.95	7.39	1.63	2.13
SDNHM 71142.21	0.92	5.58	2.02	2.22
SDNHM 71142.22	1.63	5.51	2.17	1.86
SDNHM 71142.23	1.33	4.01	2.05	1.33
SDNHM 71142.24	0.76	3.62	2.09	1.48
SDNHM 71142.25	0.84	2.73	1.84	1.64
SDNHM 71142.27	0.92	3.98	1.51	1.59
SDNHM 71142.28	0.95	3.19	1.49	1.24
SDNHM 71142.29	0.5	2.87	1.05	1.04
SDNHM 71143	6.82	25.04	7.04	8.09
SDNHM 75551	1.61	3.21	1.5	1.57

UCMP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
UCMP 148001	Mioc, CA	36.58	36.27	12.88	35.39	38.35	7.62	8.56
UCMP 148002	Mioc, CA	34.59	33.11	23.67	30.62	30.37	19.03	6.95
UCMP 148003	Mioc, CA	20.33	20.33	11.75	19.84	20.75	8.58	4.37
UCMP 148005	Mioc, CA	20.38	20.14	10.93	19.85	21.42	8.38	4.98
UCMP 148006	Mioc, CA	21.37	21.37	10.79	21.2	21.2	7.6	4.33
UCMP 148007	Mioc, CA	20.38	20.33	9.83	20.2	22.46	7.07	3.63
UCMP 148008	Mioc, CA	15.53	15.38	7.81	14.76	13.52	4.11	7.13
UCMP 148009	Mioc, CA	20.67	20.63	10.43	20.2	19.61	9.35	3.84
UCMP 148010	Mioc, CA	30.19	30.14	13.76	29.19	27.35	11.17	5.38
UCMP 148011	Mioc, CA	21.82	21.59	10.98	21.13	20.58	7.9	3.85
UCMP 148012	Mioc, CA	28.72	28.31	16.49	25.89	24.69	11.17	5.56
UCMP 148017	Mioc, CA	20.51	20.1	10.1	19.49	19.34	5.77	5.04
UCMP 148020	Mioc, CA	16.55	16.22	14.85	12.16	12.03	11.65	4.75
UCMP 148021	Mioc, CA	11.81	11.69	7.78	10.39	9.99	5.49	2.54
UCMP 148025	Mioc, FL	33.45	33.32	15.52	33.5	32.68	10.21	5.85
UCMP 148026	Mioc, FL	32.57	30.7	15.65	32.23	33.84	10.44	5.24
UCMP 148027	Pleist, CA	30.26	29.94	15.62	27.26	26.92	10.31	6.43
UCMP 148028	Pleist, CA	9.57	9.53	6.31	8.52	8.1	4.45	2.26
UCMP 148029	Pleist, CA	7.35	7.34	5.53	5.98	6.45	3.8	1.97
UCMP 148031	Pleist, CA	13.71	13.54	9.82	12.41	10.71	7.88	2.56
UCMP 148032	Mioc, FL	21.94	21.81	9.99	21.12	23.33	4.82	4.01
UCMP 148033	Mioc, CA	14.16	13.85	8.78	11.93	11.45	6.12	3.08
UCMP 148035	Mioc, CA	19.54	19.23	9.22	18.37	20.62	5.34	4.45
UCMP 148041	Mioc, CA	12.2	12.12	8.81	10.27	10.7	6.98	2.79
UCMP 148044	Mioc, MD	18.19	17.76	8.7	16.77	17.71	7.67	4.78
UCMP 148045	Pleist, CA	17.08	16.96	12.07	14.43	13.37	9.08	4.53
UCMP 148046	Pleist, CA	16.37	14.95	14.73	12.99	14.06	12.77	4.23
UCMP 148047	Pleist, CA	10.77	10.75	7.55	9.16	8.27	5.43	2.94
UCMP 148048	Pleist, CA	10.19	9.94	7.54	8.43	9.38	5.52	2.58
UCMP 148049	Pleist, CA	12.46	12.27	15.03	10.33	11.16	10.47	2.88

UCMP - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
UCMP 148001	4.82	6.68	10.95	5.09
UCMP 148002	5.44	18.79	8.14	12.22
UCMP 148003	4.92	8.78	3.66	5.9
UCMP 148005	5.35	8.63	4.04	5.41
UCMP 148006	5.87	8.61	4.27	9.4
UCMP 148007	5.33	6.4	3.7	7.13
UCMP 148008	4.21	4.96	5.5	4.26
UCMP 148009	6.43	8.65	3.99	8.91
UCMP 148010	6.91	9.79	6.18	8.06
UCMP 148011	5.73	7.97	5.06	8.47
UCMP 148012	6.12	12.27	5.66	9.14
UCMP 148017	6.43	6.95	4.83	8.89
UCMP 148020	1.68	12.32	3.54	2.46
UCMP 148021	2.41	5.44	2.4	2.77
UCMP 148025	8.17	10.71	7.41	17.03
UCMP 148026	6.69	9.65	7.03	8.66
UCMP 148027	7.39	10.74	6.17	12
UCMP 148028	1.72	4.56	1.99	1.94
UCMP 148029	1.49	3.73	1.7	1.57
UCMP 148031	2.95	7.87	4.23	4.21
UCMP 148032	6.95	4.55	4.76	7.09
UCMP 148033	1.82	6.46	2.57	2.78
UCMP 148035	5.13	5.53	4.3	6.76
UCMP 148041	1.8	6.87	2.43	3.1
UCMP 148044	3.7	7.28	3.83	4.36
UCMP 148045	2.96	8.27	6.16	2.9
UCMP 148046	4.04	11.91	4.72	2.06
UCMP 148047	1.98	5.39	2.99	3.69
UCMP 148048	1.97	5.41	2.16	2.3
UCMP 148049	1.37	10.28	2.29	2.29

UCMP - Fossil Shark Centra Measurements

Specimen #	Locality	Diameter 1	Diameter 2	Max Length	Waist Width	Waist Heigth	D Foram L	D Foram W
UCMP 148050	Pleist, CA	13.53	13.24	8.8	12.08	10.16	7.11	3.86
UCMP 148053	Pleist, CA	6.45	6.27	6.48	5.35	5.03	5.24	1.55
UCMP 148054	Pleist, CA	6.99	6.93	5.1	5.75	5.68	3.47	2.01
UCMP 148056	Pleist, CA	5.71	5.67	4.76	4.65	4.06	3.47	1.34
UCMP 148058	Plioc, CA	14.73	14.12	14.79	11.72	12.22	11.69	3.61
UCMP 148059	Pleist, CA	15.36	14.87	12.29	12.25	12.5	9.85	2.69
UCMP 148061	Pleist, CA	14.18	14.06	15.16	9.63	11.44	12.31	3.59
UCMP 148062	Pleist, CA	15.95	15.13	10.97	12.89	12.12	6.95	4.77
UCMP 148064	Pleist, CA	14.73	14.64	9.22	12.55	12.2	5.51	3.04
UCMP 148065	Pleist, CA	15.03	14.58	11.1	12.58	11.48	8.59	4.09
UCMP 148066	Pleist, CA	11.03	10.88	10.38	8.98	9.55	7.67	2.71
UCMP 148068	Pleist, CA	12.36	12.25	6.51	11	11.73	5.07	3.11
UCMP 148069	Pleist, CA	9.69	9.65	6.94	8.02	8.97	5.11	2.39
UCMP 148070	Pleist, CA	10.21	10.07	6.54	8.04	8.29	5.06	2.8
UCMP 148072	Pleist, CA	9.47	9.46	6.09	8.53	7.72	4.38	1.92
UCMP 148073	Pleist, CA	6.21	5.86	4.69	4.99	4.43	3.67	1.5
UCMP 148074	Pleist, CA	5.64	5.59	4.36	4.53	4.73	3.7	1.61
UCMP 148077	Pleist, CA	9.67	9.12	6.17	9.12	8.48	4.48	2.04
UCMP 148078	Pleist, CA	5.72	5.72	6.75	4.15	4.43	5.84	1.77
UCMP 148079	Pleist, CA	8.97	8.78	6.31	8.27	8.72	4.29	2.16
UCMP 148080	Pleist, CA	8.83	9.01	6.17	7.6	7.92	4.71	2.29

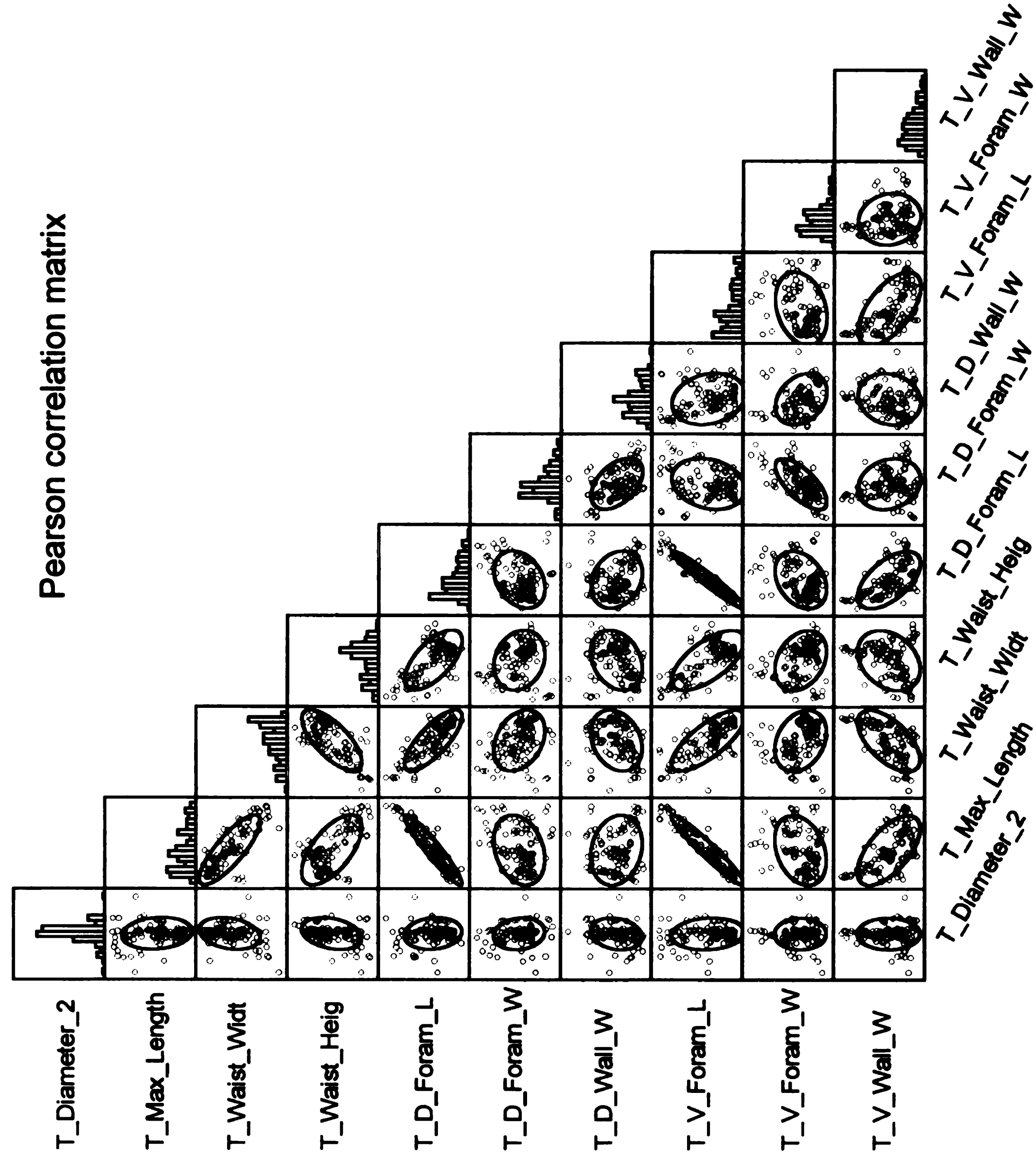
UCMP - Fossil Shark Centra Measurements

Specimen #	D Wall W	V Foram L	V Foram W	V Wall W
UCMP 148050	2.92	6.29	2.91	7.37
UCMP 148053	0.91	5.22	1.71	1.33
UCMP 148054	0.8	3.97	1.98	1.27
UCMP 148056	0.75	3.42	1.37	0.92
UCMP 148058	2.87	10.99	4.32	3.42
UCMP 148059	3.78	9.45	3.28	2.76
UCMP 148061	2.34	11.38	2.71	2.33
UCMP 148062	1.67	7.3	3.82	2.77
UCMP 148064	2.39	6.02	2.78	2.8
UCMP 148065	3.53	8.02	5.29	2.9
UCMP 148066	1.92	7.78	3.99	1.76
UCMP 148068	1.29	4.93	3.61	3.55
UCMP 148069	1.73	5.31	2.65	1.8
UCMP 148070	1.51	4.92	2.38	1.81
UCMP 148072	1.31	4.16	1.94	2.7
UCMP 148073	0.53	3.2	1.31	1.35
UCMP 148074	0.74	3.69	1.69	1.19
UCMP 148077	1.32	4.13	2.06	2.01
UCMP 148078	0.56	5.84	1.75	0.96
UCMP 148079	1.63	4.55	2.15	2.83
UCMP 148080	0.86	4.58	2.25	2.24

APPENDIX B. Pearson correlation matrix

	TDiameter2	TMaxLength	TWaistWidt	TWAaistHeig	TDForamL	TDForamW	TDWallW	TVForamL	TVForamW	TVWallW
T_DIAMETER_2	1.00									
T_MAX_LENGTH	-0.14	1.00								
T_WAIST_WIDT	0.25	-0.82	1.00							
T_WAIST_HEIG	0.29	-0.64	0.71	1.00						
T_D_FORAM_L	-0.13	0.95	-0.78	-0.65	1.00					
T_D_FORAM_W	-0.13	0.26	-0.31	-0.19	0.30	1.00				
T_D_WALL_W	0.20	-0.18	0.26	0.27	-0.22	-0.46	1.00			
T_V_FORAM_L	-0.11	0.96	-0.76	-0.66	0.97	0.22	0.20	1.00		
T_V_FORAM_W	-0.01	0.30	-0.28	-0.30	0.31	0.70	-0.30	0.26	1.00	
T_V_WALL_W	0.00	-0.63	0.60	0.29	-0.58	-0.19	0.14	-0.60	-0.10	1.00

Number of observations: 116


Pearson correlation matrix
T_Diameter_2
T_Max_Length
T_Waist_Widt
T_Waist_Heig
T_D_Foram_L
T_D_Foram_W
T_D_Wall_W
T_V_Foram_L
T_V_Foram_W
T_V_Wall_W

APPENDIX C. Discriminant analysis results

1. Discriminant analysis on Recent centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.0729    df =    10     2   113
 Approx. F=    28.1148    df =    20   208     prob =  0.0000


Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3    %correct
 1                   31         0         0      100
 2                    0        66         3       96
 3                    0         0        16      100

    Total            31        66        19       97

Jackknifed classification matrix
--------------------------------
                      1         2         3    %correct
 1                   31         0         0      100
 2                    2        63         4       91
 3                    0         1        15       94

    Total            33        64        19       94
```

2. Backwards Stepwise discriminant analysis on Recent centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.0617    df =     6     2   113
 Approx. F=    54.4438    df =    12   216     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1          2          3  %correct
 1                   31          0          0       100
 2                    0         68          1        99
 3                    0          0         16       100

    Total            31         68         17        99

Jackknifed classification matrix
--------------------------------
                      1          2          3  %correct
 1                   30          1          0        97
 2                    1         65          3        94
 3                    0          0         16       100

    Total            31         66         19        96
```

3. Discriminant analysis on Recent centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0120    df =    10     6   109
 Approx. F=    11.6830    df =    60   528      prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3         4         5         7         9  %correct
 1                  10         0         0         0         1         0         0        91
 2                   0         5         0         0         0         0         0       100
 3                   2         1        12         0         0         0         0        80
 4                   2         0         0        44         3         0         3        85
 5                   0         0         0         0        12         0         0       100
 7                   0         0         0         0         0         5         0       100
 9                   0         0         0         0         0         0        16       100

    Total           14         6        12        44        16         5        19        90

Jackknifed classification matrix
--------------------------------
                     1         2         3         4         5         7         9  %correct
 1                  10         0         0         0         1         0         0        91
 2                   0         5         0         0         0         0         0       100
 3                   2         2        10         0         1         0         0        67
 4                   2         0         0        43         3         0         4        83
 5                   0         0         0         1        11         0         0        92
 7                   0         1         0         1         0         3         0        60
 9                   0         0         0         1         1         0        14        88
```

4. Backwards Stepwise discriminant analysis on Recent centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.0076    df =     8     6   109
 Approx. F=    17.8044    df =    48   505     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3         4         5         7         9  %correct
 1                   10         0         1         0         0         0         0        91
 2                    0         5         0         0         0         0         0       100
 3                    2         0        13         0         0         0         0        87
 4                    0         0         0        48         3         0         1        92
 5                    0         0         0         1        11         0         0        92
 7                    0         0         0         0         0         5         0       100
 9                    0         0         0         0         0         0        16       100

    Total            12         5        14        49        14         5        17        93

Jackknifed classification matrix
--------------------------------
                      1         2         3         4         5         7         9  %correct
 1                    8         0         1         0         2         0         0        73
 2                    0         5         0         0         0         0         0       100
 3                    2         0        13         0         0         0         0        87
 4                    1         0         0        44         3         1         3        85
 5                    0         0         0         1        11         0         0        92
 7                    0         0         0         0         0         5         0       100
 9                    0         0         0         0         0         0        16       100

    Total            11         5        14        45        16         6        19        88
```

5. Discriminant analysis on Recent centra data (including *Negaprion and Rhizoprionodon*), with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.0726    df =    10     2   118
 Approx. F=    29.5631    df =    20   218     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3  %correct
 1                   31         0         0       100
 2                    0        71         3        96
 3                    0         0        16       100

    Total            31        71        19        98

Jackknifed classification matrix
--------------------------------
                      1         2         3  %correct
 1                   31         0         0       100
 2                    0        70         4        95
 3                    0         1        15        94

    Total            31        71        19        96
```

6. Discriminant analysis on Recent centra data (including *Negaprion* and *Rhizoprionodon*), with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0067    df =    10     8   112
 Approx. F=     9.9247    df =    80   661     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3         4         5         6         7         8         9
%correct
 1         10         0         0         0         1         0         0         0         0        91
 2          0         5         0         0         0         0         0         0         0       100
 3          1         0        14         0         0         0         0         0         0        93
 4          2         0         0        40         3         4         0         0         3        77
 5          0         0         0         0        12         0         0         0         0       100
 6          0         0         0         1         0         1         0         0         0        50
 7          0         0         0         0         0         0         4         1         0        80
 8          0         0         0         0         0         0         2         1         0        33
 9          0         0         0         0         0         0         0         0        16       100

  Total    13         5        14        41        16         5         6         2        19        85

Jackknifed classification matrix
--------------------------------
            1         2         3         4         5         6         7         8         9  %correct
 1          9         0         1         0         1         0         0         0         0        82
 2          0         4         1         0         0         0         0         0         0        80
 3          1         2        11         0         1         0         0         0         0        73
 4          2         0         0        39         3         4         1         0         3        75
 5          0         0         0         1        11         0         0         0         0        92
 6          0         0         0         2         0         0         0         0         0         0
 7          0         0         0         1         0         0         2         2         0        40
 8          0         0         0         0         0         0         3         0         0         0
 9          0         0         0         1         1         0         0         0        14        88

  Total    12         6        13        44        17         4         6         2        17        74
```

7. Discriminant analysis on CMMV centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.1027    df =    10     2   135
 Approx. F=    26.7246    df =    20   252     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   0        85         5        94
 3                   1         0        16        94

    Total           32        85        21        96

Jackknifed classification matrix
--------------------------------
                     1         2         3  %correct
 1                  30         0         1        97
 2                   1        83         6        92
 3                   2         1        14        82

    Total           33        84        21        92
```

8. Discriminant analysis on CMMV centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0183    df =    10     6   131
 Approx. F=    12.2994    df =    60   644     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3         4         5         7         9  %correct
 1                   11         0         0         0         0         0         0       100
 2                    0         5         0         0         0         0         0       100
 3                    2         0        13         0         0         0         0        87
 4                    2         0         0        64         3         0         3        89
 5                    0         0         0         0        12         0         0       100
 7                    0         0         0         0         0         6         0       100
 9                    0         0         1         0         1         0        15        88

    Total            15         5        14        64        16         6        18        91

Jackknifed classification matrix
--------------------------------
                      1         2         3         4         5         7         9  %correct
 1                    9         0         2         0         0         0         0        82
 2                    0         5         0         0         0         0         0       100
 3                    2         2        10         0         1         0         0        67
 4                    3         0         0        62         3         1         3        86
 5                    0         0         0         1        11         0         0        92
 7                    0         1         0         1         0         4         0        67
 9                    0         2         1         0         1         0        13        76

    Total            14        10        13        64        16         5        16        83
```

9. Discriminant analysis on UF centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.1230    df =    10     2   126
 Approx. F=    21.6587    df =    20   234     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   3        72         6        89
 3                   0         1        16        94

    Total           34        73        22        92

Jackknifed classification matrix
--------------------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   4        68         9        84
 3                   1         1        15        88

    Total           36        69        24        88
```

10. Discriminant analysis on UF centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0155    df =    10     8   120
 Approx. F=     8.2754    df =    80   712     prob =  0.0000


Classification matrix (cases in row categories classified into columns)
---------------------
                     1        2        3        4        5        6        7        8        9  %correct
 1                   9        0        1        0        1        0        0        0        0        82
 2                   0        5        0        0        0        0        0        0        0       100
 3                   0        0       14        0        0        0        0        1        0        93
 4                   1        1        0       44        3        0        0        1        5        80
 5                   0        0        0        0       12        0        0        0        0       100
 6                   0        0        0        2        0        3        0        0        0        60
 7                   0        0        0        0        0        0        4        1        0        80
 8                   0        1        0        0        0        0        2        1        0        25
 9                   0        0        0        0        2        0        0        0       15        88

   Total            10        7       15       46       18        3        6        4       20        83

Jackknifed classification matrix
--------------------------------
                     1        2        3        4        5        6        7        8        9  %correct
 1                   7        0        1        0        3        0        0        0        0        64
 2                   0        5        0        0        0        0        0        0        0       100
 3                   0        2       12        0        0        0        0        1        0        80
 4                   1        2        0       40        3        1        1        1        6        73
 5                   0        0        0        1       11        0        0        0        0        92
 6                   0        0        0        4        0        0        0        0        1         0
 7                   0        0        0        1        0        0        3        1        0        60
 8                   0        1        0        0        0        0        3        0        0         0
 9                   0        0        0        0        2        0        0        1       14        82

   Total             8       10       13       46       19        1        7        4       21        71
```

11. Discriminant analysis on BMNH centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.0860    df =    10     2   129
 Approx. F=    28.9251    df =    20   240     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   1        80         3        95
 3                   0         1        16        94

    Total           32        81        19        96

Jackknifed classification matrix
--------------------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   3        76         5        90
 3                   0         2        15        88

    Total           34        78        20        92
```

12. Discriminant analysis on BMNH centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0146    df =    10     6   125
 Approx. F=    12.6585    df =    60   612      prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3         4         5         7         9  %correct
 1                  11         0         0         0         0         0         0       100
 2                   0         5         0         0         0         0         0       100
 3                   1         0        14         0         0         0         0        93
 4                   2         0         0        58         3         0         3        88
 5                   0         0         0         1        12         0         0        92
 7                   0         0         0         1         0         4         0        80
 9                   0         0         0         1         0         0        16        94

    Total           14         5        14        61        15         4        19        91

Jackknifed classification matrix
--------------------------------
                     1         2         3         4         5         7         9  %correct
 1                  10         0         1         0         0         0         0        91
 2                   0         4         1         0         0         0         0        80
 3                   1         1        12         0         1         0         0        80
 4                   3         0         0        56         3         1         3        85
 5                   0         0         0         1        12         0         0        92
 7                   0         1         0         1         0         3         0        60
 9                   0         0         0         1         1         0        15        88

    Total           14         6        14        59        17         4        18        85
```

13. Discriminant analysis on SDNHM centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.1313    df =    10     2   152
 Approx. F=    25.1696    df =    20   286     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3  %correct
 1                   60         1         0        98
 2                    3        71         3        92
 3                    0         0        17       100

    Total            63        72        20        95

Jackknifed classification matrix
--------------------------------
                      1         2         3  %correct
 1                   57         4         0        93
 2                    3        69         5        90
 3                    1         1        15        88

    Total            61        74        20        91
```

14. Discriminant analysis on SDNHM centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0229    df =    10     6   148
 Approx. F=    12.9108    df =    60   733     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3         4         5         7         9  %correct
 1                  22         1         1         0         5         0         0        76
 2                   0         9         1         0         0         0         0        90
 3                   2         0        19         0         1         0         0        86
 4                   1         0         0        51         5         0         3        85
 5                   0         0         0         0        12         0         0       100
 7                   0         0         0         1         0         4         0        80
 9                   0         0         0         0         1         0        16        94

    Total           25        10        21        52        24         4        19        86

Jackknifed classification matrix
--------------------------------
                     1         2         3         4         5         7         9  %correct
 1                  21         1         1         1         5         0         0        72
 2                   0         9         1         0         0         0         0        90
 3                   2         1        16         0         3         0         0        73
 4                   1         0         0        50         5         0         4        83
 5                   0         0         0         1        11         0         0        92
 7                   0         1         0         1         0         3         0        60
 9                   0         0         0         0         2         0        15        88

    Total           24        12        18        53        26         3        19        81
```

15. Discriminant analysis on ANSP centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.2039    df =    10     2   210
 Approx. F=    24.4166    df =    20   402     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3  %correct
 1                   32         0         2        94
 2                    4       124        14        87
 3                    5         1        31        84

   Total             41       125        47        88

Jackknifed classification matrix
--------------------------------
                      1         2         3  %correct
 1                   31         0         3        91
 2                    4       123        15        87
 3                    6         3        28        76

   Total             41       126        46        85
```

16. Discriminant analysis on ANSP centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0660    df =    10      6   206
 Approx. F=    11.7562    df =    60   1037     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3         4         5         7         9  %correct
 1                  13         0         0         0         0         0         1        93
 2                   0         5         0         0         0         0         0       100
 3                   1         0        14         0         0         0         0        93
 4                   2         0         0       105         2         2        10        87
 5                   0         0         0         1        13         0         1        87
 7                   1         0         0         1         0         4         0        67
 9                   1         2         3         0         2         0        29        78

    Total           18         7        17       107        17         6        41        86

Jackknifed classification matrix
--------------------------------
                     1         2         3         4         5         7         9  %correct
 1                  13         0         0         0         0         0         1        93
 2                   0         4         1         0         0         0         0        80
 3                   2         1        12         0         0         0         0        80
 4                   2         1         0       103         1         3        11        85
 5                   0         0         0         1        12         0         2        80
 7                   0         1         0         1         1         3         0        50
 9                   1         2         3         1         6         0        24        65

    Total           18         9        16       106        20         6        38        80
```

17. Discriminant analysis on USNM centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.1469    df =    10     2   154
 Approx. F=    23.3286    df =    20   290     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3  %correct
 1                  31         0         0       100
 2                   4        84         9        87
 3                   4         3        22        76

    Total           39        87        31        87

Jackknifed classification matrix
--------------------------------
                     1         2         3  %correct
 1                  30         0         1        97
 2                   5        79        13        81
 3                   4         3        22        76

    Total           39        82        36        83
```

18. Discriminant analysis on USNM centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =      0.0463    df =     10      6   150
 Approx. F=      9.8783    df =     60    743      prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3         4         5         7         9  %correct
 1                   10         0         1         0         0         0         0        91
 2                    0         5         0         0         0         0         0       100
 3                    2         0        13         0         0         0         0        87
 4                    2         0         1        65         3         0         8        82
 5                    0         0         0         0        12         0         1        92
 7                    0         0         0         0         0         4         1        80
 9                    1         0         4         1         2         0        21        72

    Total            15         5        19        66        17         4        31        83

Jackknifed classification matrix
--------------------------------
                      1         2         3         4         5         7         9  %correct
 1                    9         0         2         0         0         0         0        82
 2                    0         5         0         0         0         0         0       100
 3                    3         0        11         0         0         0         1        73
 4                    2         0         1        64         3         0         9        81
 5                    0         0         0         0        12         0         1        92
 7                    0         1         0         0         3         0         1         0
 9                    1         0         6         1         3         0        18        62

    Total            15         6        20        65        21         0        30        76
```

19. Discriminant analysis on UCMP centra data, with FAMILY as grouping variable:

```
Wilks' lambda
   Lambda =     0.1322    df =    10      2   160
 Approx. F=    26.4336    df =    20    302     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                      1         2         3  %correct
 1                   57         1         0        98
 2                    3        75         9        86
 3                    2         0        16        89

    Total            62        76        25        91

Jackknifed classification matrix
--------------------------------
                      1         2         3  %correct
 1                   57         1         0        98
 2                    5        73         9        84
 3                    2         0        16        89

    Total            64        74        25        90
```

20. Discriminant analysis on UCMP centra data, with GENUS as grouping variable:

```
Wilks' lambda
   Lambda =     0.0264    df =    10     6   156
 Approx. F=    12.9225    df =    60   775     prob =  0.0000

Classification matrix (cases in row categories classified into columns)
---------------------
                     1         2         3         4         5         7         9  %correct
 1                  26         0         2         0         2         0         0        87
 2                   2         7         0         0         0         0         0        78
 3                   1         2        16         0         0         0         0        84
 4                   1         1         0        57         4         0         4        85
 5                   1         0         0         0        14         0         0        93
 7                   0         0         0         1         0         4         0        80
 9                   0         1         1         0         0         0        16        89

    Total           31        11        19        58        20         4        20        86

Jackknifed classification matrix
--------------------------------
                     1         2         3         4         5         7         9  %correct
 1                  24         0         4         0         2         0         0        80
 2                   3         6         0         0         0         0         0        67
 3                   1         3        15         0         0         0         0        79
 4                   1         2         0        53         6         0         5        79
 5                   2         0         0         0        13         0         0        87
 7                   0         1         0         1         0         3         0        60
 9                   0         2         1         0         1         0        14        78

    Total           31        14        20        54        22         3        19        79
```

APPENDIX D: PHYLOGENETIC ANALYSIS CHARACTERS

A list of centrum characters and their states coded for the matrix

1. Centra typically fluted cylinder shaped (0); centra typically non–fluted cylinder shaped (1).
2. All centra non–hourglass shaped (0); at least some centra hourglass shaped (1).
3. All centra non–modified cylinder shaped (0); at least some centra modified cylinder shaped (1).
4. Medio–lateral breadth > dorso–ventral height (0); medio–lateral breadth = dorso–ventral height (1); medio–lateral breadth < dorso–ventral height (2).
5. Centrum length/diameter ratio typically > 0.95 (0); centrum length/diameter ratio typically between 0.6 and 0.95 (1); centrum length/diameter ratio typically < 0.6 (2).
6. Width at apices of double cone/diameter ratio < 0.85 (0); width at apices of double cone/diameter ratio typically > 0.85 (1).
7. Basidorsal and basiventral arch–cartilage foramina oval (0); Basidorsal and basiventral arch–cartilage foramina square or rectangular in some centra of the vertebral column (1).
8. Basidorsal and basiventral arch–cartilage foramina extend into centrum rims (0); basidorsal and basiventral arch–cartilage foramina do not extend into rims (1).
9. Basidorsal arch–cartilage foramina length/diameter ratio typically > 0.57 (0); basidorsal arch–cartilage foramina length/diameter ratio typically < 0.57 (1).
10. Basidorsal arch–cartilage foramina length/ basidorsal arch–cartilage foramina width ratio typically >3.0 (0); basidorsal arch–cartilage foramina length/ basidorsal arch–cartilage foramina width ratio typically < 3.0 (1).

11. Basidorsal arch–cartilage foramina width/dorsal interforaminal wall width ratio typically > 1.0 (0); basidorsal arch–cartilage foramina width/dorsal interforaminal wall width ratio typically < 1.0 (1).
12. Dorsal interforaminal wall width/width at apices of the double cone ratio typically < 0.28 (0); dorsal interforaminal wall width/width at apices of the double cone ratio typically > 0.28 (1).
13. Basiventral arch–cartilage foramina length/diameter ratio typically > 0.54 (0); basiventral arch–cartilage foramina length/diameter ratio typically < 0.54 (1).
14. Basiventral arch–cartilage foramina length/basiventral arch–cartilage foramina width ratio typically >2.5 (0); basiventral arch–cartilage foramina length/basiventral arch–cartilage foramina width ratio typically < 2.5 (1).
15. Pores absent (0); pores small (1); pores large (2).
16. Pores absent (0); pores dense at rim (1); pores encircling rims and foramina (2); pores scattered (3).
17. Interior angle of intermedialia acute in some centra (0); interior angle of intermedialia at 90 degrees or obtuse (1).
18. Diagonal calcified lamellae absent (0); diagonal calcified lamellae length less than one–half the distance to the surface of the centrum (1); diagonal calcified lamellae length typically more than one–half the distance to the surface of the centrum (2).
19. Diagonal calcified lamellae absent (0); diagonal calcified lamellae typically thick (1); Diagonal calcified lamellae typically thin (2).
20. Calcified projections surrounding the basidorsal and basiventral cartilages absent (0); calcified projections surrounding the basidorsal and basiventral cartilages present (1).

21. Basidorsal and basiventral cartilages bulbous in cross–sectional view (0); basidorsal and basiventral cartilages straight in cross–sectional view (1).

22. Basidorsal and basiventral cartilage margins smooth (0); basidorsal and basiventral cartilage margins irregularly shaped (1).

23. Basiventral cartilages project from the calcified double cone in a straight path (0); basiventral cartilages project from the calcified double cone in a bowed path in some centra (1).

A list of whole specimen characters and their states coded for the matrix

The following list of apomorphies for Carcharhiniformes was taken directly from Compagno (1988). When present in a taxon, each of these apomorphies is coded as 1. When an apomorphy is absent, it is coded as 0.

1. First dorsal over pelvic bases
2. Loss of eyelid depressor muscle
3. Reduction of second dorsal fin
4. Reduction of clasper parts
5. Loss of rostral node
6. Postorbital processes expanded laterally
7. Occiput expanded
8. Loss of fourth lower extrabranchial cartilages
9. Triakid tooth type with anaulacorhizous roots
10. Strongly developed orbital notches on the cranium
11. Bifurcated (triakids) or hornlike ("higher" groups) postorbital processes
12. Possibly loss of a fused clasper groove
13. Lateral teeth asymmetrical and semibladelike
14. Pleats variably developed on claspers
15. Nasal capsules laterally expanded and ovoid
16. Cranium broader
17. Differentiation of dentition into compressed, broadened anteroposterior teeth differentiated from the smaller, narrower medials

18. Ectethmoid condyles present

19. Subethmoid fossa present

20. Posterior part of the subnasal plate expanded anteriorly under ectethmoid chamber

21. A pair of medial ectethmoid condyles present

22. Subnasal plate expanded anteriorly, separating the ectethmoid fossa from the nasal fontanelle

23. Mouth triangular

24. Teeth developed as pavement

25. Lower teeth enlarged at symphysis

26. Teeth expanded onto the underside of the lower jaw

27. Internal NLEs with very deep subocular pouches

28. General reduction of spiracles (except Galeocerdo)

29. Stronger monognathic heterodonty

30. Presence of precaudal pits

31. Plesodic pectoral fins

32. Mesorhipidion on the clasper

33. Rippled dorsal caudal margin

34. Nasal fontanelles separate from nasal apertures or lost

35. Primary supraorbital crests lost

36. Extension of levator palatoquadrati muscles into orbits

37. Loss of oral and gill raker papillae?

38. Increase in fin size

39. Anterior movement of first dorsal base

40. Loss of clasper hooks
41. Increase in size
42. Increase in length of distal pectoral radials
43. Extremely strong monognathic and dignathic heterodonty (paralleled in more derived carcharhinids)
44. Aortic and efferent hyoidian arterial canals present
45. Further enlargement of gill openings (three or more times eye length)
46. Lower jaw truncated at symphysis
47. Distal crown edges of upper anterolateral teeth arcuate, not angled
48. Mesial serrations on upper teeth and some lowers in adults and subadults
49. A toothless space at the upper and lower symphysis
50. Many tooth rows with imbricate overlap
51. Basal ledge ad groove absent from teeth
52. Shift to osteodonty (living species)
53. Second dorsal more reduced (less than 0.6 of first dorsal length)
54. Shortened terminal lobe of caudal
55. Reduced nasal fontanelles
56. Greatly elongated and narrowed anterior fontanelle with deflected edges
57. Keel on basal plate very strong
58. Keel present in subethmoid fossa
59. Efferent hyoidian canals greatly expanded and opening under hyomandibular facets
60. Postorbital processes reduced, not triangular and broad–based, with cylindrical base and expanded, hastate tip

61. Sphenopterotic ridges reduced

62. Ectethmoid foramina present

63. Scroll intestinal valve present

64. Second dorsal fin more or less reduced relative to the first

65. Uniquely enlarged, modified, inflated otic capsules, that extend in front of orbital fissures

66. Postorbital processes situated about at midlengths of otic capsules

67. Lengthened upper labial furrows, longer than those of hemigaleids, *Rhizoprionodon*, and triakids

68. Broadly arched tooth crowns with heavy serrations and serrated cusplets, secondarily anaulacorhizous tooth roots

69. Keels on caudal peduncle (also in *Prionace*)

70. Ectotic processes and precerebral pit and keel on cranium

71. High vertebral counts

72. Unique color pattern

73. Cusplets replaced by blades on teeth (also *Scoliodon* and Sphyrnidae)

74. Greatly elongated preanal ridges and anal radial segments supporting them

75. Very narrow basal plate at orbital notches

76. Stapediocarotid foramina present of basal plate

78. Posterodorsal medial ectethmoid foramina on the ectethmoid condyles

79. Shortening of labial furrows

80. Posterodorsal medial ectethmoid foramina on the ectethmoid condyle

81. Slender body

82. Curved–triangular teeth

83. Enlarged medial upper teeth

84. Gill rakers

85. Long, narrow pectorals (also in some large *Carcharhinus* species)

86. Weak keels on the caudal peduncle

87. A dorsal flare and large epiphysial foramen on the anterior fontanelle

88. Broad–based preorbital processes

89. Gradually sloping sides on otic capsules

90. Blue coloration

91. Brow ridge above eyes

92. Erect, narrow–cusped teeth in both jaws, with serrations reduced or almost entirely absent.

93. Cephalofoil present

94. Endonarial grooves present

95. Labial furrows vestigial or absent (also lost in some carcharhinids)

96. Greatly depressed medial rostral cartilage

97. Expanded, platelike rostral node

98. Depressed and laterally expanded nasal capsules and internasal septum

99. Nasal capsules entirely lateral to cerebral cavity

100. Subethmoid fossa a transverse slot

101. Slitlike nasal apertures

102. Ectethmoid chambers lateral to ectethmoid condyles

103. Ventral edge of anterior fontanelle at base of medial rostral cartilage

104. Double parietal fossae

105. No paired dorsal aortae

106. A single pair of efferent hyoidian foramina on basal plate (paralleled in the carcharhinid Rhizoprionodontini)

107. Development of sphyrnid secondary supraorbital crest

108. Preorbital process far distal on the nasal capsules

109. Postorbital processes extending through middle of levator palatoquadrati muscles

110. Levator nictitans muscles far distal on cephalofoil

111. Originating on proximal shaft of postorbital processes

112. Labial cartilages absent

113. Clasper rhipidion lost

Data matrix of centrum characters for Carcharhiniformes

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0
Haploblepharus	0	0	0	0	0	0	0	0	0	9	9	9	0	9	0	0	1	1	1	9	0	0	0
Triakis	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Galeorhinus	0	0	0	1	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0
Mustelus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0
Hemipristis	1	0	0	1	2	1	0	1	1	1	0	0	1	1	2	3	1	2	1	1	1	1	0
Galeocerdo	1	0	1	1	1	0	1	1	1	1	0	0	1	1	2	2	1	1	2	0	1	0	0
Rhizoprionodon	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	2	1	0	0	0
Prionace	1	0	0	1	2	0	1	0	1	1	0	0	1	1	1	1	1	0	0	1	1	0	0
Negaprion	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	3	1	2	2	1	1	0	1
Carcharhinus	1	0	1	1	2	1	1	1	1	1	1	1	1	1	1	3	1	2	2	1	1	0	1
Sphyrna	1	1	1	2	1	0	1	1	1	1	1	0	1	0	1	3	1	1	2	1	1	1	1
Indet 1	1	0	0	0	2	1	0	1	1	0	0	0	1	0	1	2	1	0	0	0	1	0	0
Indet 2	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	3	1	0	0	0	1	1	0

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
without centrum characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Scyliorhinus	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0
Mustelus	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1
Hemipristis	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Galeocerdo	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Rhizoprionodon	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Prionace	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Negaprion	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Carcharhinus	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
Sphyrna	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
without centrum characters	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustelus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemipristis	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Galeocerdo	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Rhizoprionodon	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Prionace	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Negaprion	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Carcharhinus	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Sphyrna	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
without centrum characters	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustelus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemipristis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Galeocerdo	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Rhizoprionodon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Prionace	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Negaprion	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Carcharhinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Sphyrna	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
without centrum characters	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustelus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemipristis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeocerdo	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhizoprionodon	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Prionace	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Negaprion	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Carcharhinus	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Sphyrna	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125
without centrum characters	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustelus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemipristis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeocerdo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhizoprionodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prionace	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Negaprion	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Carcharhinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphyrna	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1

Data matrix of whole specimen characters for Carcharhiniformes, derived from Compagno (1988)

with centrum characters	126	127	128	129	130	131	132	133	134	135	136
without centrum characters	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**
Scyliorhinus	0	0	0	0	0	0	0	0	0	0	0
Triakis	0	0	0	0	0	0	0	0	0	0	0
Galeorhinus	0	0	0	0	0	0	0	0	0	0	0
Mustelus	0	0	0	0	0	0	0	0	0	0	0
Hemipristis	0	0	0	0	0	0	0	0	0	0	0
Galeocerdo	0	0	0	0	0	0	0	0	0	0	0
Rhizoprionodon	0	0	0	0	0	0	0	0	0	0	0
Prionace	0	0	0	0	0	0	0	0	0	0	0
Negaprion	0	0	0	0	0	0	0	0	0	0	0
Carcharhinus	0	0	0	0	0	0	0	0	0	0	0
Sphyrna	1	1	1	1	1	1	1	1	1	1	1

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