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MORPHOLOGY AND SYSTEMATIC IMPLICATIONS OF FOSSIL AND RECENT LAMNID SHARK VERTEBRAE USING COMPUTERIZED TOMOGRAPHY (CT-SCANNING)

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Major Professor's Signature

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Date

MORPHOLOGY AND SYSTEMATIC IMPLICATIONS OF FOSSIL AND RECENT LAMNID SHARK VERTEBRAE USING COMPUTERIZED TOMOGRAPHY (CT-SCANNING)

By

Sarah Elizabeth Kraig

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ABSTRACT

MORPHOLOGY AND SYSTEMATIC IMPLICATIONS OF FOSSIL AND RECENT LAMNID SHARK VERTEBRAE USING COMPUTERIZED TOMOGRAPHY (CT-SCANNING)

By

Sarah Elizabeth Kraig

The use of CT-scanning to better understand shark anatomy is a relatively new technique. The amount of information gained from work on the internal morphology of the braincase has shown to significantly increase when CT-scanning is employed, and more importantly, having done so through non-invasive means. This project applies this technique to Lamnid shark vertebral columns with the intention of determining phylogenetically useful characters from vertebral centra without destroying the specimens, and more specifically, to shed additional light on the phylogenetic position of the fossil shark, *Carcharodon megalodon*. The use of fossil material in this project strengthens the need for non-invasive means. After scans were made, both external and internal measurements were used, as well as morphological features, to determine characters and character states. Phylogenetic analyses were mixed. The Carcharhiniform specimens (used as the outgroup) were grouped together, though they were not the most basal of the specimens: *Alopias vulpinus*, the Thresher shark, was. The *Carcharodon megalodon* specimens grouped together with other Lamnids, which in itself is promising, though not significant enough to further clarify their position. The CT-scanning was successful in identifying internal structures for study. This technique is highly influenced by the technology available for scanning, as well as by the preservation quality of the specimens.

ACKNOWLEDGEMENTS

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INTRODUCTION

The scientific study of fossil sharks has been ongoing since the mid-19th century (e.g. Agassiz, 1833-1843). Given that shark skeletons are composed almost entirely of cartilage, the parts of a shark most likely to fossilize are the teeth, which are produced in large numbers and which have a high preservation potential due to their hard enamel covering. As fossilized shark teeth are the most common vertebrate fossils in the record (Maisey, 1984), much of what we know about fossil sharks has come from their study. Otic capsules (Maisey, 1985, 2001; Jerve, 2007) and vertebrae are among the other structures that have been preserved, and they each provide potentially significant information. Studies comparing the tooth morphology of fossil and extant species have proved informative, including with regards to *Carcharodon megalodon*, the hypothesized relative of modern great white sharks (*Carcharodon carcharias*). Most of the evidence supporting this relationship comes from the morphology - generally very similar- and relative size of the teeth. This has led to the conclusion that not only is *C. megalodon* closely related to *Charcharodon carcharias*, but morphologically very similar, with the most obvious difference being relative size (*C. megalodon* was calculated as being three times the length of *C. carcharias*) (Gottfried et al., 1996). Nevertheless, Gottfried and Fordyce (2001), and Nieves-Rivera et al (2003), all concluded that isolated teeth in themselves do not provide unambiguous support for clearly defined decisions on shark phylogenetic relationships. With the discovery of fossilized *C. megalodon* vertebrae, we now have a separate basis of morphological comparison between *C. megalodon* and *C. carcharias*, and for lamnids in general.

Evolutionary convergence is rampant among shark teeth (Hubbell, 1996) and thus highlights the challenge of utilizing only teeth for a phylogenetic analysis. The analysis of fossilized cartilaginous vertebral centra allows for additional non-dental characters that can be useful in phylogenetic studies. As these are relatively rare and sometimes delicate structures in the fossil record, non-invasive means must be employed to analyze their internal structure. CT-scanning (computerized tomography) as employed here provides high-resolution images of internal structures and is an ideal technique for analyzing well-calcified centra.

CT-scanning is still a relatively new means of studying fossil sharks, though this is not the first study to employ it. Maisy (2004) CT-scanned the braincase of the extant basal shark *Notorynchus cepedianus*, and fossil sharks dating back to the Devonian Period. Again in 2005 Maisey used CT-scanning to navigate the braincase of *Cladodoides wildungensis*, another Late Devonian shark. Jerve (2007) employed CT-scanning on the skeletal labyrinth of the otic capsule of fossil carcharhinid specimens and used a comparative approach with non-fossil lamnids and carcharhinids to investigate membranous labyrinth morphology and function.

In this study, I will use CT-scanning to analyze the internal morphology of fossilized lamnid centra and Recent comparative specimens. I will identify and describe internal features preserved in both the fossil and non-fossil specimens, compare- via phylogenetic analysis- the phylogenetic position of the fossil taxa with regards to non-fossil and non-lamniform sharks (ie: specimens from their sister group, the Order Carcharhiniformes), and determine whether the use of CT-scanning provides phylogenetically informative characters from fossilized specimens.

The Vertebral Foramina

The vertebral foramina are structurally complex and potentially informative in that they preserve well when centra are preserved. During life, the foramina are 'filled' with solid basidorsal or basiventral (depending upon location) cartilages (Figure 1). The basidorsal cartilages extend dorsally and fuse medially to

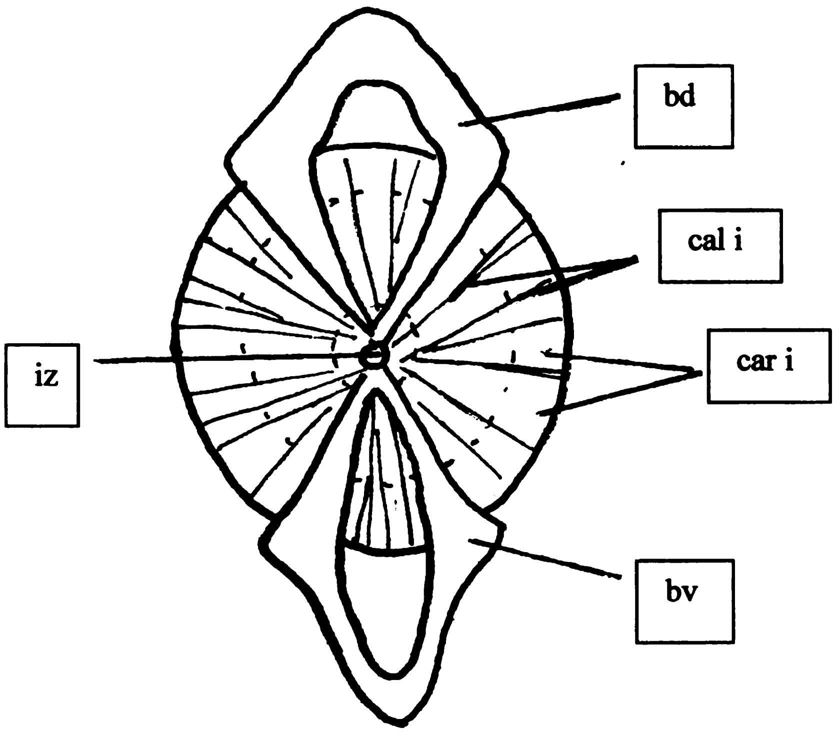


Figure 1: Generalized lamnid vertebra as appears *in vivo*. See *Anatomical Abbreviations* for descriptions of labels. Modified from Ridewood, 1921.

produce the neural arch. With the vertebrae in articulation, the arches form a 'tunnel' for passage of the spinal column. Encased in this column are the spinal cord and fluid. The basiventral cartilages extend and fuse ventrally to form the haemal arch (in the trunk and caudal region) mirroring that of the neural arch, though it is typically slightly narrower. In the thoracic (mid-body) region, the ribs extend ventrally without fusing, forming the haemal canal. The haemal canal and arch enclose the haemal artery. The calcified regions of the intermediale extend to the edges of the centrum and are thus exposed to the naked eye in a fossilized specimen. They are known as lamellae (Figure 3). In modern centra, a thin external layer of cartilage may still be present, covering the lamellae, though not necessarily preventing their identification.

The angles formed between the foramina are approximately equal within a given vertebrae- this is due to the fact that the dorsal and ventral foramina (when viewed axially) form an 'X.' These angles, however, are not necessarily identical between the Orders Lamniformes and Carcharhiniformes, or even among genera within an order, and are thus systematically valuable (Hildebrand et al., 2001). Although non-genetic factors such as sheer-stresses along the spine over time could potentially affect these angles, the assumption here is that these are not significant enough factors to produce large distortions.

As vertebral centra are virtually symmetrical if sliced laterally (through the inner zone, separating the two articulating halves), it is usually impossible to determine posterior from anterior without reference to the rest of the column. Therefore, no attempt to do so is made in this study. Additionally, it is impossible to determine the age of a specimen (juvenile or adult) or the exact location along the spine from where a given centrum originated.

Anatomical Abbreviations

bd	basidorsal cartilage
bv	basiventral cartilage
iz	inner zone
cal i	calcified areas of the intermediale
car i	cartilaginous parts of intermediale

MATERIALS AND METHODS

Specimens

A complete listing of specimens studied is given in Appendix A. Institutional catalogue numbers are used when available. In the case of multiple individual centra under one catalogue number, the catalogue number is expanded to include letters by adding a period after the number, and then the letter. For example, the two associated centra of *Carcharodon carcharias* from CAS with the catalogue number 25844 have been expanded to CAS 25844.a and CAS 25844.b (Note: some catalogue numbers include dashed letters, as with BMP 5821-a. These were pre-existing and should not be confused with the letters added for this study.)

The orders Lamniformes and Carcharhiniformes are both represented (Appendix A), with Carcharhiniformes serving as the outgroup.

Institutional Abbreviations

AMNH: American Museum of Natural History, New York, New York
BMNH: The Natural History Museum, London, England
CAS: California Academy of Sciences, San Fransisco, California
CMMV: Calvert Marine Museum, Solomons, Maryland
FM: The Field Museum, Chicago, Illinois
PV: Charleston Museum, Charleston, South Carolina

CT Scans

Initial scans were made at Sparrow Hospital in Lansing, Michigan in May 2007. Later CT scans were made at the Michigan State University Radiology Clinic in January 2008. Specimens scanned at Sparrow Hospital were scanned on a Toshiba Aquilion 64 medical scanner with slice thickness of 0.3mm and slice intervals of 0.5mm. All specimens scanned at the MSU Radiology Center were examined using a GE Discovery

STE medical scanner with slice thickness of 0.625 mm, slice intervals of 0.625 mm, and a helical rotation speed of 1.0 sec. All data were saved as DICOM files and opened and analyzed using OSIRIX Medical Imaging software. All measurements were taken using calipers (Mitutoyo) or the measurement option in the OSIRIX program.

Photographs

All photographs were taken with a Nikon Coolpix S200 digital camera and manipulated using Macintosh iPhoto.

Centrum Measurements

Measurements were taken, when possible, on the specimen first (using Mitutoyo digital calipers – measurements to 0.001 mm), and from the CT scans secondarily. BMNH2316 (see Figure 13) was used initially. This is a sectioned vertebrae, and thus two foramina are exposed, along with the inner zone. Internal measurements were taken using both the calipers and then also using the measurement tool in OSIRIX to determine fidelity between the two. The differences averaged 2*um* on foramina that are approximately 4.8-4.9cm in length. Therefore, fidelity is assumed.

When more than one vertebra was available under a given catalogue number (and thus, from the same individual), two practices were followed: 1) if there was no obvious distinction to be made among the centra, then the best representative was measured, and 2) if there was a distinction to be made (such as size), then each was assigned its own letter (see 'Specimens') and measured. In the case of the latter, the centra were treated as individuals during the phylogenetic analysis.

Eleven external measurements (see Figure 2 and Figure 3) were taken on each fossil and recent centrum (modified after Burris, 2005). The measurements are as follows:

1) Diameter 1: Diameter of centrum measured across the face of the centrum. Anterior and posterior are impossible to determine from isolated centra; therefore, the larger of the two measurements taken is used as Diameter 1.
2) Diameter 2: The smaller of the two diameter measurements, as described in Diameter 1.
3) Centrum length: Centrum length measured anterioposteriorly from rim to rim.
4) Centrum width at apices of the double cone: Width at apices of the double cone. Lamniform centrum walls are convex at this location.
5) Centrum height: height of centrum measured at the apices of the double cone. Measured at 90° from Diameters 1 and 2.
6) Dorsal foramen length: Length measured anterioposteriorly from margin to margin of a single dorsal foramen. Because fossil centra are sometimes imperfectly preserved, the length was measured on whichever of the two foramina was best preserved. On recent centra preserved with the cartilaginous foraminal arches still attached (thus obscuring the foramina), these measurements were taken from the CT scans.
7) Dorsal foramen width: Maximum width of the same dorsal foramen that was measured for length, measured laterally.
8) Dorsal interforaminal width: Width of the wall separating the two dorsal foramina.

9) Ventral foramen length: Length measured anteriorposteriorly from margin to margin of a single ventral foamen. Because fossil centra are sometime 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.

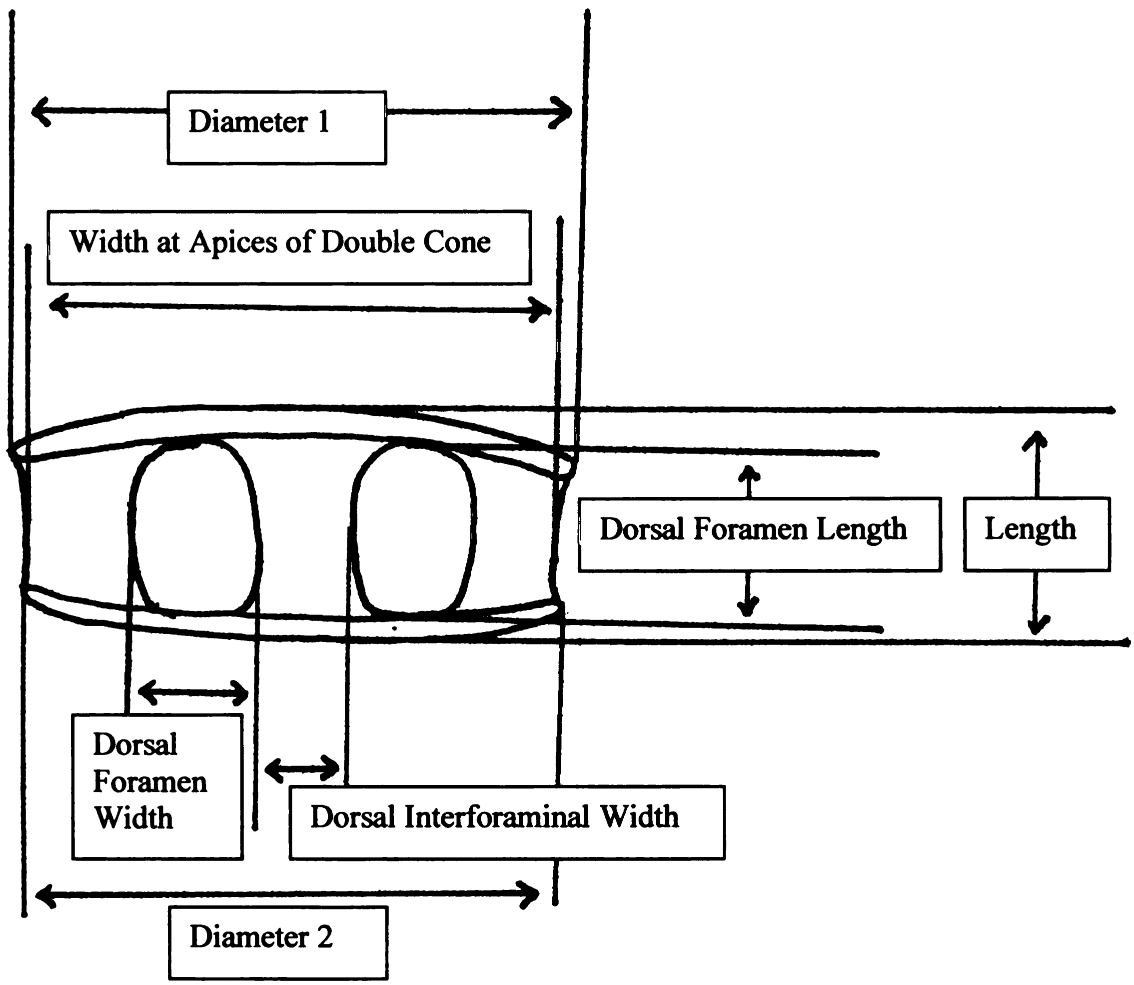


Figure 2: External measurements on a vertebral centrum (dorsal view).
Modified from Burris, 2004.

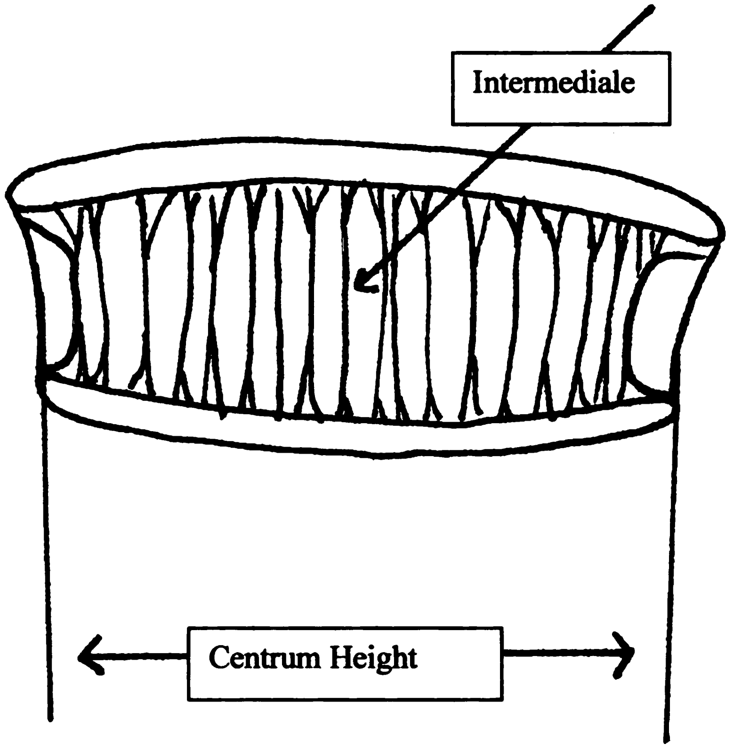


Figure 3: External measurements on a vertebral centrum (lateral view).
Modified from Burris, 2004.

Fourteen internal measurements (Figure 4) were taken from each centrum using the CT-scanned images. They are listed here:

1) Inner zone height: length of inner space, measured from dorsal to ventral.
2) Inner zone width: length of inner space, measured from side to side.
3) Dorsal inner foramen width: Maximum width of the dorsal foramen, measured laterally.
4) Ventral inner foramen width: Maximum width of the ventral foramen, measured laterally.
5) Dorsal depth: Length of the dorsal foramen from mid-point of inner foramen width to the mid-point of the outer foramen width.

6) Ventral depth: Length of the ventral foramen from mid-point of inner foramen width to the mid-point of the outer foramen width.

7) Dorsal foramen angle: Angle of the dorsal foramen, as taken from the external foraminal 'corners,' to the mid-point of the inner foramen.

8) Ventral foramen angle: Angle of the ventral foramen, as taken from the external foraminal 'corners,' to the mid-point of the inner foramen.

9) Dorsal interforaminal inner distance: Width of the inner wall separating the two dorsal foramina. Located closest to the inner zone.

10) Ventral interforaminal inner distance: Width of the inner wall separating the two ventral foramina. Located closest to the inner zone.

11) Dorsal interforaminal angle: Angle of the space between the dorsal foramina. Taken from the external foraminal 'corners' bordering the interforaminal area, to the mid-point of the inner foramen.

12) Ventral interforaminal angle: Angle of the space between the ventral foramina. Taken from the external foraminal 'corners' bordering the interforaminal area, to the mid-point of the inner foramen.

13) Dorsal foramen area: Area of the dorsal foramen, calculated as ½ab, where a=dorsal length and b=dorsal outer foramen width.

14) Ventral foramen area: Area of ventral foramen, calculated as ½ab, where a=ventral length and b=ventral outer foramen width.

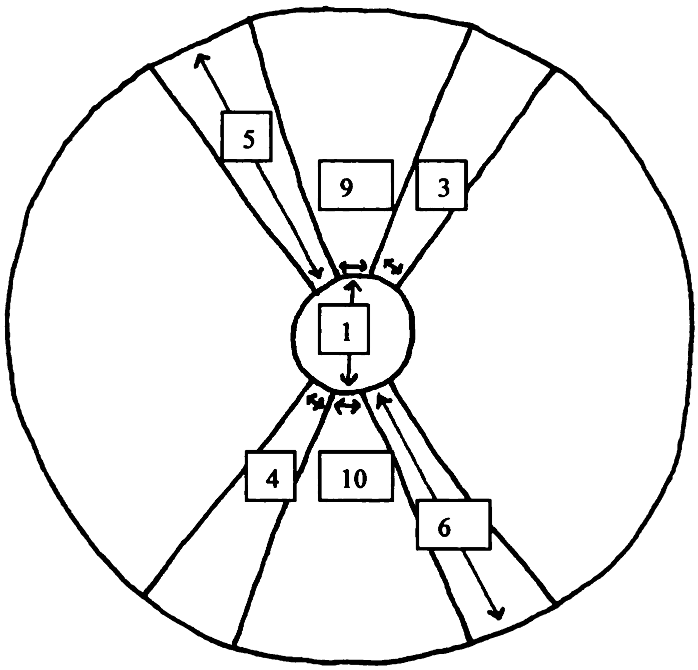


Figure 4-a: Internal measurements 1, 3, 4, 5, 6, 9, and 10 on a vertebral centrum (Axial, or anterioposterior, view) as explained in text. *Please note that while measurements 3 and 5 and then 4 and 6 are measured on different foramina, the dorsal and ventral measurements are each taken from the same foramen. They are shown on different sides for ease of viewing.

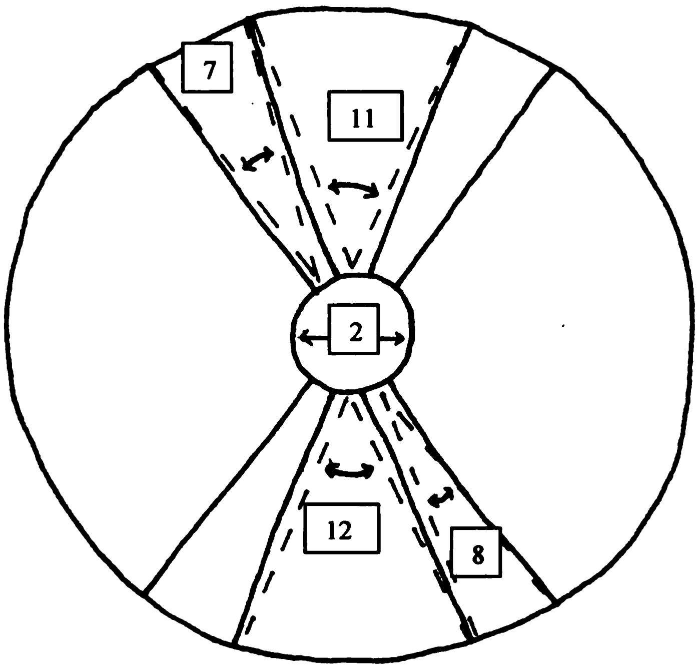


Figure 4-b: Internal measurements 2, 7, 8, 11, and 12 on a vertebral centrum (Axial, or anterioposterior, view).

Technique for Taking Internal Measurements

The technique that has been developed for taking internal measurements is based upon the identification of the inner zone of a centrum, which marks the zone through which the notochord passes. The centrum is viewed axially (if scans were not taken in this position, then they are manipulated). While moving axially though the centrum, the inner zone can typically be identified as a dark circular structure in the middle of the centrum, and is located approximately midway as you move axially. The CT-scan slice used for taking measurements is the one that has the smallest diameter inner zone for the purposes of this study, the inner zone height was measured to make this determination. This slice is designated the central slice and is where the foramina are largest because the foramina are conical and come to a point at the center of the inner zone. Once this slice is identified, measurements can be taken using the measurement tool of the viewing software (OSIRIX).

MORPHOLOGICAL DESCRIPTIONS

Specimens in this section are organized systematically to better facilitate comparisons. Both fossil and recent specimens are included; specimens are Recent unless noted as 'fossil.' Refer to the Materials and Methods section for definitions and descriptions of morphological terms. Also, please refer to Appendices B and C for complete tables of internal (B) and external (C) measurements.

Class CHONDRICTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order LAMNIFORMES Compagno, 1973

Family ALOPIIDAE Bonaparte, 1838

***Alopias* Rafinesque, 1810**

CAS 65976 -- *Alopias vulpinus*

This specimen of *Alopias vulpinus* (the Thresher shark) was caught off of Pt. San Pedro, California in 1952 in 200 feet of clear water. It is a dry preserved specimen with the both the dorsal and ventral arches still attached, the ventral arch being complete. This makes visual inspection of the foramina difficult, though a distinction between dorsal and ventral is still possible based upon the outer interforaminal distances. There is little taphonomic distortion of the vertebrae. The outer edges of the centra are stippled, not striated. When viewed dorso-ventrally and laterally the centra have a slight hourglass shape. The specimen was scanned while sitting on an angle (not at an exact 90o to the CT machine), and thus the dorsal and ventral ends are not clearly visible in the same image. Therefore there are two images for this specimen (necessary for retrieving all of the measurements).

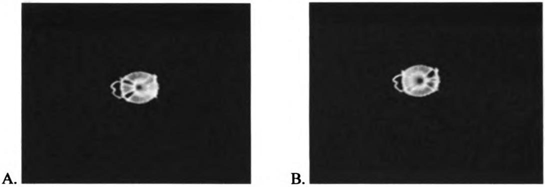


Figure 5: CAS 65976. *Alopias vulpinus*. A shows the ventral arch, and B shows the dorsal end of the vertebra. Scale bar is 5 cm.

Family ODONTASPIDIDAE Müller and Henle, 1839

***Odontaspis* Agassiz, 1838**

BMNH 5821-a – *Odontaspis sp.* (fossil)

Specimen BMNH 5821-a is a fossilized series of associated disarticulated vertebrae. Still preserved *in situ*, the vertebrae have a mudstone matrix within many of the foramina. All of the vertebrae fall within 23.50-26.00 mm in diameter range. Since there is some taphonomic distortion, measurements have been taken from those vertebrae exhibiting the least evidence of weathering. The edges are striated axially. When viewed both laterally and dorso-ventrally, there is no hourglass shape to the vertebrae; axially, there is some dorso-ventral compression (lateral elongation), though this is slight. Internal measurements were not possible, as they were unclear and not well resolved.

Family LAMNIDAE Müller and Henle, 1838

Carcharodon Smith, 1838

BMNH P.8983 – *Carcharodon ? auriculatus* (fossil)

BMNH P.8983 (figure 6) is the largest centrum in this study. It was collected from the London Clay deposit (Lower Eocene) and is remarkably well preserved. There is little taphonomic distortion along the outer edge of the centrum. The dorsal foramina are nearly perfect with only a little wear on one of the foramen. Thus, the other, more well preserved foramen was measured. The ventral foramina have more wear, with one having its wear extend into the rim above and below. The other foramen is worn at the corners, so the areas where measurements were taken (along the sides and the top and bottom) are intact enough for accurate measurements.

There is a slight lateral elongation when viewed axially, as well as the slightest hint of a waist when viewed dorso-ventrally. There is no waist when viewed laterally. There is some sediment covering the innermost part of one of the articulating facets (where one centrum articulates with the next), though they do not inhibit taking measurements. There are a few cracks running though the outer layers of the centra, though after inspecting the CT scans, they do not extend into the interior of the specimen, and thus do not affect the internal measurements.

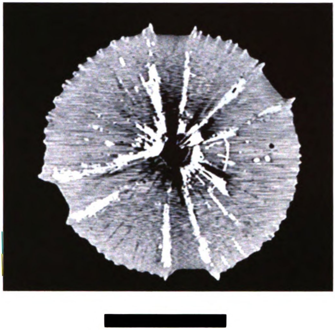


Figure 6: BMNH P.8983. *Carcharodon ? auriculatus*. Scale bar is 5 cm.

CAS 25844.a, 25844.b -- *Carcharodon carcharias*

These two centra are from the same specimen, catalogue numbers CAS 25844.a and CAS 25844.b (figures 7-a and 7-b). Collected off of Malibu, CA in 1936. Dry preserved vertebrae, CAS 25844.a is larger (and longer) than CAS 25844.b. The dorsal and ventral foramina of both centra are well preserved with no taphonomic deterioration. Both have striated edges, though they do look stippled. There is an hourglass appearance when viewed both laterally and dorso-ventrally.

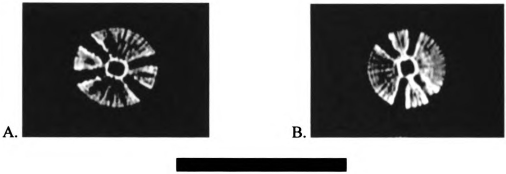


Figure 7: CAS 25844.a. *Carcharodon carcharias*. A is the larger specimen (dorsal end is to the right), and B is the smaller specimen (dorsal end is towards top). Scale bar is 5 cm.

CAS 26678 – *Carcharodon carcharias*

CAS 26678 (figure 8) is an articulated column of eight adult great white shark vertebae. Collected in 1959 off of La Selva Beach near Santa Cruz, CA. As described in Materials and Methods, no obvious morphological distinctions are apparent among the vertebra; therefore one representative centrum was selected to be measured. The specimen is wet-preserved with considerable soft tissue still attached to the cartilage, making external measurements a near impossibility. All measurements were taken using the CT-scans of the specimen. The centra are striated, as this is visible through the layers of soft tissue.

Figure 8: CAS 26678. *Carcharodon carcharias*. The vertebra measured is the second from the top (with a few of the measurements still shown). This is a lateral view. Scale bar is 5 cm.

PV4808, PV4809, BM PV4810 -- *Carcharodon megalodon* (fossil)

Two of the fossil *Carcharodon megalodon* vertebrae from the Charleston Museum (PV4808, PV4809; Figures 9-a and 9-b) are mid-Pliocene in age and were collected from the Goose Creek formation while dredging the bottom of the Wando River near Charleston, South Carolina. PV4810 (Figure 9-c) is thought to be late-Miocene in age, and was collected whilst dredging in either the Cooper or Wando Rivers in Charleston, South Carolina.

PV4808 (Figure 9-a) is a near-perfectly preserved *Carcharodon megalodon* centrum. The dorsal and ventral foramina are clearly visible, with little taphonomic distress, except along the external edges of the foramina. One side (an articulating face) of the vertebrae is infilled with sediment, though this does not affect the foramina.

PV4809 (figure 9-b) is a second *C. megalodon* centrum. Slightly larger in size than PV4808, it too has some infilling on one of its articulating faces. There is also more taphonomic wear on the ventral rim of one facet (it is unclear whether it is the anterior or posterior facet). This is a non-issue for foraminal measurements, as only one foramen is affected.

PV4810 (figure 9-c) is the third and best-preserved *C. megalodon* centrum. One entire facet is infilled to the point where the sediment protrudes beyond the level of the rim on that side. There is no significant taphonomic distress.

All of the specimens are striated along the outer edges of their intermediale. There is no hourglass shape for any of the specimens when viewed either laterally or dorso-ventrally.

Figure 9-a: PV 4808. *Carcharodon megalodon.* Note the slight taphonomic wear on the external edges of the foramina.

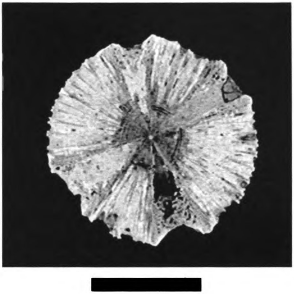


Figure 9-b: PV 4809. *Carcharodon megalodon.*

Figure 9-c: PV 4810. *Carcharodon megalodon.* The largest of the three *C. megalodon* vertebrae.

BMNH 35860 – *Carcharodon sp.* (fossil)

BMNH 35860 (figure 10) is one of two fossil *Carcharodon* sp. vertebrae. They were collected at the Red Crag Formation in Suffolk, England. Only one of the two is usable; the unusable one is so highly eroded that the internal parts of the intermediale are now exposed (the edges are worn away).

The remaining centrum is missing some of one of the rims, though not the areas near the foramina. However, this does allow only one diameter measurement to be taken, and thus it is identified as diameter 1. There are some large cracks running through the centrum.

The edges of the intermediale have striated lamellae; however, there are also pores present. They are medium in size and are scattered on the lamellae themselves.

There is a dorso-ventral elongation when viewed axially. There are no waists (either when viewed dorso-ventrally or laterally).

This centrum is so poorly preserved that the internal structures are not distinguishable from the CT scans. It is therefore not included in some of the phylogenetic analyses (ie: those using the internal characters).

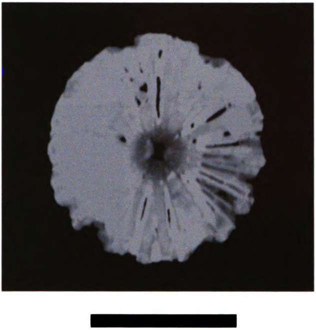


Figure 10: BMNH 35860-1. *Carcharodon sp*. Note how much darker and pooer in quality this image is than the others. This is due to poor preservation.

Isurus Rafinesque, 1810

CAS SU40902.a, SU40902.b – *Isurus glaucus*

CAS SU40902.a (figure 11-a) and CAS SU4090.b (figure 11-b) are two centra from a Mako shark. CAS SU40902.a is smaller overall, while CAS SU40902.b is larger and has a distinct 'ridge' on one of its articulating faces (this does not interfere with any of the measurements for this study). Collected between Pt. Dune and San Pedro near Los Angeles, CA in 1943. Because they were collected from commercial fisherman, there is no way to tell if they are from the same specimen, and thus they will be treated as though they originated from different individuals.

CAS SU40902.a is a perfectly preserved dry specimen. It is nearly circular in shape, with a slight lateral elongation.

CAS SU 40902.b is also a perfectly preserved dry specimen with a slight lateral elongation.

Both have striated edges and some stippling is present on the striations. When viewed both dorso-ventrally and laterally, there is no 'waist' – that is to say, there is no hourglass shape to the centra.

A.  B. 

Figure 11: CAS SU40902.a. *Isurus glaucus*. A is the smaller of the two vertebrae (top in the photo), and B is the larger of the two vertebrae (bottom in photo). Scale bar is 5 cm.

Lamna **Cuvier, 1816**

CAS 26710.a, CAS 26710.b – *Lamna ditropis*

Collected 6-7 miles offshore from Monterey Bay, CA in 1957. CAS 26710.a (figure 12-a) and CAS 26710.b (figure 12-b) are both specimens of Salmon shark. CAS 26710.a is the larger of the two and has a slight 'egg-shaped' distortion towards the ventral (haemal) end. It is also distinguishable by having a small pink spot on it, most likely made soon after it was dry-prepared. CAS 26710.b is the smaller and slightly 'egg-shaped' towards the dorsal (neural) side. There is no taphonomic distortion and both are striated.

CAS 26710.a has no waist either dorso-ventrally or laterally; however, CAS 26710.b does have a slight waist in both views.

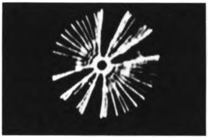
A.  B. 

Figure 12: CAS 26710.a. A is the larger *Lamna ditropis* vertebra, and B is the smaller *Lamna ditropis* vertebra. Scale bar is 5 cm.

Family CETORHINIDAE Gill, 1862

***Cetorhinus* Blainville, 1816**

BM2316 -- *Cetorhinus maximus* (fossil)

BMNH 2316 (Figure 13) is a fossil *Cetorhinus maximus* (Basking shark) vertebra from the Pliocene of Antwerp, Belgium. Only one half of the vertebra (either the dorsal or ventral – it is impossible to determine without the other present) is preserved. It has also subsequently been sectioned dorso-ventrally at the inner zone. This allows for direct observation of the mineralization patterns, as well as access to the internal morphology of the vertebrae. As the foramina are exposed, direct measurements are possible of the internal morphology. There is little taphonomic distortion on the external surfaces, and it is quite possible to see the striated lamellae along the external edges of the intermediale. There is a slight waist when viewed axially.

Since this is only a half specimen, the foramina that are present are taken as dorsal.

Figure 13: BMNH 2316. *Cetorhinus maximus* centrum. Notice the clarity of the scan in comparison with other vertebrae. This is because it has been thin-sectioned.

CAS 224630 – *"Tetroras" (=Cetorhinus) maximus*

CAS 224630 (Figure 14) is a dry-preserved specimen of a Basking shark. It was collected near Sharp Park in San Mateo Co., CA. There is severe lateral compression on one end of the vertebra (either dorsal or ventral) due to the conditions under which it was preserved. This has created distortions for a few of the measurements, such as: centrum width at the apices of the double cones, diameter 1, diameter 2, and centrum height. The dorsal and ventral (neural and haemal) arches are still attached and preserved, making visual identification of the foramina difficult. Thus, they were identified and measured from the CT scans that were taken. Though the edges of the centrum are covered with dried cartilage, the striations are still visible.

Figure 14: CAS 224630. CT-scan of *"Tetroras" (=Cetorhinus) maximus*. Note the severe lateral compression of the vertebra in the upper left-hand corner.

Order CARCARHINIFORMES Compagno, 1973 (Carcharhinida White, 1936)

All of the specimens scanned in the Order Carcharhiniformes were scanned with a lower resolution. This was because the images were unclear when scanned at the same resolution as the other specimens. Therefore, they are less 'sharp' and detailed. The foramina are however, still clearly visible thus the internal measurements are still possible.

SDSNH 63154

This specimen (Figure 15) has been identified only as a member of the Order Carcharhiniformes. Collected in the Rancho del Rey Condo Hill in the San Diego Formation in San Diego Co., CA in May 1995. Its neural foramina are ovoid, while the haemal are more rectangular. There is a slight hourglass shape to the centrum when viewed dorso-ventrally, and when viewed laterally, this shape is greatly reduced, almost to the point of being non-existent. When viewed axially, there is a lateral elongation (it is dorso-ventrally compressed). This should not be mis-construed as a taphonomic deformation, but rather as the natural state of the centrum. Striated lamellae are absent; indeed, the only markings along the edges of the intermediale are some scattered pores along the lateral edges, as well as some in the interforaminal space.

Family CARCHARHINIDAE, Jordan and Evermann, 1896

SDSNH 65993

This specimen (Figure 16) has been identified to the Family Carcharhinidae within Carcharhiniformes. Collected in 1984 in the Mission Hills Quarry, part of the San Diego Formation, in San Diego Co., CA. The neural foramina are ovoid and the hemal are rectangular. There is an hourglass shape with viewed dorso-ventrally; this is less pronounced when viewed laterally. There is a lateral elongation when viewed axially (dorso-ventrally compressed). This is the natural state of the centrum and is not a taphonomic deformation. There are no striated lamellae along the outer edges of the intermediale, but small pores are present, scattered along the intermediale edge.

Family TRIAKIDAE, Gray, 1851

SDSNH 75551

SDSNH 75551 (figure 17) has been identified to the Family Triakidae within the order Carcharhiniformes. The specimen was collected near Rancho del Rey, a part of the San Diego Formation, in San Diego Co., CA in 1990. The neural foramina are ovoid and curve in slightly at the waist, while the hemal are rectangular and do not curve in at the waist. There is an hourglass shape when viewed dorso-ventrally; this is less pronounced when viewed laterally. When viewed axially there is a lateral elongation (dorso-ventral compression). A significant point is that one lateral side is much longer than the other. As one cannot tell posterior from anterior, it is impossible to say if this is the left or right side of the animal; however, it is possible that this is due to a preference on the part of the animal for movement on one side more than the other. Additionally, it could be due to the fact that since this is a very small centrum (the smallest in the study, of either order), the individual was a juvenile with this defect and died as a result.

There are very small pores (barely visible to the naked eye) on both the dorsal and ventral interforaminal areas, as well as on the lateral edges of the intermediale.

SDSNH 71143

SDSNH 71143 (figure 18) has been identified as belonging to the Family Triakidae in the Order Carcharhiniformes. It was collected in Shell Hill in Rancho del Rey, a part of the San Diego Formation in San Diego Co., CA in 1989. The dorsal foramina are ovoid and curve in at the waist, like a kidney bean. The ventral foramina are rectangular and do not curve in at the waist. Viewed dorso-ventrally, there is a distinct hourglass shape; this disappears when viewed laterally. When viewed axially, the centrum is laterally compressed (dorso-ventrally elongated), the only Carcharhiniform to have this shape. There are randomly scattered very small pores all over the intermediale edges.

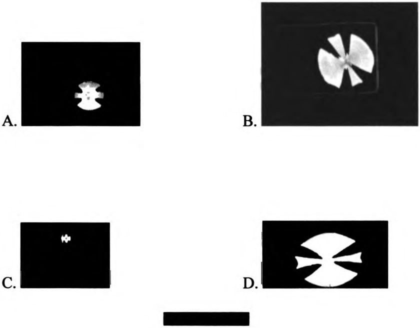


Figure 15: Plate of Charcharhiniformes. A: SDSNH 63154, a Carcharhiniform (dorsal end to left); B: SDSNH 65993 from the Family Carcharhinidae (dorsal end to lower right); C: SDSNH 75551 from the Family Triakidae (dorsal end on bottom); D: SDSNH 71143 from the Family Triakidae (dorsal end to right side).

QUANTITATIVE ANAYLYSIS

Characters

Characters were developed based upon both the internal and external morphology. The eleven external measurements, the thirty-two internal measurements, and the below-mentioned additional characters, were used and recorded into Microsoft Excel, coded, and then transferred into PAST (Hammer and Harper, 2006) for analysis. See Appendix D for a list of characters and the coded states. See Appendix E for a list of the specimens with their coded states.

Phylogenetic Analysis Background

Phylogenetic analysis, though not fool-proof in providing true evolutionary histories, is the most sound approach to the question of determining which of a multitude of phylogenetic reconstructions is the best. Parsimony operates on the theory of Occam's razor: the simplest theory is often the best.

Heuristic (TBR) Search: A heuristic search searches a 'subset of all possible trees' (Hammer and Harper, 2006). This is done to minimize the length of time needed to do an analysis with an exhaustive or branch-and-bound parameters. Because it is not guaranteed to find the absolute most parsimonious tree (due to the subset being tested), this is often used with more than 15 specimens, and was thus used for this analysis.

TBR (tree bisection and reconnection), one of three available algorithms for heuristic searching, is used here due to its advanced 'branch-swapping' abilities. Though it takes longer than the other two algorithms, NNI (nearest neighbor) and SPR (subtree pruning and regrafting), it often finds shorter trees.

Branch-and-Bound Search: A variant of an exhaustive search, branch-and-bound continuously calculates the tree length and automatically disregards trees whose branch length exceeds the shortest completed tree found so far. Thus there is the guarantee of finding the shortest trees().

Wagner optimization: Characters analyzed using the Wagner optimization are reversible and ordered so that a change from 0 to 2 costs more than a change from 0 to 1 or 1 to 2, yet is the same as a change from 2 to 0 (Hammer and Harper, 2006). There is also polarity in the character states, with the primitive state coded as 0.

Outgroup: The Order Carcharhiniformes is used as the outgroup in this study, and thus has its character states coded as 0. The Carcharhinid with the fewest non-zero character states was listed first in PAST (the program will automatically code the first specimen listed as the outgroup).

Specimen Identifications in Phylogenetic Results

1. Carcharhiniformes
2. Carcharhinidae
3. Triakidae
4. Triakidae
5. *Alopias vulpinus*
6. *Odontaspis* sp.
7. *Carcharodon ? auriculatus*
8. *Carcharodon carcharias*
9. *Carcharodon carcharias*
10. *Carcharodon carcharias*
11. *Carcharodon megalodon*
12. *Carcharodon megalodon*
13. *Carcharodon megalodon*
14. *Carcharodon* sp.
15. *Isurus glaucus*
16. *Isurus glaucus*
17. *Lamna ditropis*
18. *Lamna ditropis*

19. *Cetorhinus maximus*
20. *"Tetroras" (=Cetorhinus) maximus*

Phylogenetic Results

An analysis with all specimens and all characters using a Heuristic (TBR) search and Wagner optimization produced one MPT with a tree length of 115 and an ensemble CI of 0.4286.

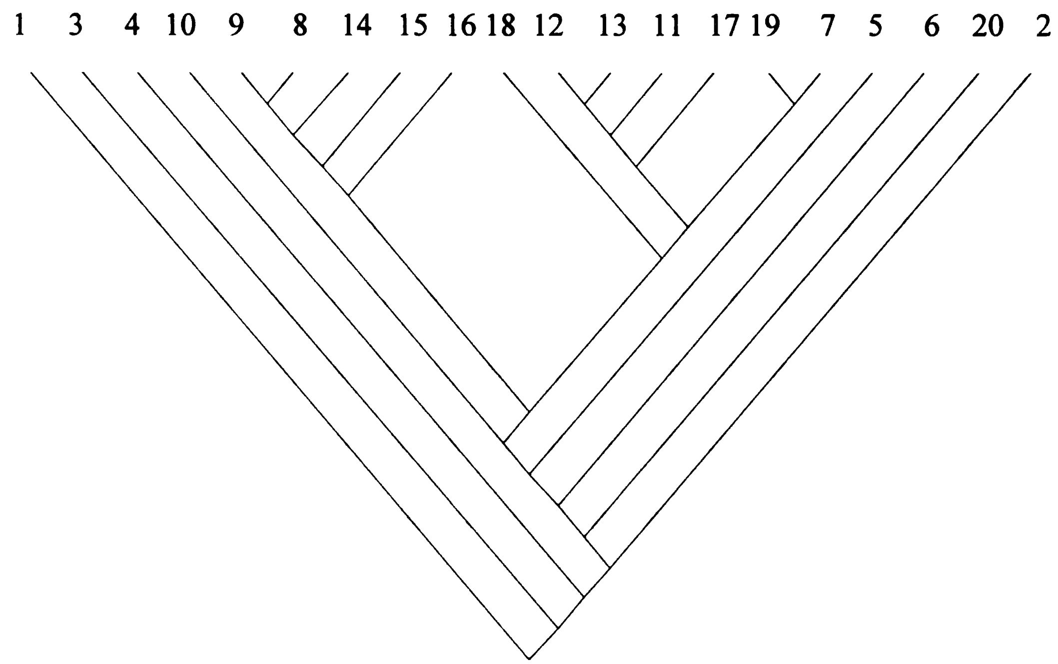


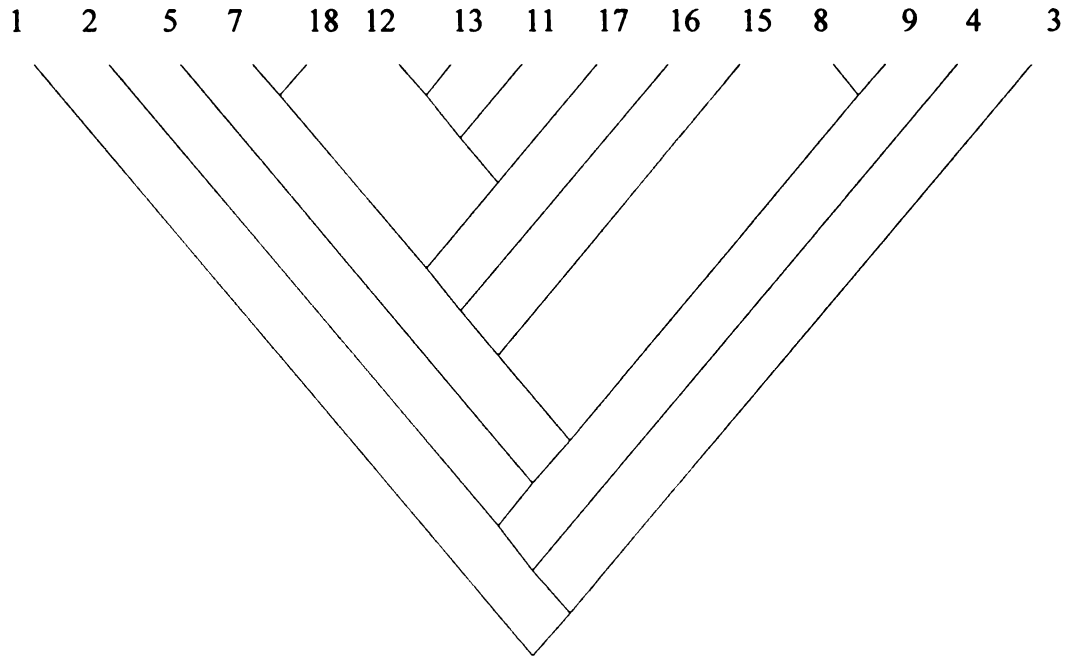
Figure 16: One MPT in analysis of all specimens and all characters.

This analysis most notably shows a distinction between the Carcharhinids and the Lamnids, with the exception of the Carcharhinidae specimen. In addition, all three *Carcharodon megalodon* specimens group together.

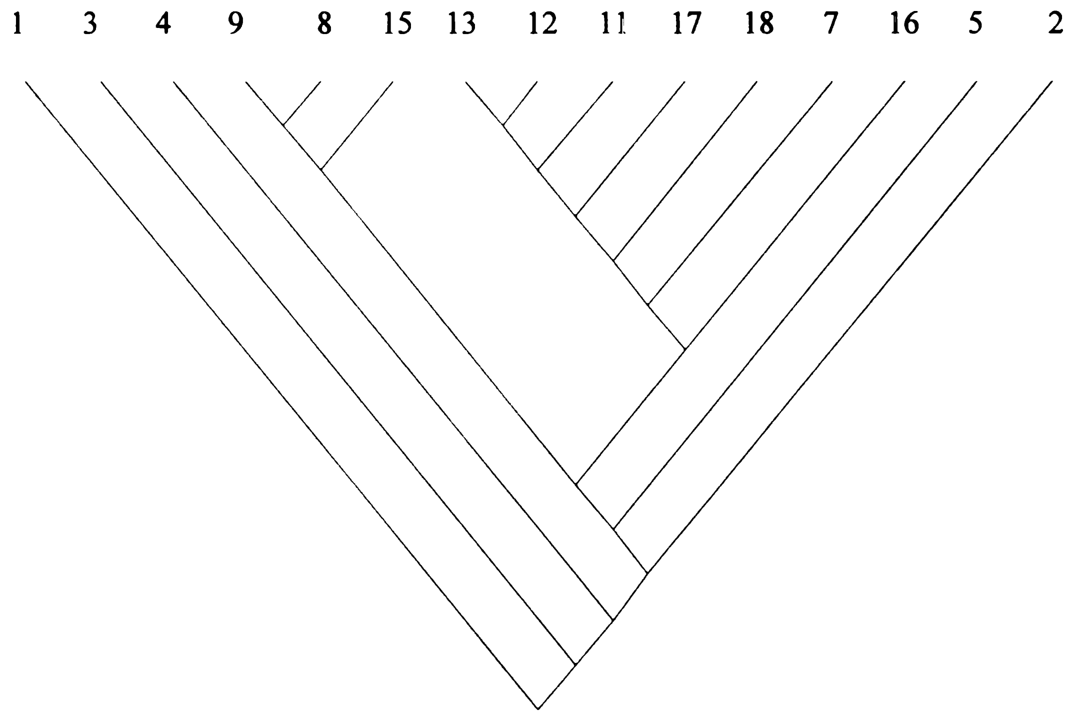
Removal of Specimens 6,10,14,19,20

Specimens 6, 10, 14, 19, and 20 (BMNH P.5821-a, *Odontaspis sp.*; CAs 26678, *Carcharodon carcharias*; BMNH 35860-1, *Carcharodon sp.*; BMNH 2316, *Cetorhinus maximus*; and CAS 224630, *Tetroras [Cetorhinus] maximus*) were removed due to poor preservation quality, which led to either the inability to take measurements (and thus resulting in ?'s for some characters) or, in the case of specimen 10 (CAS 26678, *Carcharodon carcharias*), the inability to take measurements on the specimen and observe certain morphological characteristics (i.e.: the presence or absence of pores) due to the presence of flesh that obscures these from view. *Tetroras (Cetorhinus) maximus* and *Cetorhinus maximus* were removed from further testing, due to their severe distortion (as described in the qualitative analysis section). While this further reduces the number of taxa represented, neither are good representatives of their species as they provide unreliable data. Additionally, *Odontaspis sp.* and *Carcharodon sp.* were removed from the study. Again, as they are the only representatives of their taxa, their removal reduces the taxonomic diversity; however, as internal measurements were not possible for both, there are many characters that are coded at '?' and are therefore phylogenetically not useful.

After the removal of these specimens, a new phylogenetic analysis produced ten MPT's with tree lengths of 99.



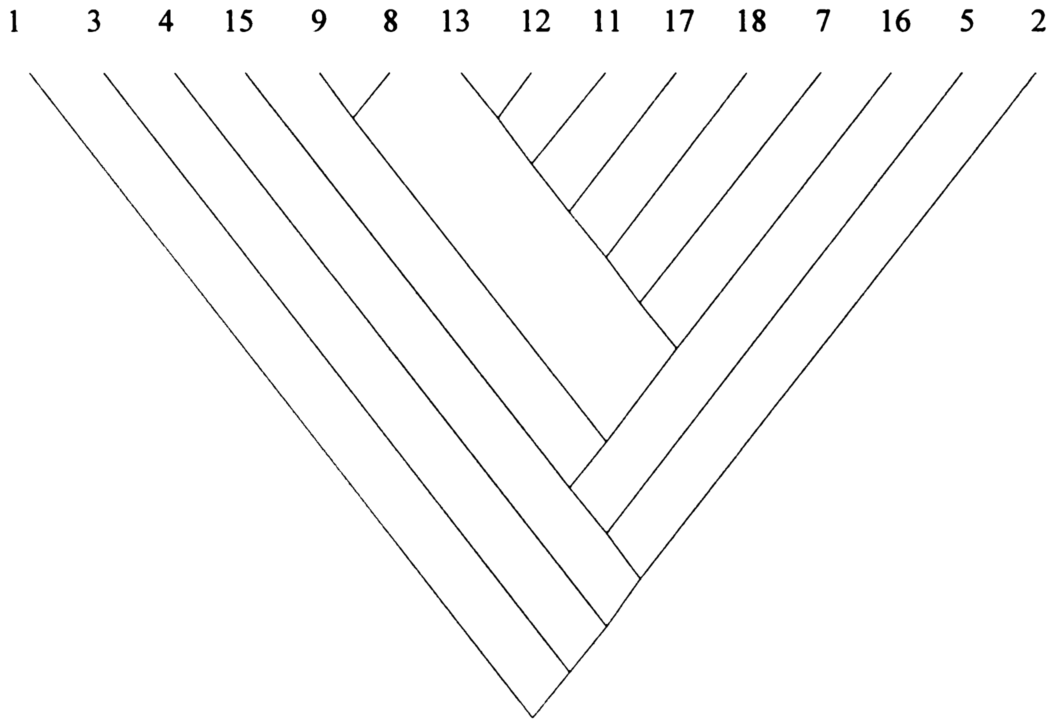
A.



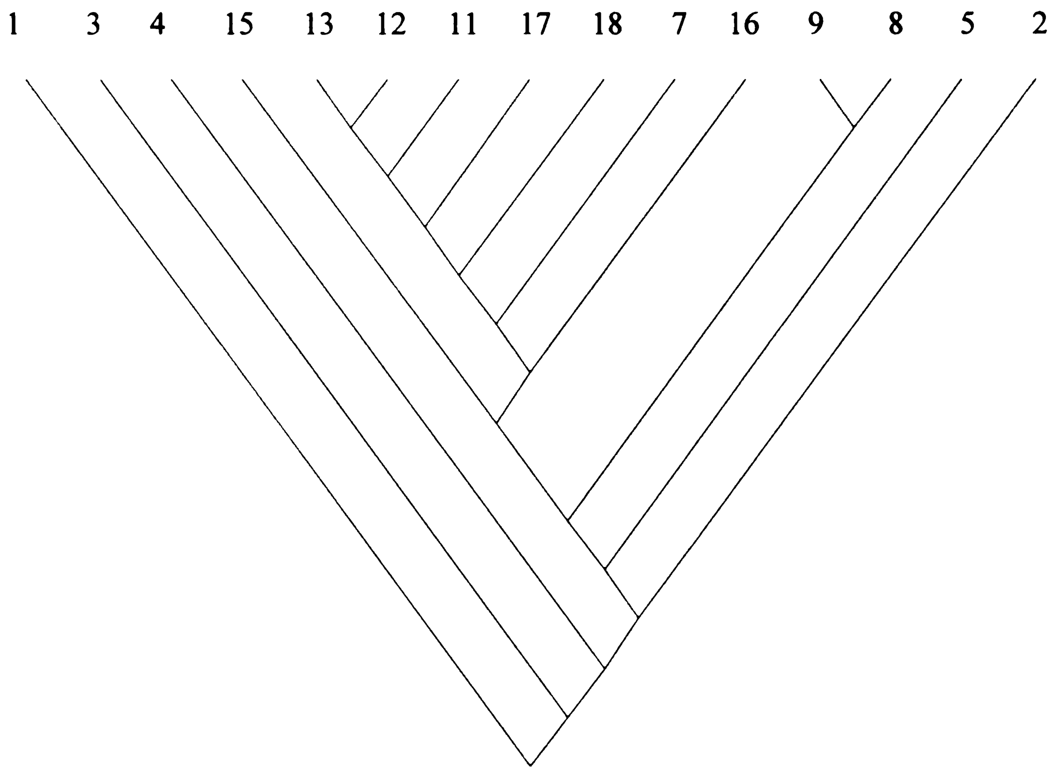
B.

Figure 17: Ten MPT's of analysis without specimens 6, 10, 14, 19, and 20. A, B, C, D, E, F, G, H, I, and J are the ten MPT's; K is the Strict consensus tree; L is the Majority consensus tree.

Figure 17 Continued

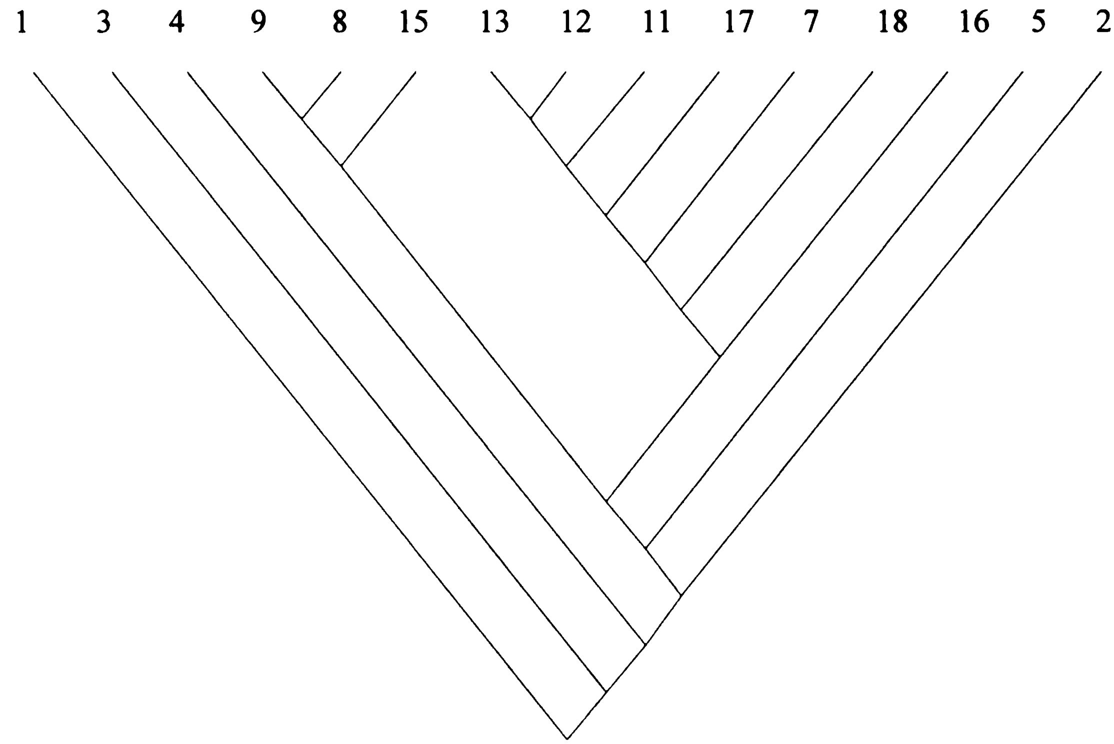


C.

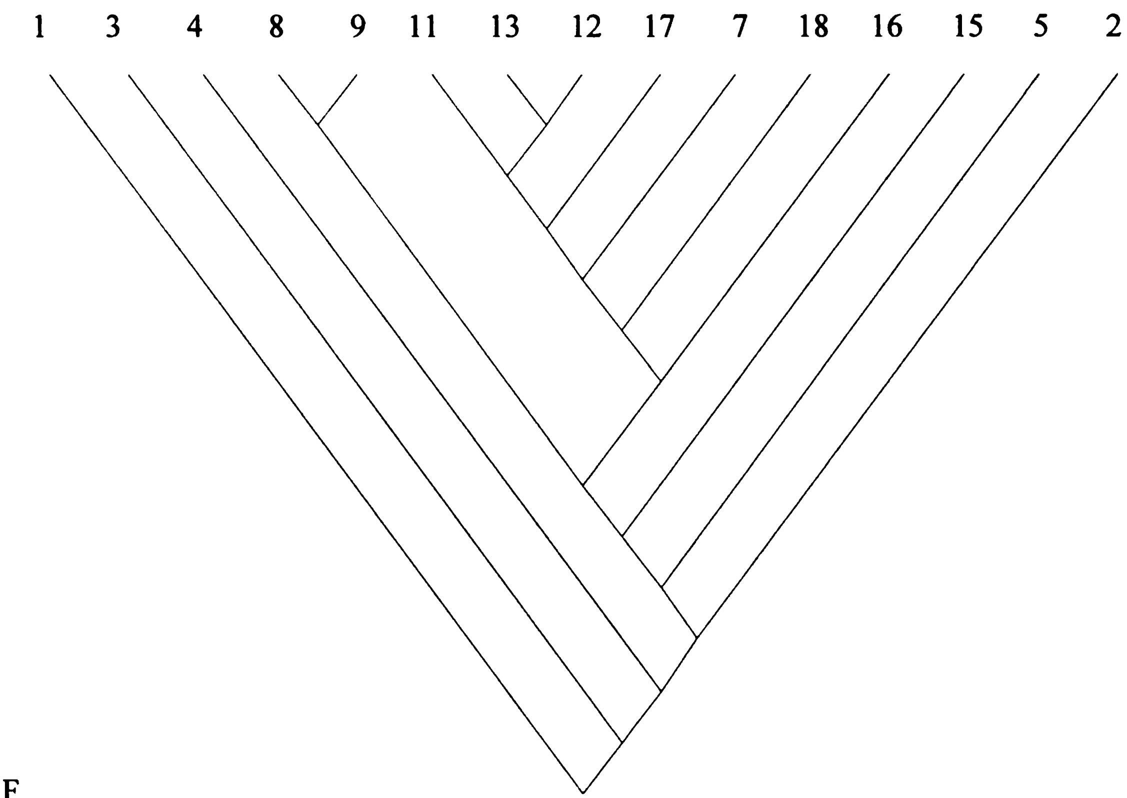


D.

Figure 17 Continued

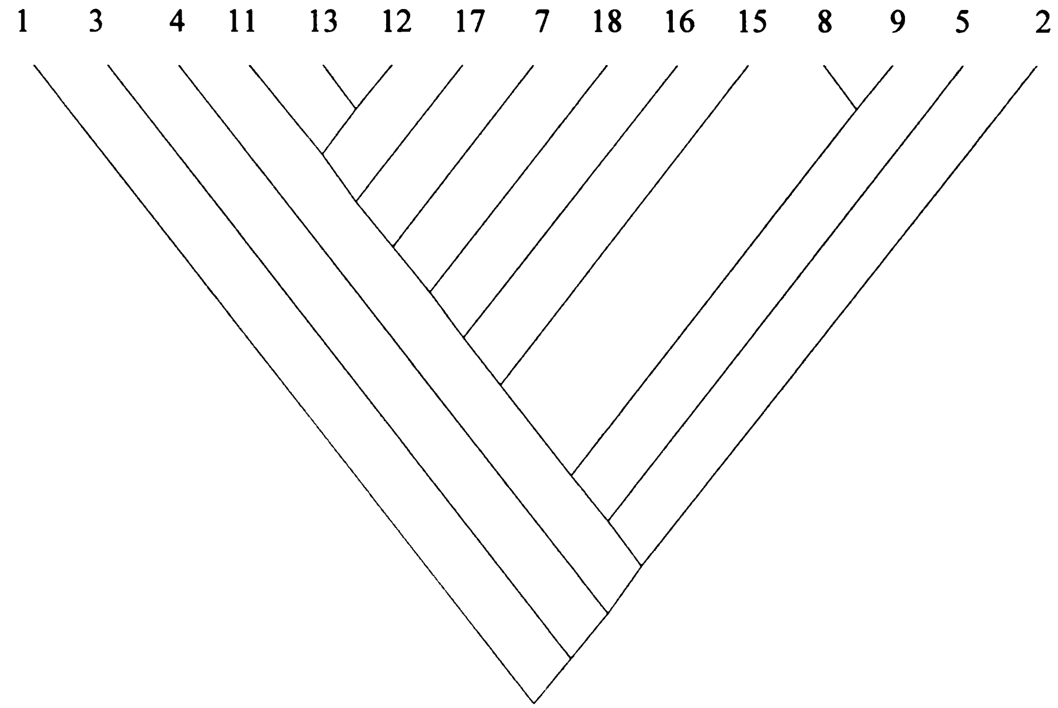


E.

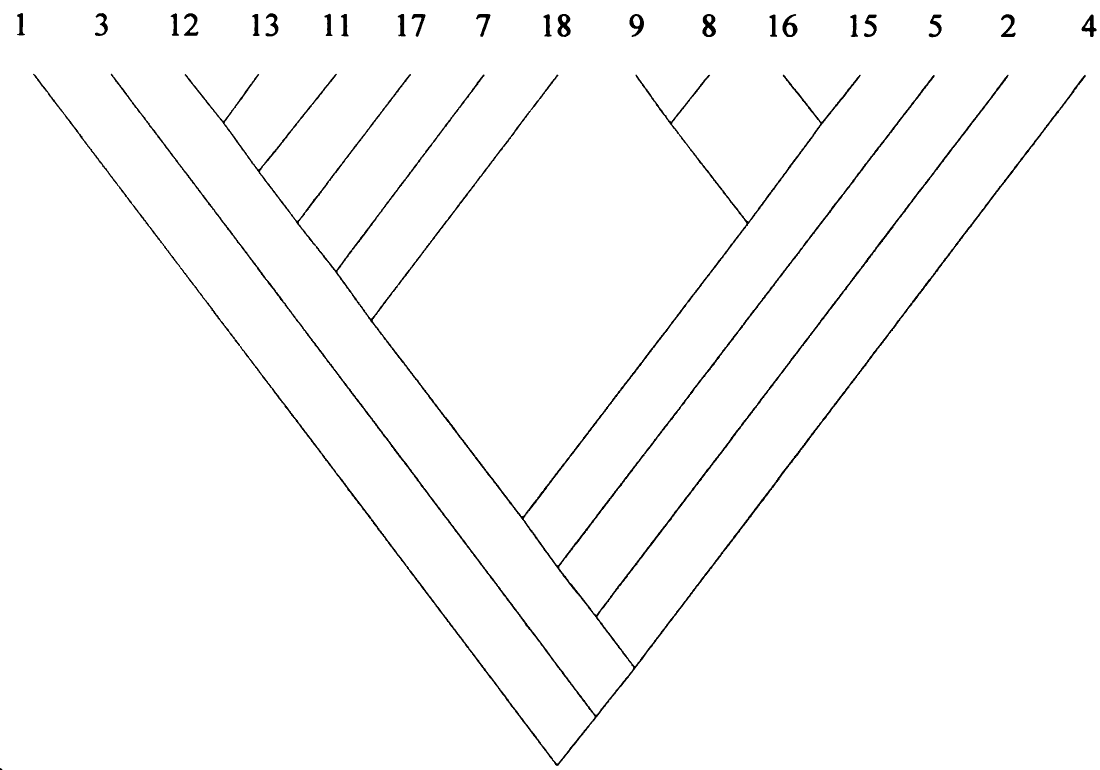


F.

Figure 17 Continued

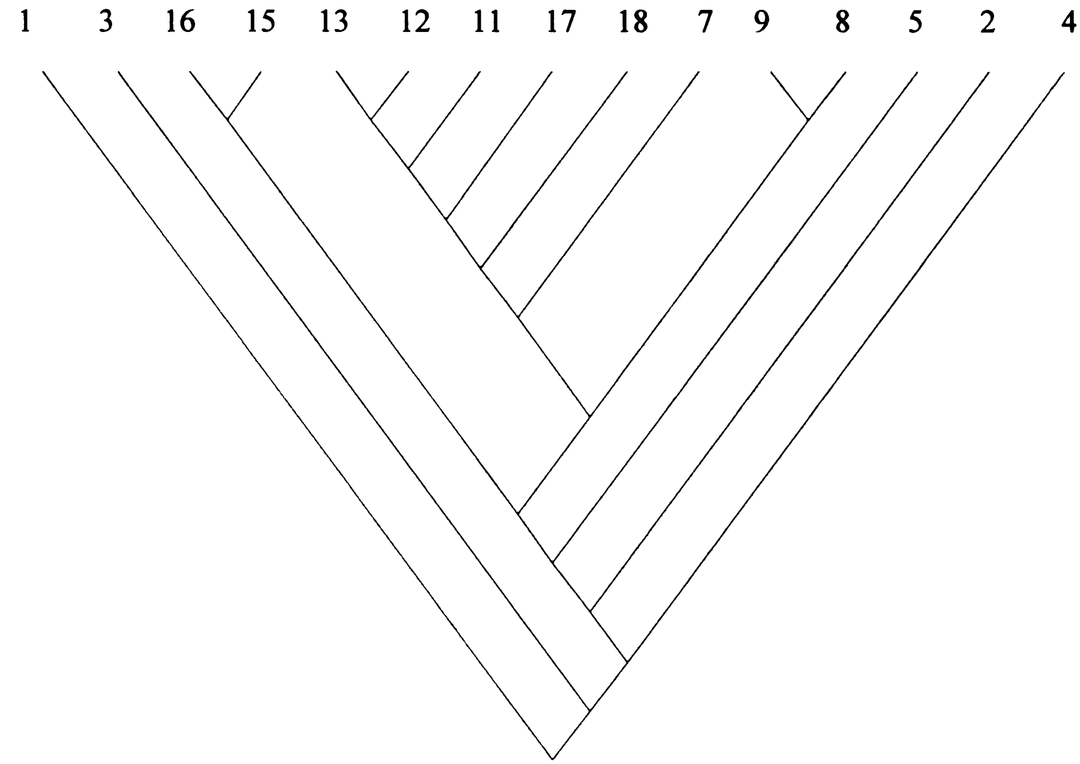


G.

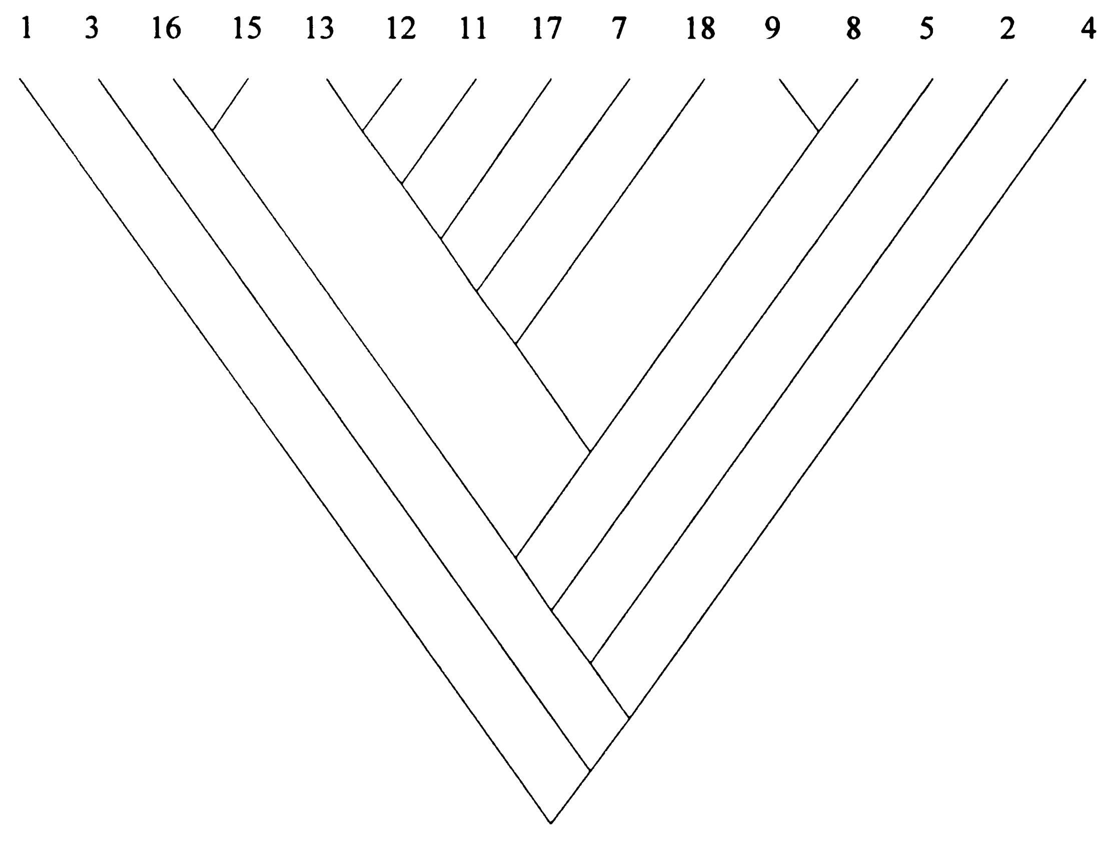


H.

Figure 17 Continued

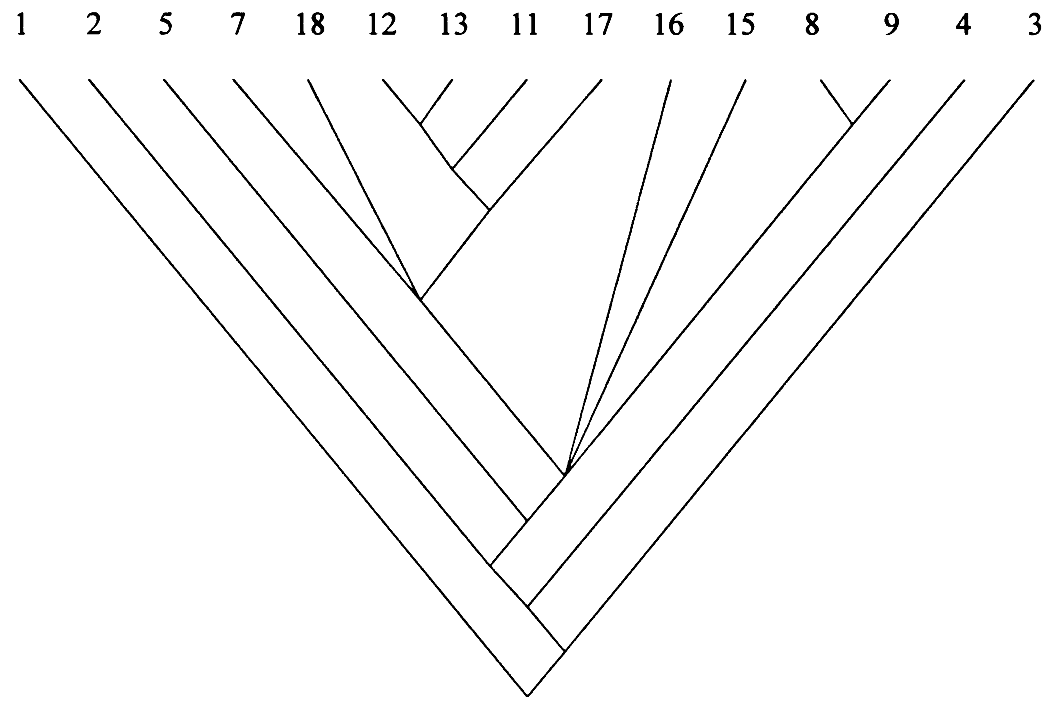


I.

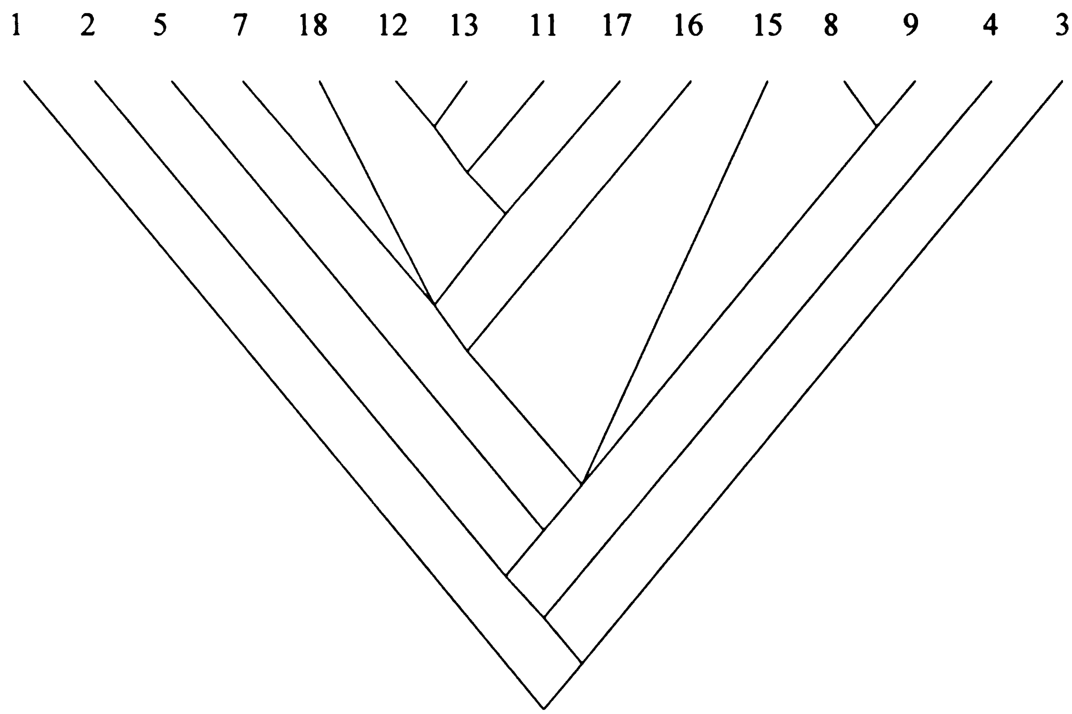


J.

Figure 17 Continued



K.

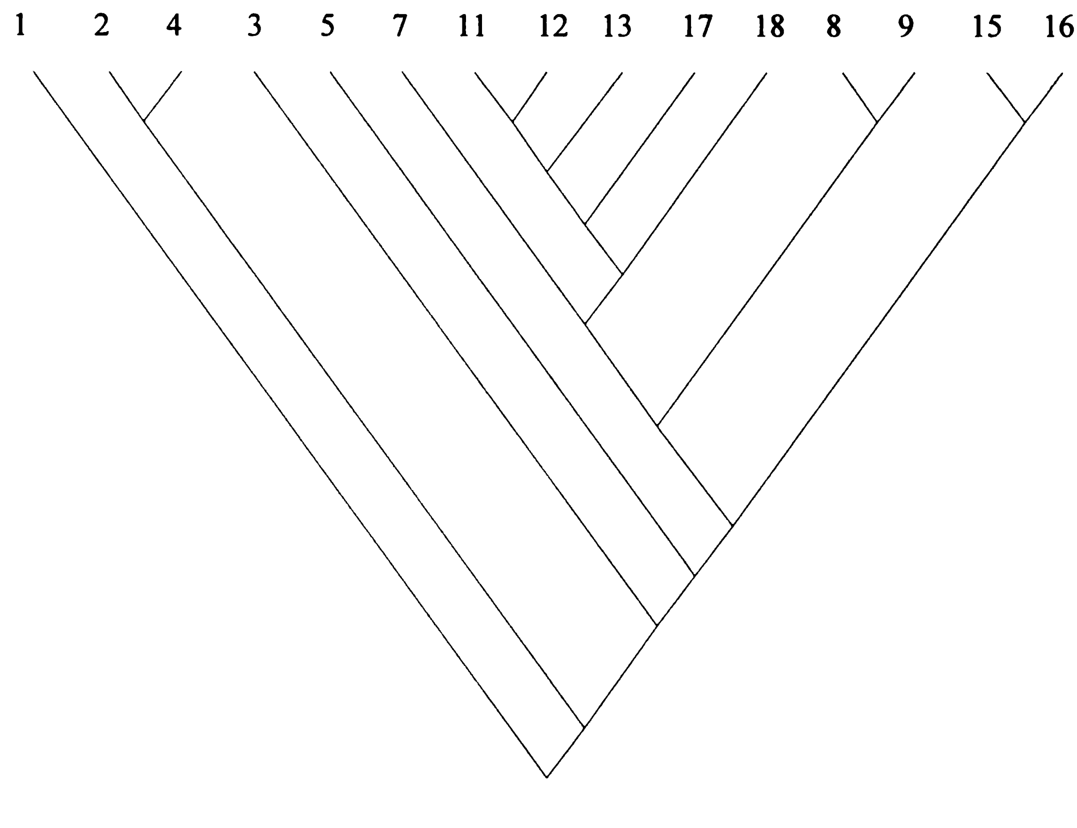


L.

Removal of Characters 1, 11, 12, 13, 15, 19, 24

Characters were removed due to their low CI values (as determined during the initial analysis with all specimens and characters. See Table 1). Removal was based upon a CI of <0.3.

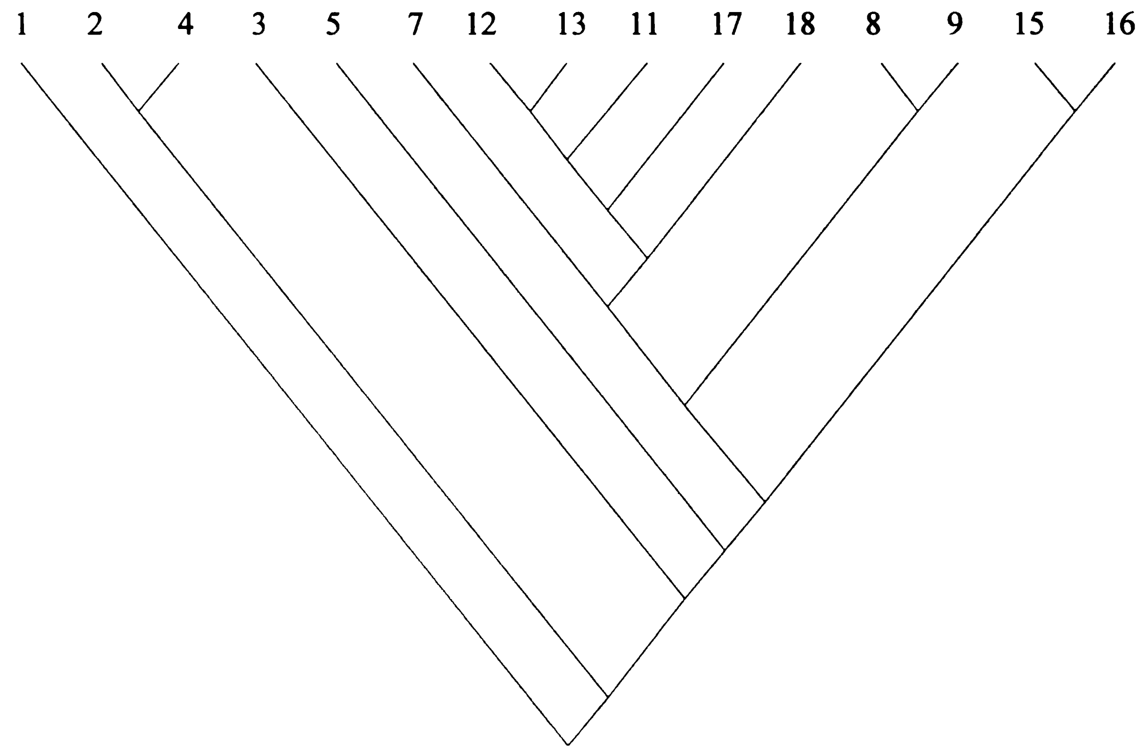
With this combination of the removal of specimens 6, 10, 14, 19 and 20 and characters 1, 11, 12, 13, 15, 19, and 24 there are five MPT's with a length of 67.



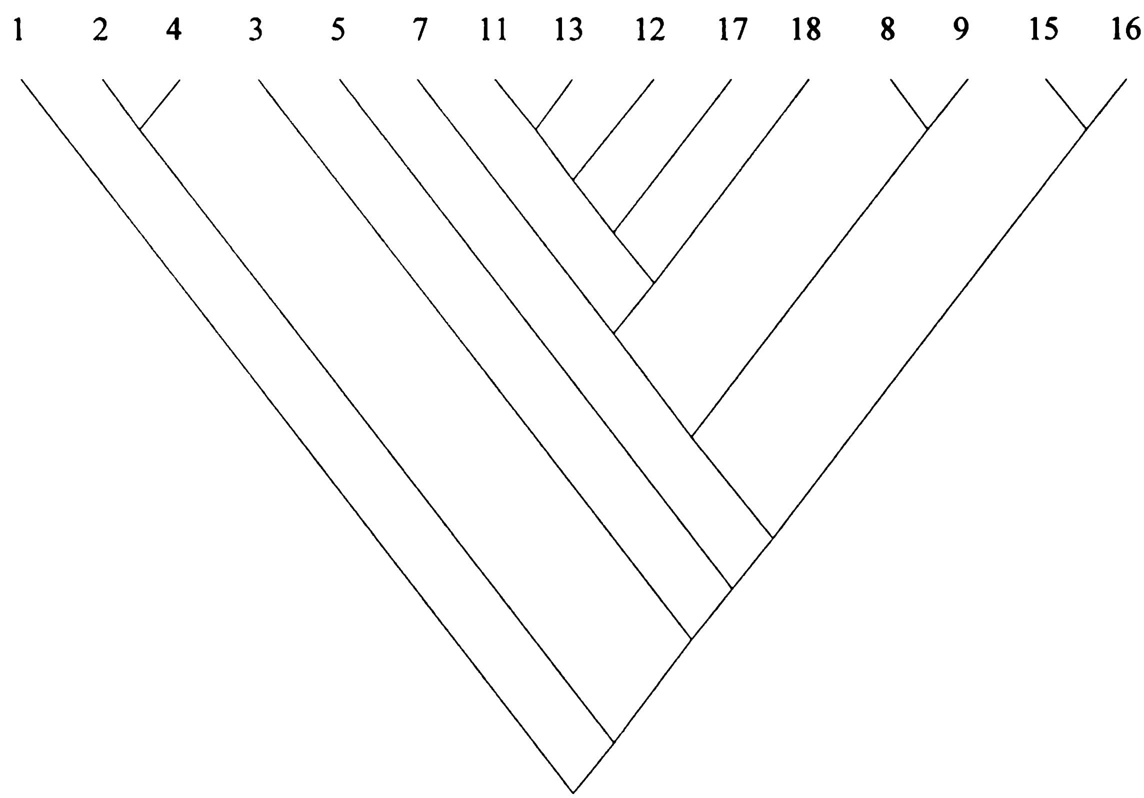
A.

Figure 18: Five MPT's produced with the removal of specimens 6, 10, 14, 19, and 20 and the removal of characters 1, 11, 12, 13, 15, 19, and 24. A, B, C, D, and E are the five MPT's; F is the Strict Consensus tree; G is the Majority Consensus tree.

Figure 18 Continued

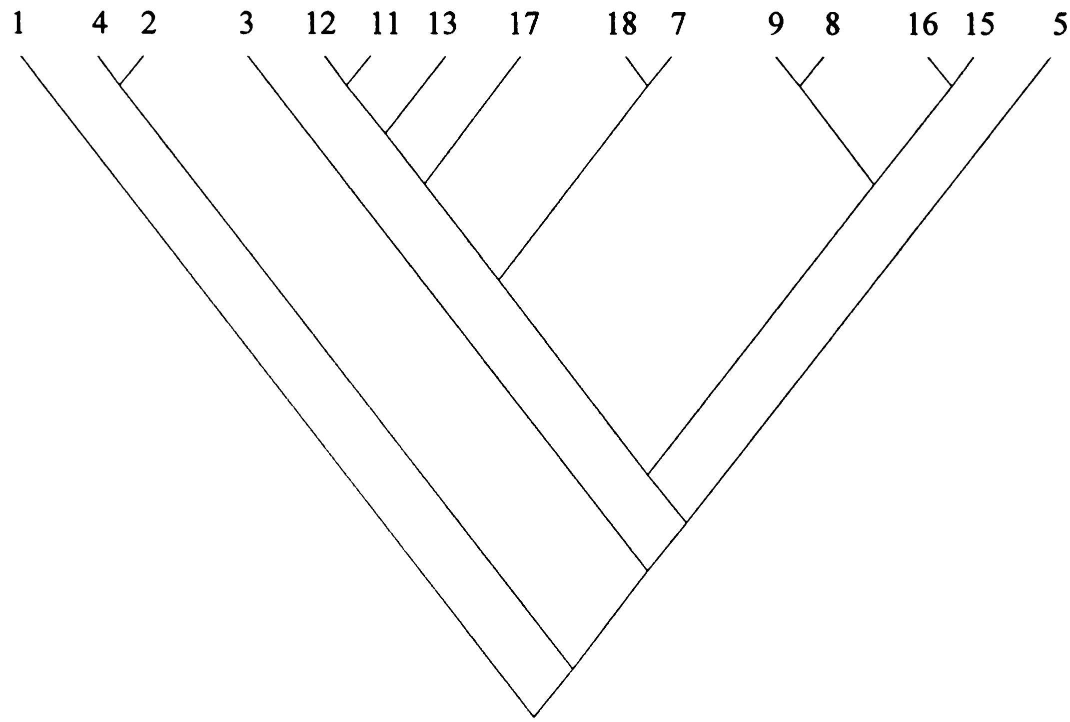


B.

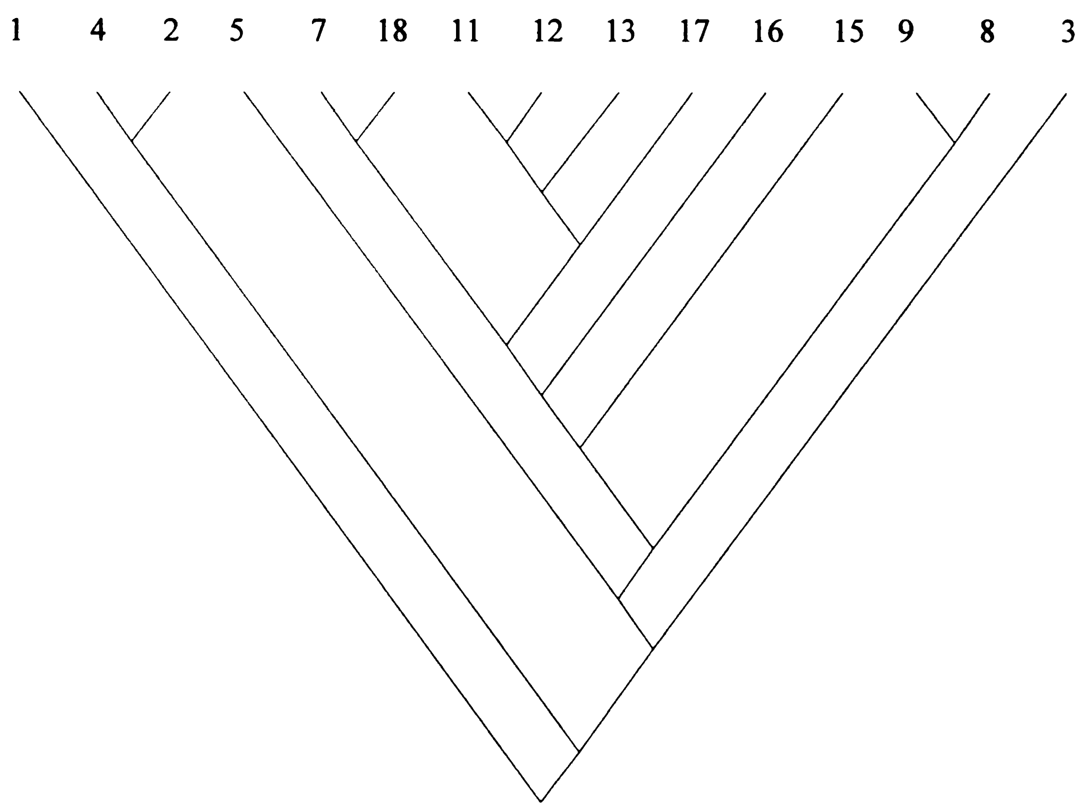


C.

Figure 18 Continued

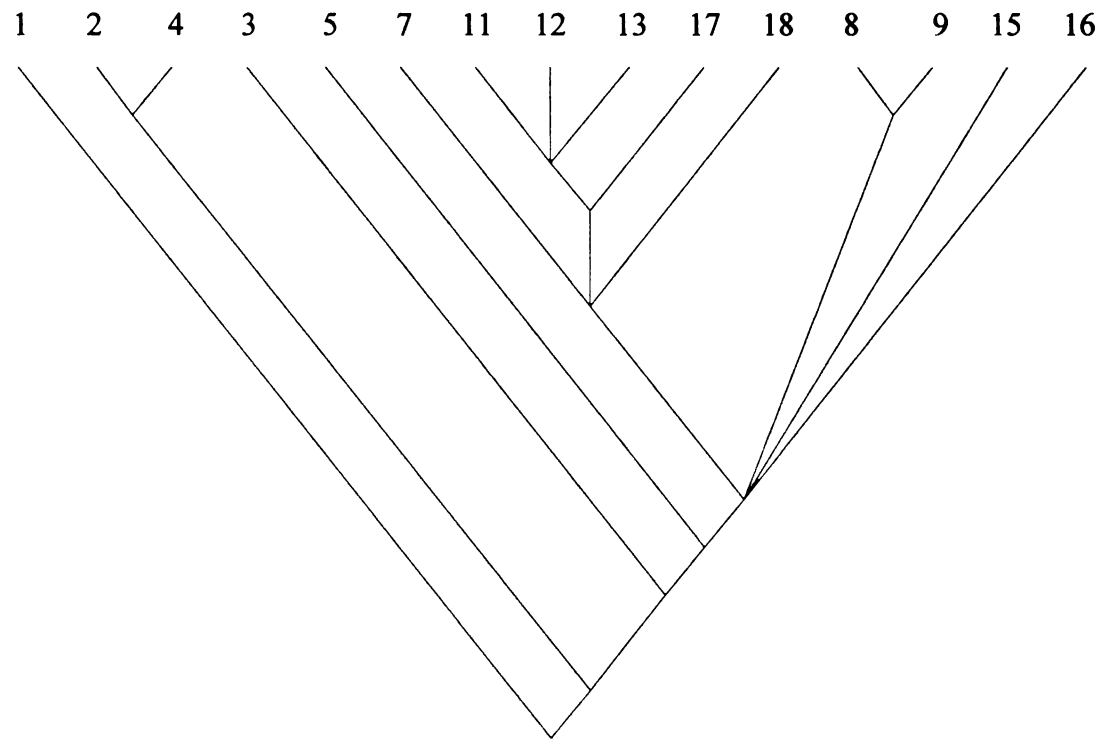


D.

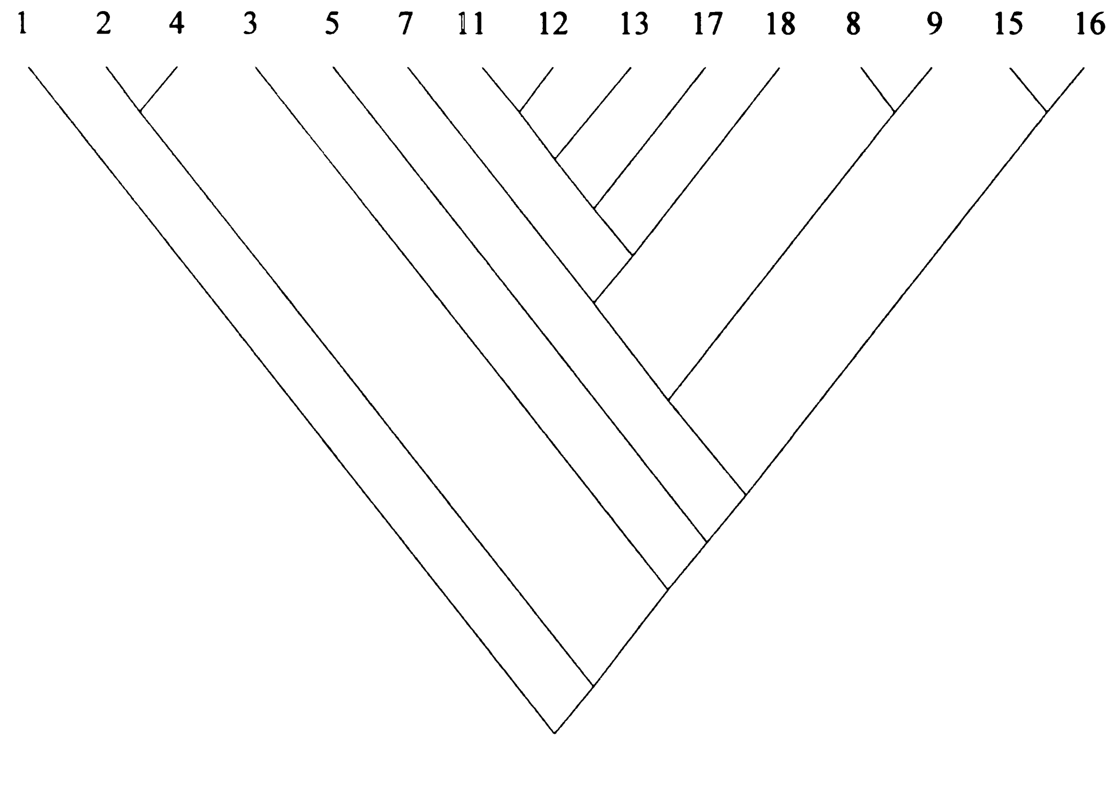


E.

Figure 18 Continued



F.



G.

Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
CI Value	N/A	1	0.67	0.4	0.5	0.33	1	1	1	1	0.17	0.17
Convergence Likely ? (Y/N)	Y	N	N	N	N	N	N	N	N	N	Y	Y
Character	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
CI Value	0.25	1	0.25	0.5	0.5	0.5	0.25	1	1	1	1	0.22
Convergence Likely ? (Y/N)	Y	N	Y	N	N	N	Y	N	N	N	N	Y
Character	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	
CI Value	0.33	0.5	0.33	0.5	0.33	0.5	0.5	0.33	0.33	0.4	0.5	
Convergence Likely ? (Y/N)	N	N	N	N	N	N	N	N	N	N	N	

Table 1: List of characters and their consistency indices. Based upon phylogenetic analysis using all specimens and all characters.

DISCUSSION

Initial Analysis with all Specimens and Characters

Interestingly, the species that groups next closest to *C. megalodon* is *Lamna ditropis*, the salmon shark, a relationship not previously suggested. There is a not much finer resolution, thus leading to further analysis. This includes removing specimens that have poor preservation quality and analyzing the characters for convergence using their CI values. A CI value of 1 is indicative of there being no convergence and a CI of 0 indicates convergence is likely. The results of the characters are given in Table 1.

Analysis with Removal of Specimens 6, 10, 14, 19, and 20

With this combination of specimens and characters, there is resolution, but not any that makes sense. There are specimens of the same species that are separated and those from multiple species lumped together. This is indicative of redundancy and of the existence of non-phylogenetically useful characters, as well as a possible indication of convergence among characters.

Analysis with Removal of Specimens 6, 10, 14, 19, and 20 and Characters 1, 11, 12, 13, 15, 19, and 24

In the final analysis (with the removal of both the poorly preserved specimens and the convergent characters), both the strict and majority consensus trees show nearly identical results. The Carcharhinids are basal to the Lamnids, as is to be expected with their assignation as the outgroup. Recovery of phylogenetically useful information is indicative that shark vertebral centra retain some degree of phylogenetic signal. This is shown through the recovery of the *Carcharodon megalodon* speciemens (11, 12, and 13) together. Additionally, the *Lamna ditropis* specimens group together, as do the *Carcharodon carcharias* (8 and 9) and *Isurus glaucus* (15 and 16) specimens.

It is interesting to note that the species that grouped closest to *Carcharodon megalodon* are *Carcharodon auriculatus (?)* and *Lamna ditropis*. As *C. auriculatus* is another member of the genus *Carcharodon* (and another large, fossil shark), their close association is not surprising. *Lamna ditropis'* close association is, however, a relationship not previously suggested in the literature and provides a new possibility for *C. megalodon* placement within the Lamnids

Also of note is the close association between the *Carcharodon carcharias* specimens and the *Isurus glaucus* specimens, as these are often touted as close cousins of one another. Therefore, these results are significant regarding the usefulness of shark vertebral centra in phylogenetics.

The placement of *Alopias vulpinus* as the most basal Lamnid is also not surprising as they are the most physically distinct species in the analysis, possessing the elongate caudal fin which gives the species its common name of Thresher Shark.

Limitations

Specimen preservation was a large limitation during the analysis, as specimens which were poorly preserved (either taphonomically, or during museum preparation) resulted in removal from the study due to lack of reliable data. Additionally, there is a relatively poor availability of skeletonizes shark specimens, both of fossil and recent specimens. Due to their scarcity in the fossil record and the existence of protective laws for the capture of living animals, specimens available for study are often reliant upon those that are already present in museum collections. This leads to the limitation of having mostly only individual vertebrae as opposed to fully vertebral columns. Not knowing where along the spinal column an individual vertebrae comes from could be significant. This is because vertebral vary both in size and shape along the column due to the function each section has (i.e.: neck, thoracic, lumbar, or caudal). Additionally, the age of the specimen could be significant. Varying ontogenetic stages may alter the measurements of the vertebrae. As an individual ages, stresses along the column may change and may thus manifest themselves in varied ways. Without a standardized set of acceptable variation for specimens ate different developmental stages, results will only be as good as the identifications on the collections labels.

CONCLUSION

CT Scanning

The use of CT scanning on fossil vertebrates, though not a new technique has shown in this case to be useful for the identification and subsequent study of new phylogenetic characters.

Carcharodon megalodon *affinities with* C. carcharias

The hypothesis that *Carcharodon carcharias* is a sister taxa to *Carcharodon megalodon* is not supported in this analysis. Placement of *C. megalodon* specimens nearer to *C. carcharias* specimens does not occur, though they are separated from the Carcharhinifomes. Specimens 11, 12, and 13, (BMNH 4808, BMNH 4809, and BMNH 4810, all *Carcharodon megalodon*) do group together, though specimens 17 and 18 (CAS 26710.a and CAS 26710.b, both *Lamna ditropis*) are closest to them. The two *Lamna ditropis* specimens should theoretically group together, as they are from the same individual. In addition, all of the various members of the genus *Carcharodon* should also group, and they do not. We do see specimens 8 and 9 (both modern Great White *Carcharodon carcharias* specimens) together as well as a closer association of the *C. megalodon* specimens with the *C. auriculatus* specimen, though the presence of the *Lamna ditropis* specimens is unsettling.

The Mako specimens (15 and 16, CAS SU40902.a and CAS SU40902.b) group together and share a node with the modern *Carcharodon carcharias* specimes. This is significant as they closely related specimens.

Directions for Future Research

Though the images produced with computerized tomography were satisfactory enough to allow for internal examination, more precise and more detailed images will only serve to increase confidence with respect to the internal measurements taken. In addition, more powerful imaging software will allow for great manipulation of the images.

Development of a database of various species' ontogenetic (including stress factors due to use/aging) differences will allow for a greater understanding of the variances in specimens due to accountable factors. This will also allow us to focus on the differences due to species, not because of growth or stresses along the skeletal frame. Additionally, including information on the location of a single vertebrae along the spinal column will also account for the observed variation among specimens.

The use of a more powerful phylogenetic analysis program will also produce results with more impact. A program such as PAUP would be able to handle larger test runs (such as with branch-and-bound testing) and would therefore take into account all possible phylogenetic trees. Convergence among characters, though taken into consideration in this study, can still be addressed in future work. As always, the inclusion of more characters and more specimens will greatly increase the impact of the results.

Combining vertebral data with preexisting data sets (most notably those of teeth) will form a larger, more inclusive data set. This will help to fortify the conclusions this study has drawn (i.e.: the presence of *Lamna ditropis* as the sister taxa to *Carcharodon megalodon*).

APPENDIX A: SPECIMEN LIST

Specimen #	**Identification**
CAS 65976	*Alopias vulpinus*
BM P.5821-a	*Odontaspis sp.*
BM P.8983	*Carcharodon auriculatus (?)*
CAS 25844.a	*Carcharodon carcharias*
CAS 25844.b	*Carcharodon carcharias*
CAS 26678	*Carcharodon carcharias*
BM PV4808	*Carcharodon megalodon*
BM PV4809	*Carcharodon megalodon*
BM PV4810	*Carcharodon megalodon*
BM 35860-1	*Carcharodon sp.*
CAS SU40902.a	*Isurus glaucus*
CAS SU40902.b	*Isurus glaucus*
CAS 26710.a	*Lamna ditropis*
CAS 26710.b	*Lamna ditropis*
BM 2316	*Cetorhinus maximus*
CAS 224630	*"Tetroras" (=Cetorhinus) maximus*
SDSNH 63154	Carcharhiniformes (Order-level)
SDSNH 65993	Carcharhinidae (Family-level)
SDSNH 75551	Triakidae (Family-level)
SDSNH 71143	Triakidae (Family-level)

APPENDIX B: EXTERNAL MEASUREMENTS

Specimen	Identification	Diameter 1	Diameter 2	Centrum Length	Centrum Width
CAS 65976	*Alopisa vulpinus*	1.090	1.079	0.327	1.002
BM P.5821-a	*Odontaspis sp.*	2.342	2.232	1.200	2.461
BM P.8983	*Carcharodon auriculatus*	10.776	10.703	3.975	10.251
CAS 25844.a	*Carcharodon carcharias*	2.468	2.433	0.961	2.288
CAS 25844.b	*Carcharodon carcharias*	2.353	2.347	0.629	2.304
CAS 26678	*Carcharodon carcharias*	5.815	5.697	2.789	5.774
BM PV4808	*Carcharodon megalodon*	8.490	8.441	3.262	8.375
BM PV4809	*Carcharodon megalodon*	9.513	9.421	3.499	9.262
BM PV4810	*Carcharodon megalodon*	9.257	9.029	3.442	8.983
BM 35860-1	*Carcharodon sp.*	7.591	N/A	2.818	7.650
CAS SU40902.a	*Isurus glaucus*	1.299	1.286	0.480	1.277
CAS SU40902.b	*Isurus glaucus*	1.358	1.367	0.558	1.339
CAS 26710.a	*Lamna ditropis*	3.148	3.131	1.025	3.136
CAS 26710.b	*Lamna ditropis*	3.028	2.982	1.160	2.953
BM 2316	*Cetorhinus maxiums*	10.268	9.463	2.911	9.507
CAS 224630	*Teroras (=Cetorhinus) maximus*	6.441	6.421	3.718	4.633

Specimen	Identification	Centrum Height	D Foram L	D Foram W	D Interforam W
CAS 65976	*Alopisa vulpinus*	1.098	0.298	0.296	0.144
BM P.5821-a	*Odontaspis sp.*	2.462	0.889	0.454	0.665
BM P.8983	*Carcharodon auriculatus*	9.794	2.036	1.845	3.244
CAS 25844.a	*Carcharodon carcharias*	2.530	0.476	0.347	0.615
CAS 25844.b	*Carcharodon carcharias*	2.368	0.137	0.373	0.521
CAS 26678	*Carcharodon carcharias*	5.786	1.730	1.027	0.903
BM PV4808	*Carcharodon megalodon*	8.661	2.077	11.568	3.048
BM PV4809	*Carcharodon megalodon*	9.313	2.327	1.932	3.689
BM PV4810	*Carcharodon megalodon*	9.059	2.199	2.266	3.439
BM 35860-1	*Carcharodon sp.*	8.291	1.499	1.219	2.270
CAS SU40902.a	*Isurus glaucus*	1.258	0.244	0.271	0.281
CAS SU40902.b	*Isurus glaucus*	1.306	0.276	0.211	0.312
CAS 26710.a	*Lamna ditropis*	3.233	0.732	0.449	0.739
CAS 26710.b	*Lamna ditropis*	2.937	0.810	0.516	0.655
BM 2316	*Cetorhinus maxiums*	N/A	N/A	2.002	2.826
CAS 224630	*Teroras (=Cetorhinus) maximus*	5.053	N/A	1.071	0.427

Specimen	Identification	V Foram L	V Foram W	V Interforam W
CAS 65976	*Alopisa vulpinus*	0.276	0.138	0.408
BM P.5821-a	*Odontaspis sp.*	0.937	0.475	1.165
BM P.8983	*Carcharodon auriculatus*	1.576	2.251	4.773
CAS 25844.a	*Carcharodon carcharias*	0.455	0.308	0.653
CAS 25844.b	*Carcharodon carcharias*	0.210	0.289	0.582
CAS 26678	*Carcharodon carcharias*	1.571	0.814	2.356
BM PV4808	*Carcharodon megalodon*	2.123	2.148	3.399
BM PV4809	*Carcharodon megalodon*	2.196	1.625	3.744
BM PV4810	*Carcharodon megalodon*	2.189	1.920	3.558
BM 35860-1	*Carcharodon sp.*	1.173	1.200	3.066
CAS SU40902.a	*Isurus glaucus*	0.238	0.227	0.461
CAS SU40902.b	*Isurus glaucus*	0.252	0.228	0.410
CAS 26710.a	*Lamna ditropis*	0.694	0.625	0.856
CAS 26710.b	*Lamna ditropis*	0.686	0.486	0.879
BM 2316	*Cetorhinus maxiums*	N/A	N/A	N/A
CAS 224630	*Teroras (=Cetorhinus) maximus*	N/A	1.250	1.325

Specimen	Identification	Diameter 1	Diameter 2	Centrum Length	Centrum Width
SDSNH 63154	Carcharhiniformes (Order)	3.596	3.538	1.894	3.249
SDSNH 65993	Carcharhinidae (Family)	2.094	2.030	1.277	1.815
SDSNH 75551	Triakidae (Family)	0.661	0.644	0.539	0.582
SDSNH 71143	Triakidae (Family)	3.836	3.800	3.131	3.318

Specimen	Identification	Centrum Height	D Foram L	D Foram W	D Interforam W
SDSNH 63154	Carcharhiniformes (Order)	3.236	1.550	0.816	0.671
SDSNH 65993	Carcharhinidae (Family)	1.797	0.953	0.415	0.417
SDSNH 75551	Triakidae (Family)	0.539	0.319	0.140	0.161
SDSNH 71143	Triakidae (Family)	4.008	2.527	0.702	0.676

Specimen	Identification	V Foram L	V Foram W	V Interforam W
SDSNH 63154	Carcharhiniformes (Order)	1.715	0.745	0.751
SDSNH 65993	Carcharhinidae (Family)	0.949	0.332	0.482
SDSNH 75551	Triakidae (Family)	0.278	0.140	0.170
SDSNH 71143	Triakidae (Family)	2.502	0.726	0.776

APPENDIX C: INTERNAL MEASUREMENTS

Specimen	Identification	Inner Zone H	Inner Zone W	D Inner Foram W	V Inner Foram W
CAS 65976	*Alopisa vulpinus*	0.167	0.144	0.02361	0.0435
BM P.5821-a	*Odontaspis sp.*	N/A	N/A	N/A	N/A
BM P.8983	*Carcharodon auriculatus*	0.797	0.818	0.355	0.301
CAS 25844.a	*Carcharodon carcharias*	0.490	0.413	0.203	0.199
CAS 25844.b	*Carcharodon carcharias*	0.446	0.393	0.198	0.181
CAS 26678	*Carcharodon carcharias*	0.792	0.526	0.105	0.117
BM PV4808	*Carcharodon megalodon*	0.180	0.180	0.157	0.114
BM PV4809	*Carcharodon megalodon*	0.167	0.204	0.0807	0.09786
BM PV4810	*Carcharodon megalodon*	0.114	0.161	0.105	0.104
BM 35860-1	*Carcharodon sp.*	N/A	N/A	N/A	N/A
CAS SU40902.a	*Isurus glaucus*	0.166	0.192	0/05701	0.07433
CAS SU40902.b	*Isurus glaucus*	0.208	0.185	0.05602	0.05014
CAS 26710.a	*Lamna ditropis*	0.293	0.266	0.05319	0.09402
CAS 26710.b	*Lamna ditropis*	0.315	0.277	0.6649	0.04205
BM 2316	*Cetorhinus maxiums*	0.734	0.792	0.236	N/A
CAS 224630	*Teroras (=Cetorhinus) maximus*	0.131	0.0807	0.117	0.211

Specimen	Identification	D Depth	V Depth	D Foram Angle	V Foram Angle
CAS 65976	*Alopisa vulpinus*	0.433	0.434	51.683	24.053
BM P.5821-a	*Odontaspis sp.*	N/A	N/A	N/A	N/A
BM P.8983	*Carcharodon auriculatus*	3.971	4.172	21.589	24.252
CAS 25844.a	*Carcharodon carcharias*	0.884	0.903	30.076	26.949
CAS 25844.b	*Carcharodon carcharias*	0.759	0.816	31.453	26.282
CAS 26678	*Carcharodon carcharias*	2.480	2.612	23.035	19.902
BM PV4808	*Carcharodon megalodon*	3.829	3.685	23.772	28.338
BM PV4809	*Carcharodon megalodon*	4.049	4.167	26.767	24.461
BM PV4810	*Carcharodon megalodon*	4.458	4.352	31.044	30.061
BM 35860-1	*Carcharodon sp.*	N/A	N/A	N/A	N/A
CAS SU40902.a	*Isurus glaucus*	0.348	0.421	36.216	30.466
CAS SU40902.b	*Isurus glaucus*	0.464	0.468	25.852	23.928
CAS 26710.a	*Lamna ditropis*	1.393	1.471	21.884	28.301
CAS 26710.b	*Lamna ditropis*	1.290	1.239	25.206	24.083
BM 2316	*Cetorhinus maxiums*	4.316	N/A	24.354	N/A
CAS 224630	*Teroras (=Cetorhinus) maximus*	1.762	1.775	30.845	40.138

Specimen	Identification	D Int Foram Inner W	V Int Foram Inner W	D Int Foram Anlge
CAS 65976	*Alopisa vulpinus*	0.07084	0.144	24.146
BM P.5821-a	*Odontaspis sp.*	N/A	N/A	N/A
BM P.8983	*Carcharodon auriculatus*	0.183	0.295	38.115
CAS 25844.a	*Carcharodon carcharias*	0.161	0.107	49.646
CAS 25844.b	*Carcharodon carcharias*	0.232	0.194	47.812
CAS 26678	*Carcharodon carcharias*	0.314	0.431	26.505
BM PV4808	*Carcharodon megalodon*	0.149	0.193	44.957
BM PV4809	*Carcharodon megalodon*	0.204	0.149	46.260
BM PV4810	*Carcharodon megalodon*	0.149	0.161	39.718
BM 35860-1	*Carcharodon sp.*	N/A	N/A	N/A
CAS SU40902.a	*Isurus glaucus*	0.065	0.03606	26.809
CAS SU40902.b	*Isurus glaucus*	0.03546	0.03964	33.586
CAS 26710.a	*Lamna ditropis*	0.196	0.196	37.646
CAS 26710.b	*Lamna ditropis*	0.208	0.244	34.442
BM 2316	*Cetorhinus maxiums*	0.197	N/A	32.381
CAS 224630	*Teroras (=Cetorhinus) maximus*	0.138	0.360	12.364

Specimen	Identification	V Int Foram Angle	D Foram Area	V Foram Area
CAS 65976	*Alopisa vulpinus*	58.671	0.064	0.030
BM P.5821-a	*Odontaspis sp.*	N/A	N/A	N/A
BM P.8983	*Carcharodon auriculatus*	58.195	3.663	4.696
CAS 25844.a	*Carcharodon carcharias*	50.092	0.153	0.139
CAS 25844.b	*Carcharodon carcharias*	51.528	0.142	0.118
CAS 26678	*Carcharodon carcharias*	60.082	1.273	1.063
BM PV4808	*Carcharodon megalodon*	44.128	3.002	3.958
BM PV4809	*Carcharodon megalodon*	47.150	3.911	3.386
BM PV4810	*Carcharodon megalodon*	41.809	5.051	4.178
BM 35860-1	*Carcharodon sp.*	N/A	N/A	N/A
CAS SU40902.a	*Isurus glaucus*	53.893	0.047	0.048
CAS SU40902.b	*Isurus glaucus*	51.546	0.049	0.053
CAS 26710.a	*Lamna ditropis*	38.518	0.313	0.460
CAS 26710.b	*Lamna ditropis*	48.257	0.333	0.301
BM 2316	*Cetorhinus maxiums*	N/A	4.320	N/A
CAS 224630	*Teroras (=Cetorhinus) maximus*	37.153	0.944	1.109

Specimen	Identification	Inner Zone H	Inner Zone W	D Inner Foram W	V Inner Foram W
SDSNH 63154	Carcharhiniformes (Order)	0.05253	0.07895	0.05874	0.07443
SDSNH 65993	Carcharhinidae (Family)	0.05884	0.05263	0.190	0.200
SDSNH 75551	Triakidae (Family)	0.02632	0.02543	0.03576	0.03478
SDSNH 71143	Triakidae (Family)	0.05263	0.05884	0.05884	0.08322

Specimen	Identification	D Depth	V Depth	D Foram Angle	V Foram Angle
SDSNH 63154	Carcharhiniformes (Order)	0.425	0.333	54.008	54.008
SDSNH 65993	Carcharhinidae (Family)	1.189	1.296	33.723	33.723
SDSNH 75551	Triakidae (Family)	0.105	0.09488	53.455	53.455
SDSNH 71143	Triakidae (Family)	1.660	1.548	24.312	24.312

Specimen	Identification	D Int Foram Inner W	V Int Foram Inner W	D Int Foram Angle
SDSNH 63154	Carcharhiniformes (Order)	0.263	0.396	43.632
SDSNH 65993	Carcharhinidae (Family)	0.132	0.243	30.082
SDSNH 75551	Triakidae (Family)	0.08322	0.07444	46.507
SDSNH 71143	Triakidae (Family)	0.250	0.346	23.408

Specimen	Identification	V Int Foram Angle	D Foram Area	V Foram Area
SDSNH 63154	Carcharhiniformes (Order)	54.693	0.1734	0.124
SDSNH 65993	Carcharhinidae (Family)	30.922	0.247	0.215
SDSNH 75551	Triakidae (Family)	49.028	0.007	0.00664
SDSNH 71143	Triakidae (Family)	27.028	0.583	0.562

APPENDIX D: LIST OF CHARACTERS

Those with a double asterisk (**) are after Burris, 2004. They are as follows:

1) Internal foraminal shape is conical (0); internal foraminal shape is cuboid (1)
2) External dorsal and ventral foraminal shapes are same (1); are different (0)
3) External appearance of centrum (as seen from a birds-eye or side view) is striated (2); external appearance of centrum is striated with pores (1); external appearance has pores (0).
4) Pores absent (2); pores small (0); pores large (1). **
5) Pores absent (2); pores on lamellae and around foramina (1); pores scattered (0)**
6) Centrum is non-hourglass shaped when viewed axially (2); centrum has a slight hourglass shape when viewed axially (1); centrum has an obvious hourglass shape when viewed axially (0).
7) Lamellae do not extend into interior of inner part of foramina (1); lamellae extend into inerior part of foramina (0).
8) Space exists between inner zone and inner edge of foramina (0); inner zone extends to inner edge of foramina (1).
9) Centrum length/diameter ratio < 0.50 (1); centrum length/diameter ratio > 0.50 (0).
10) Centrum length/height ratio < 0.5 (1); centrum length/height ratio > 0.50 (0).
11) Centrum diameter 1/ height ratio < 1.0 (1); centrum diameter 1/height ratio >1.0 (0).
12) Inner zone height/inner zone width ratio < 1.0 (0); inner zone height/inner zone width ratio > 1.0 (1).

13) Dorsal foramen length/dorsal foramen width ratio < 1.3 (2); dorsal foramen length/dorsal foramen width ratio 1.3-1.95 (1); dorsal foramen length/dorsal foramen width ratio >1.95 (0).

14) Ventral foramen length/ventral foramen width ratio < 1.50 (1); ventral foramen length/ventral foramen width ratio >1.50 (0).

15) Dorsal foramen length/ventral foramen length ratio < 1.0 (1); dorsal foramen length/ventral foramen length ratio > 1.0 (0).

16) Width at apices of double cone/diameter ratio > 1.0 (2); width at apices of double cone/diameter ratio 0.90 – 1.0 (1); width at apices of double cone/diameter ratio < 0.9 (0). **

17) Dorsal external interforaminal width/ventral external interforaminal width < 0.60 (2); dorsal external interforaminal width/ventral external interforaminal width 0.60 - 0.80 (1); dorsal external interforaminal width/ventral external interforaminal width > 0.80 (0).

18) Dorsal interforaminal wall width/width at apices of the double cone ratio < 0.30 (0); dorsal interforaminal wall width/width at apices of the double cone ratio > 0.30 (1). **

19) Ventral interforaminal wall width/width at apices of the double cone ratio > 0.30 (1); ventral interforaminal wall width/width at apices of the double cone ratio < 0.30 (0).

20) Dorsal interforaminal angle < 25 (2); dorsal interforaminal angle 25 – 35 (1); dorsal interforaminal angle > 35 (0).

21) Striated between foramina (1); solid between foramina (0).

22) Dorsal foramen length/dorsal foramen depth ratio < 0.50 (2); dorsal foramen length/dorsal foramen depth ratio 0.50 – 0.75 (1); dorsal foramen length/dorsal foramen depth ratio > 0.75 (0).

23) Ventral foramen length/ventral foramen depth ratio < 0.60 (2); ventral foramen length/ventral foramen depth ratio 0.60 – 1 (1); ventral foramen length/ventral foramen depth ratio > 1.0 (0).

24) Dorsal foramen angle/ventral foramen angle ratio > 1.10 (2); dorsal foramen angle/ventral foramen angle ratio 1.0 – 1.10 (1); dorsal foramen angle/ventral foramen angle ratio <1.0 (0).

25) Dorsal interforaminal angle/ventral interforaminal angle ratio < 0.95 (0); dorsal interforamina angle/ventral interforaminal angle ratio > 0.95 (1).

26) Dorsal foraminal angle/ventral interforaminal angle ratio < 0.60 (2); dorsal foraminal angle/ventral interforaminal angle ratio 0.60 – 0.90 (1); dorsal foraminal angle/ventral interforaminal angle ratio > 1.0 (0).

27) Ventral foraminal angle/dorsal interforaminal angle ratio < 0.70 (2); ventral foraminal angle/dorsal interforaminal angle ratio 0.70 – 1.10 (1); ventral foraminal angle/dorsal interforaminal angle ratio > 1.10 (0).

28) Dorsal inner foraminal width/dorsal external foraminal width ratio < 0.30 (0); dorsal inner foraminal width/dorsal external foraminal width ratio > 0.30 (1).

29) Ventral inner foraminal width/ventral external foraminal width ratio < 0.30 (0); ventral inner foraminal width/ventral external foraminal width ratio > 0.30 (1).

30) Inner zone height/dorsal foramen length ratio > 0.10 (1); inner zone height/dorsal foramen length ratio < 0.10 (0).

31) Inner zone height/ventral foramen length > 0.10 (1); inner zone height/ventral foramen length ratio > 0.10 (0).

32) Inner zone area/dorsal foramen area ratio > 0.10 (1); inner zone area/dorsal foramen area ratio < 0.10 (0).

33) Inner zone area/ventral foramen area ratio > 0.10 (1); inner zone area ventral foramen area ratio < 0.10 (0).

34) Dorsal foramen length/centrum length ratio < 0.50 (2); dorsal foramen length/centrum length ratio 0.50 – 0.70 (1); dorsal foramen length/centrum length ratio > 0.70 (0).

35) Ventral foramen length/centrum length ratio < 0.50 (1); ventral foramen length/centrum length ratio > 0.5 (0).

APPENDIX E: CODED CHARACTERS

Specimen	Identification	1	2	3	4	5	6	7	8	9	10	11	12
CAS 65976	*Alopisa vulpinus*	0	1	0	2	2	1	1	0	1	1	1	1
BM P.5821-a	*Odontaspis sp.*	?	1	0	2	2	2	1	?	0	1	1	?
BM P.8983	*Carcharodon auriculatus*	?	1	2	2	2	1	1	0	0	1	0	0
CAS 25844.a	*Carcharodon carcharias*	0	1	1	1	1	1	1	0	0	1	1	1
CAS 25844.b	*Carcharodon carcharias*	0	1	1	1	1	1	1	0	0	1	1	1
CAS 26678	*Carcharodon carcharias*	0	1	1	1	1	1	1	0	0	1	0	1
BM PV4808	*Carcharodon megalodon*	0	1	2	2	2	2	1	1	0	1	1	1
BM PV4809	*Carcharodon megalodon*	0	1	2	2	2	2	1	1	0	1	0	0
BM PV4810	*Carcharodon megalodon*	0	1	2	2	2	2	1	1	0	1	0	0
BM 35860-1	*Carcharodon sp.*	?	1	1	1	1	2	1	0	0	1	1	?
CAS SU40902.a	*Isurus glaucus*	0	1	1	0	1	2	1	0	0	1	0	0
CAS SU40902.b	*Isurus glaucus*	0	1	1	0	1	2	1	0	0	1	0	1
CAS 26710.a	*Lamna ditropis*	0	1	2	2	2	2	1	0	0	1	1	1
CAS 26710.b	*Lamna ditropis*	0	1	2	2	2	1	1	0	0	1	0	1
BM 2316	*Cetorhimus maxiums*	0	?	2	2	2	0	1	1	0	?	?	0
CAS 224630	*Teroras (=Cetorhimus) maximus*	0	1	2	2	2	1	1	0	1	0	0	1

Specimen	Identification	13	14	15	16	17	18	19	20	21	22	23	24	25
CAS 65976	*Alopisa vulpimus*	2	0	0	1	2	0	1	1	1	1	1	2	0
BM P.5821-a	*Odontaspis sp.*	0	0	1	2	2	0	1	?	1	?	?	?	?
BM P.8983	*Carcharodon auriculatus*	2	1	0	1	1	1	1	1	1	1	2	0	0
CAS 25844.a	*Carcharodon carcharias*	1	1	0	1	0	0	0	1	1	1	2	2	1
CAS 25844.b	*Carcharodon carcharias*	2	1	1	1	0	0	0	2	1	2	2	2	0
CAS 26678	*Carcharodon carcharias*	1	0	0	1	2	0	1	1	1	1	1	2	0
BM PV4808	*Carcharodon megalodon*	1	1	1	1	0	1	1	1	1	1	2	0	1
BM PV4809	*Carcharodon megalodon*	2	1	0	1	0	1	1	1	1	1	2	1	1
BM PV4810	*Carcharodon megalodon*	2	1	0	1	0	1	1	1	1	1	2	1	1
BM 35860-1	*Carcharodon sp.*	2	1	0	2	1	0	1	?	1	?	?	?	?
CAS SU40902.a	*Isurus glaucus*	2	1	0	1	1	0	1	1	1	1	2	2	0
CAS SU40902.b	*Isurus glaucus*	1	1	0	1	1	0	1	1	1	1	2	1	0
CAS 26710.a	*Lamna ditropis*	1	1	0	1	0	0	0	1	1	1	2	0	1
CAS 26710.b	*Lamna ditropis*	1	1	0	1	1	0	0	1	1	1	2	1	0
BM 2316	*Cetorhinus maxiums*	?	?	?	1	?	0	?	?	1	?	?	?	?
CAS 224630	*Teroras (=Cetorhinus) maximus*	?	?	?	0	2	0	0	?	1	?	?	0	0

Specimen	Identification	26	27	28	29	30	31	32	33	34	35
CAS 65976	*Alopisa vulpinus*	1	1	0	1	1	1	1	1	0	0
BM P.5821-a	*Odontaspis sp.*	?	?	?	?	?	?	?	?	0	0
BM P.8983	*Carcharodon auriculatus*	2	2	0	0	1	1	1	1	1	1
CAS 25844.a	*Carcharodon carcharias*	1	2	1	1	1	1	1	1	2	1
CAS 25844.b	*Carcharodon carcharias*	1	2	1	1	1	1	1	1	2	1
CAS 26678	*Carcharodon carcharias*	2	1	0	0	1	1	1	1	1	0
BM PV4808	*Carcharodon megalodon*	2	2	0	0	0	0	0	0	1	0
BM PV4809	*Carcharodon megalodon*	2	2	0	0	0	0	0	0	1	0
BM PV4810	*Carcharodon megalodon*	1	1	0	0	0	0	0	0	1	0
BM 35860-1	*Carcharodon sp.*	?	?	?	?	?	?	?	?	1	1
CAS SU40902.a	*Isurus glaucus*	1	0	0	1	1	1	1	1	1	1
CAS SU40902.b	*Isurus glaucus*	2	1	0	0	1	1	1	1	2	1
CAS 26710.a	*Lamna ditropis*	2	1	0	0	1	1	1	1	0	0
CAS 26710.b	*Lamna ditropis*	2	2	0	0	1	1	1	1	1	0
BM 2316	*Cetorhinus maxiums*	?	?	0	?	?	?	1	?	?	?
CAS 224630	*Teroras (=Cetorhinus) maximus*	1	0	0	0	?	?	0	0	?	?

Specimen	**Identification**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
SDSNH 63154	Carcharhiniformes (Order)	0	0	0	0	0	0	0	0	0	0	0	0	1
SDSNH 65993	Carcharhinidae (Family)	0	0	0	0	1	1	0	0	0	0	0	1	0
SDSNH 75551	Triakidae (Family)	0	0	0	0	0	0	0	0	0	0	0	1	0
SDSNH 71143	Triakidae (Family)	0	0	0	0	1	1	0	0	0	0	1	0	0

Specimen	Identification	14	15	16	17	18	19	20	21	22	23	24	25	26
SDSNH 63154	Carcharhiniformes (Order)	0	1	1	0	0	0	0	0	0	0	1	0	0
SDSNH 65993	Carcharhinidae (Family)	0	0	0	0	0	0	0	0	0	1	1	1	0
SDSNH 75551	Triakidae (Family)	0	0	0	0	0	0	0	0	0	0	0	0	0
SDSNH 71143	Triakidae (Family)	0	0	0	0	0	0	0	0	0	0	0	0	0

Specimen	**Identification**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
SDSNH 63154	Carcharhiniformes (Order)	0	0	0	0	0	0	0	0	0
SDSNH 65993	Carcharhinidae (Family)	1	1	1	0	0	0	0	0	0
SDSNH 75551	Triakidae (Family)	0	0	0	0	0	1	1	1	0
SDSNH 71143	Triakidae (Family)	0	0	0	0	0	0	0	0	0

BIBLIOGRAPHY

Agassiz, L. 1833–1843 [1835]. Recherches sur les poissons fossiles [5 volumes]. Imprimerie de Patitpierre, Neucha□tel, 1420 pp.

Applegate, S., and L. Espinosa-Arrubarrena. 1996. The fossil history of *Carcharodon* and its possible ancestor, *Cretolamna*: a study in tooth identification; pp. 19 –36 *in* A. Klimley and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. Academic Press, San Diego.

Bonaparte, C. L. J. L. 1838. Selachorum tabula analytica. *Nuovi Annali delle Scienze Naturali* 1: 195-214.

Burris, J. 2004. Morphology and phylogenetic implications of recent and fossil Carcharhiniform shark vertebral centra. Dissertaion for the Degree of Ph.D. Michigan State University.

Cappetta, H. 1987. Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology, v. 3B.

Compagno, L. J. V. 1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharhinidae), and related genera. Proceedings, California Academy of Science series 4, v. 38, p. 63-98.

Compagno, L. J. V. 1973. Interrelationships of living elasmobranches, *in* Greenwood, P. H., Miles, R. S., and Patterson, C., eds., Interrelationships of fishes. Zoological Journal of the Linnean Society, Supplement 1, v. 53, p. 15-61.

Compagno, L. J. V. 1984. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization (FAO) Fisheries Synopsis 4(125):1–655.

Compagno, L. J. V., Dando, M., and Fowler, S. 2005. Order Lamniformes *in* Sharks of the World. Princeton University Press, p. 175-185.

Gottfried, M. D., L. J. V. Compagno, and S. C. Bowman. 1996. Size and skeletal anatomy of the giant "megatooth" shark *Carcharodon megalodon*. In A. Klimly and D. Ainley, eds., *Great White Sharks, the Biology of Charcharodon carcharias*. Academic Press, San Diego.

Gottfried, M. D. 1999. Fossil shark vertebral centra: an overlooked data set? Journal of Vertebrate Paleontology 19(3) supplement:47A. *Charodon carcharias*. Academic Press, San Diego.

Gottfried, M. D., and R. E. Fordyce. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the Late Oligocene of New

Zealand, with comments on *Carcharodon* interrelationships. Journal of Vertebrate Paleontology, v. 21, no. 4, p. 730-739.

Gray, J. E. 1851. List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii. 160 p. British Museum (Natural History), London.

Harper, D.A.T., and P. D. Ryan, 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis.Palaeontologia Electronica 4(1): 9pp..

Hildebrand, M. and Goslow, G. E. 2001. Evolution of the spine *in* Analysis of vertebrate structure. John Wiley and Sons, Inc., p. 145-146.

Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proc. Royal Soc. London, 43:649-662.

Jervey, A. 2007. Comparative morphology of the skeletal labyrinth in Miocene-Pliocene fossil and recent sharks. Thesis for the Degree of M. S. Michigan State University.

Lariche, M.1936. *Mém. Musée Roy. D'Hist. Nat. Belgique.* 12th Ser., **3**.

Maisey, J. G. 1984. Higher elasmobranch phylogeny and biostratigraphy. Zoological Journal of the Linnean Society, v. 82, p. 33-54.

Maisey, J.G. 1985. Cranial morphology of the fossil elasmobranch *Synechodus dubrisiensis*. Amer. Mus. Nov. 2804, 28 pp.

Maisey, J. G. 2001. Remarks on the inner ear of elasmobranches and its interpretation from skeletal labyrinth morphology. Journal of Morphology, 250, p. 236-264.

Maisey J. G. 2004 Morphology of the braincase in the broadnose sevengill shark *Notorynchus* (Elasmobranchii, Hexanchiformes), based on CT scanning. Amer. Mus. Nov 3429. 52 pp.

Maisey, J. G. 2005. Braincase of the Upper Devonian shark *Cladodoides wildungensis* (Chondrichthyes, Elasnobranchii), with observations on the braincase in early chondrichthyans. Bulletin of the Anerican Museum of Natural History, 288, p. 1-103.

Müller, J., and J. Henle. 1838-1841. Systematische Beschreibung der Plagiostomen. Berlin. [un-numbered]

Nieves-Rivera, Á. M., M. Ruiz-Yantín, and M. D. Gottfried. 2003. New Record of the Lamnid Shark *Carcharodon megalodon* from the Middle Miocene of Puerto Rico. Caribbean Journal of Science. 39:2. 223-227.

Purdy, R., J. H. McLellan, V. P. Schneider, S. P. Applegate, R. Meyer, and R. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. Smithsonian Contributions to Paleobiology 90:71–202.

Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della sicilia, con varie osservazioni sopra i medisimi. Caratteri. Pls. 1-20.

Ridewood, W. G., 1921. On the calcification of the vertebral centra in sharks and rays: London, Harrison and Sons, Ltd., Philosophical Transactions of the Royal Society of London, v. 210, series B.

Tanke, D. H. and P. J. Currie. 1998. Head-biting behavior in Theropod Dinosaurs: paleopathological evidence. Gaia, no. 15, p. 167-184.

White, E. G. 1936. A classification and phylogeny of the elasmobranch fishes: American Museum Novitates, no. 837, 16 p.