QUANTIFYING HETERODONTY IN THE LATE DEVONIAN (UPPER FAMENNIAN) SHARKS *CLADOSELACHE* AND *CTENACANTHUS* FROM THE OHIO SHALE, USA

Stephen J. Jacquemin, David J. Cicimurri[#], Jun A. Ebersole[∫], Madelyn Jones*,*
Zach Whetstone & Charles N. Ciampaglio**

* Wright State University - Lake Campus, 7600 Lake Campus Drive, Celina, OH 45822.
Corresponding author: stephen.jacquemin@wright.edu

[#]South Carolina State Museum, 301 Gervais Street, Columbia, SC 29201

[∫]McWane Science Center, 200 19th Street North, Birmingham, AL 35203

Stephen J. Jacquemin, David J. Cicmurri, Jun A. Ebersole, Madelyn Jones, Zach Whetstone & Charles N. Ciampaglio. Quantifying heterodonty in the late Devonian (Upper Famennian) sharks *Cladoselache* and *Ctenacanthus* from the Ohio Shale, USA. - PalArch's Journal of Vertebrate Palaeontology 13, 1 (2016), 1-20. ISSN 1567-2158. 20 pages + 5 plates, 7 figures.

Keywords: geometric morphometrics, heterodonty, Devonian, cladodont, *Cladoselache*, *Ctenacanthus*

ABSTRACT

Differentiation of tooth size and shape within the jaw (*i.e.* heterodonty) is an expected pattern in the majority of Neoselachii sharks. Various forms of heterodonty may be observed within an individual set of jaws, which can be the result of tooth position (monognathic), upper or lower jaw position (dignathic), tooth file or developmental position (ontogeny), or between male and female in sex specific differences (gynandric). Heterodonty patterns result from natural selection as a functional linkage tied to feeding niche for both feeding performance and dietary diversity. However, the types and/or degree of heterodonty present in Devonian sharks such as *Cladoselache* and *Ctenacanthus* have not previously been discussed or quantified in the literature. The objective of this study was to analyze a number of associated dentitions from representatives of these two genera, all collected from the Cleveland Shale Member of the Ohio Shale (upper Famennian; Upper Devonian), to test for, and quantify, various types of heterodonty within and across taxonomic lineages of early cladodont sharks. Geometric morphometrics and linear measurements were used to describe tooth shape and resulting axes and measurements were regressed with jaw position, tooth file position, and upper versus lower jaw to test for differentiation associated with various types of heterodonty. Teeth from *Cladoselache* and *Ctenacanthus* dentitions that were examined did not show any variation in tooth shape consistent with heterodonty. However, tooth size did vary slightly with jaw position and the presence of symphyseal teeth at the lower jaw symphysis does indicate differentiation between upper and lower jaws. Furthermore, the long period of tooth retention characteristic of these genera create a record of ontogenetic heterodonty within a tooth file observable as an increase in tooth size lingually. Although tooth shape did not significantly co-vary with jaw position in either taxa, significant morphometric differences between the two genera were evident. These findings strengthen the taxonomic validity of the genera and recognized species within these genera and provide further insights into the niche of these Devonian sharks.

Introduction

Nearly all extant neoselachian sharks exhibit one or more forms of heterodonty (Frazzetta, 1988). These patterns in teeth manifest as predictable trends in size or shape and are a reflection of a combination of contemporary environment, variation in size, behavior, and evolutionary history. Recognized patterns in tooth size and shape include monognathic, dignathic, gynandric, and ontogenic variation. Given that the earliest sharks were likely filter feeding (*i.e.* no 'developed teeth'), and that these early taxa gave rise to lineages leading to modern sharks which exhibit both teeth and patterning within the jaw, the question of when and in what taxa these adaptations in tooth shape and size began becomes paramount to our understanding of the evolution of early fauna and paleoecology.

Monognathic heterodonty is often observed within the upper and lower dentitions and is expressed as a change in the overall shape of the teeth from the jaw symphysis to the posterior end of the tooth row (Applegate, 1965). Species that exhibit monognathic heterodonty typically possess teeth that pattern from acute to increasingly oblique angles from the anterior to posterior positions. This form of heterodonty is even evident in those species with more homodont dentitions, like *Galeocerdo* and *Squatina* (Herman *et al.*, 1992). Dignathic heterodonty is particularly evident in carcharhiniform, squaliform, and hexanchiform sharks (Herman *et al.*, 1989; Naylor, 1990; Naylor & Marcus, 1994), where the teeth within the upper jaw are markedly different from those within the lower jaw. Gynandric heterodonty has been observed in both shark (Purdy & Francis, 2007; Herman *et al.,* 1990, 1991) and batoid species where conspicuous differences between the male and female dentitions, particularly during reproductive seasons, have been observed (*i.e.*, Feduccia & Slaughter, 1974; Kajiura & Tricas, 1996). Lastly, ontogenetic heterodonty occurs in genera like *Heterodontus*, where tooth morphology changes drastically as individuals grow into adulthood (Cappetta, 2012). These differences in tooth shape are expected to be a function of feeding performance and dietary diversity as a result of selective pressures (Motta & Wilga, 2001). However, although established in modern taxa, whether differentiation in tooth shape was present in the earliest sharks, or arose later due to selective pressures, is not well understood.

Changes in tooth shape by position, within position, or between positions of the upper and/or lower dentitions can be quite drastic, and can be particularly compounded as individual sharks grow (Herman *et al.*, 1993; Shimada, 2002; Purdy & Francis, 2007). From an applied paleontological perspective, these variations in tooth morphology can make it extremely difficult to accurately identify fossil shark teeth from the earliest taxa, as a grouping of five apparently disjunct tooth morphologies could represent five biological species, or a single species exhibiting various types of heterodonty. This presents a unique problem and opportunity for the study of one of the earliest and well known Paleozoic shark groupings – the cladodont taxa, particularly *Cladoselache* (Cladoselachiformes Berg, 1937; Cladoselachidae Dean, 1894) and *Ctenacanthus* (Ctenacanthiformes Zangerl, 1981; Ctenacanthidae Dean, 1909). These two genera have the potential to serve as good case study organisms to explore these problems because they are some of the earliest sharks with teeth, they are fairly common in the fossil record, and many specimens have articulated or associated dentitions.

Cladoselache and *Ctenacanthus* are most commonly associated with the Upper Devonian (Upper Famennian) Cleveland Shale deposits of Ohio, where isolated teeth are extremely common. The environmental and biological parameters during this time, including soft anoxic sediments coupled with the likely brief amount of time between death and coverage of individuals, has facilitated a unique and extensive fossil record of these early cladodont sharks (Williams, 1990). Williams (1990) indicates that these taxa represented both a numerically and ecologically dominant component of the assemblage. However, decades of studying cladodont remains from these deposits has resulted in a lengthy treatise of splitting out or synonymizing taxonomic species based on tooth size and/or morphology (see Newberry, 1899; St. John & Worthen, 1875; St. John & Worthen, 1883; Claypole, 1893; Claypole, 1895; Dean, 1909; Ginter *et al.*, 2005; Ginter *et al.*, 2010; Ginter, 2010), which has resulted in a lack of clarity regarding basic understanding of diversity or biology.

Preserved articulated cladodont dentitions show that teeth were contained within discrete, regularly spaced files adjacent to corresponding jaw files. Individual teeth display a single central conical cusp with smaller lateral cusplets, as well as distinct features that distinguish labial and lingual sides. However, few studies have incorporated size and shape into analyses of cladodont tooth variation, or used such information to investigate the biology of individual species or explore the validity of these recognized taxa. The objective of this study was to describe tooth shape in Devonian cladodont sharks within the genera *Cladoselache* and *Ctenacanthus* and specifically test for various types of heterodonty. In addition, this study assesses interspecific differences and discusses the taxonomic and morphologic implications of information gleaned from the potential for heterodonty in these early sharks.

Methods

Hundreds of cladodont sharks were recovered during the highway salvage operations of the 1960's along Interstate 71 near Cleveland, Ohio. Recovered remains included isolated teeth, partial dentitions, finspines, and nearly complete individuals. These specimens were recovered from a single horizon (C. Ciampagalio, pers. observ.) within the Upper Devonian (upper Famennian) Cleveland Shale Member of the Ohio Shale (Williams, 2001). All specimens currently reside in the collections of the Cleveland Museum of Natural History (CMNH) in Ohio. This study is the result of the close examination of a subset of these individuals that includes prepared specimens and those preserving associated dentitions that are referable to *Cladoselache* and *Ctenacanthus*.

Specimens examined in this study were chosen based on a set of three criteria that included the preservation of associated dentitions exposing teeth from various parts of the jaw; the state of preservation; and the completeness and quality of the preparation. To meet the objectives of quantifying intraspecific tooth variation, including variation within a jaw, between upper and lower jaws, and within individual tooth files, specimens were selected based on the presence of associated teeth with evidence of their position in the jaw (*i.e.*, plates 1-4) and articulated tooth rows (and/or tooth files; *i.e.*, plates 1 & 2). Several specimens exhibited teeth in a semi-scattered state encompassing the dental arcade (plate 5), and while not informative relative to single tooth rows, still provided valuable intraspecific information. Of the specimens housed at the CMNH, 13 were found to meet the above criteria. Detailed intraspecific tooth measurements by jaw position were used to test for monognathic heterodonty within these 13 dentitions (eight *Cladoselache* [CMNH 5336, 5769, 6187, 6187.2, 8114, 8114.2, 9296, 50238] and five *Ctenacanthus* [CMNH 5835, 5956, 6219, 9207, 9440]). Detailed intraspecific tooth measurements of single articulated rows were used to quantify ontogenetic heterodonty and included information from a single representative *Cladoselache* (CMNH 50238) and *Ctenacanthus* (CMNH 5956) individuals. *Cladoselache* (CMNH 50238) and *Ctenacanthus* (CMNH 5956) individuals were also used to assess the potential for dignathic heterodonty. All available exposed teeth were ultimately pooled to test for interspecific generic and specific level variation. Elucidating the phylogeny of the studied *Cladoselache* and *Ctenacanthus* remains is beyond the scope of this paper, thus the study follows the taxonomic hierarchy and species determinations provided by Ginter (2010) and Ginter *et al.* (2010).

All specimens were photographed using a tripod mounted Nikon d3000 camera with Nikkor 60 mm lens. To minimize and avoid issues associated with image distortion, parallax, and orientation, a fixed distance from camera to specimen (consistent locations maintained) was maintained using both a mounted rail system to position the camera and remote system to capture images and to avoid any contact with the camera during imaging. Geometric morphometrics and linear measurement techniques were used to digitize individual teeth according to a series of fixed and repeatable landmarks and linear trusses. Geometric morphometrics is a landmark-based technique that summarizes shape variation between individuals through analysis of relative position between homologous points placed on specimens in a cartesian style (x, y) framework. Although geometric morphometrics can also be applied to the z axis, this was not possible for this study given the *in situ* nature of the fossils. Prior to spatial analysis of landmark data, size, rotation, and translation are removed from these landmark data through a Procrustes analysis (Zelditch *et al.*, 2004). While this technique is different from traditional linear measurements, these measurements can still provide specific detail regarding specific raw sizes, ratios, and relative distances between a few specific locales that could be difficult to interpret using geometric morphometrics.

In this study, geometric morphometrics was used to test for overall interspecific generic level differences and intraspecific variation associated with monognathic heterodonty, whereas linear measurements were used to provide an assessment of size and ratio difference potential in monognathic heterodonty as well as test for dignathic heterodonty and to quantify ontogenetic heterodonty within and across tooth files. Landmark placement for geometric morphometrics and linear measurements were done in the software tpsDig (Rohlf, 2008, *life.bio.sunysb.edu/morph*; figure 1). Linear measurements were taken to the nearest 100th of a millimeter. Broken or overly worn teeth were not digitized because their inclusion could skew the results of the shape analysis. To assess monognathic variation in tooth shape by position in the jaw, a continuous number from anterior to posterior position was assigned for all visible teeth and landmark data of individual teeth in position was ordinated using relative warp analysis (software tpsRelw; Rohlf, 2007, *life.bio.sunysb.edu/morph*). Resulting multivariate axes were interpreted using percent variation explained and tooth shape was compared by tooth position using linear regression models in tpsRegr (Rohlf, 2011, *life.bio.sunysb.edu/morph*). These models indicated significance of relationship between tooth shape and tooth position and specifically quantified the degree of which using percent variation explained.

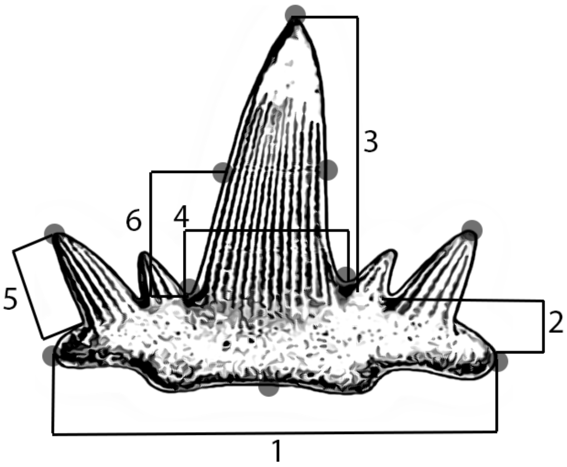

Figure 1. Representative cladodont tooth with landmarks and linear measurements utilized in descriptions and analyses. Landmarks represent distal and medial points associated with the root and each cusp while linear measurements encompass maximum depth, width, and height of the root and each cusp.

Linear measurements were used in addition to shape to assess variation in specific size aspects of each tooth by position. The following six linear measurements were taken of each tooth exposed within an articulated tooth row (figure 1): 1) greatest mesiodistal root width; 2) greatest baso-apical root height; 3) maximum crown height; 4) mesiodistal width of crown base; 5) greatest outer cusplet height; and 6) greatest baso-apical ornamentation height. To assess dignathic heterodonty, tooth shape and size, as well as the presence/absence of symphyseal tooth rows, was used to provide inference into the potential for differences. To assess ontogenetic variation in a single tooth file a subset of linear measurements to encompass the exposed root width and root height were used. These two metrics are commonly exposed in articulated tooth files and provide an accurate reflection of tooth size and shape as no specimen with all teeth exposed completely still in file position was observed. To assess overall interspecific variation between taxa, relative warp axes (multivariate analysis of landmark data) of teeth were combined in a MANOVA analysis using taxa (*i.e.*, *Cladoselache* vs. *Ctenacanthus*) as the grouping variable.

Systematic Paleontology

Chondrichthyes
Ctenacanthiformes Zangerl, 1981 (sensu
Ginter & Maisey, 2008)
Ctenacanthidae Dean, 1909
Ctenacanthus Agassiz, 1835

Plates 1 & 4

Material examined – CMNH 9440, 9207, 6219, 5956, 5835.

Description – According to Ginter (2010), dental characters that distinguish this genus include: 1) tooth crowns consisting of a relatively short and triangular central cusp that is convex lingually and flat labially, flanked by one or two pairs of lateral cusplets (with the first pair smaller than second); 2) the tooth base has a shallow basiolabial depression (concavity of the basal surface at labial edge), a short and straight basiolabial shelf (a ridge-like structure at labial edge of tooth base), and a moderately developed and straight orolingual ridge (a ridge-like structure on upper surface of the base, between the crown foot and lingual margin of the base).

Discussion – Ginter (2010) recognized three species of *Ctenacanthus* within the Cleveland Shale, and these are based on tooth size, ornamentation, and development of lateral cusplets. Of the three species, *Ct. terrelli* and *Ct. concinnus* are similar to each other in gross morphology but differ in overall size and development of crown ornamentation, and *Ct. tumidus*, the largest species, is distinguished by having only a single pair of lateral cusplets (also Ginter *et al.*, 2010). The additional cusplets present in *Ct. terrelli* and *Ct. concinnus* appear to increase relative root width to height ratios when compared with *Ct. tumidus*.

Cladoselachidae
Cladoselache Dean, 1894

Plates 2, 3, 5

Material examined – CMNH 50238, 9296, 8114, 8114.2, 6187, 6187.2, 5769, 5336.

Description – Morphological criteria used to identify teeth of this genus include: 1) crowns bearing an elongated, triangular central cusp that is convex lingually and flat labially, flanked by single pair of cusplets; 2) tooth base has a deep basiolabial depression, and the basiolabial shelf consists of two separate protuberances (Ginter *et al.*, 2010).

Discussion – Ginter *et al.* (2010) concluded that *Cladoselache* was monospecific and recognized only *Cl. fyleri* as a valid species. Isolated teeth of *Cladoselache* can be differentiated from those of *Ctenacanthus* using the morphological criteria outlined above, and another Cleveland Shale genus, *Tamiobatis*, is distinguished from the latter two taxa by the presence of numerous accessory cusplets along the labial face of the tooth (Williams, 1998; Duffin & Ginter, 2006).

Results

A total of 87 teeth from the 13 specimens were digitized, including 59 from associated dentitions of *Cladoselache* and 28 from dentitions representing *Ctenacanthus*. Relative warp analysis (RWA) elicited shape along three significant axes that explained 72% of the total variation. MANOVA indicated significant overall differences between *Ctenacanthus* and *Cladoselache* (Wilks' lambda = 0.72, df 6, 80, F 5.05, P<0.001; figure 2). The primary axis (RWA1: 51% variation, eigenvalue 1.2) differentiated individuals by central cusp relative height and tended to separate comparatively broad-toothed *Ctenacanthus* individuals from narrow-toothed *Cladoselache* individuals (figures 2 & 3). The second axis (RWA2: 12% variation, eigenvalue 0.57) separated individuals according to side cusp relative height and tended to separate comparatively low cusped *Ctenacanthus* individuals from higher cusped *Cladoselache* individuals (figures 2 & 3). The third axis (RWA3: 10% variation, eigenvalue 0.54) separated individuals according to degree of cusp curvature and did not differentiate taxa.

Monognathic heterodonty was not supported in regression analysis of overall tooth shape with jaw position in either *Cladoselache* (Wilks' lambda = 0.66; P = 0.86; Percent unexplained = 98.9%) or *Ctenacanthus* (Wilks' lambda = 0.22; P = 0.16; Percent unexplained = 95.3%; figure 4). Independent of shape, subsequent linear measurements (*i.e.* root width, crown width, crown height, root height, and ornamentation height) of teeth found that the largest teeth in a row were the most anterior and that linear measurements of teeth did not significantly change with jaw position. For example, the crown heights for the exposed teeth from the right posterior to anterior positions in specimen CMNH 50238 (plate 2) measured: (R1) 4.43 mm, (R2) 2.05 mm, (R3) 3.37 mm, (R4) 3.45 mm, (R5) 2.53 mm, (R6) 2.98 mm, (R7) 3.32 mm, (R8) 2.69 mm, (R9) 2.84 mm, (R10) 2.84 mm, and (R11) 2.61 mm, respectively. While the largest tooth measured was from the anterolateral position (R1, measuring 4.43 mm), crown heights of the remaining teeth showed no consistency in terms of changes in size (*Pearson's* P > 0.7). All remaining measurements taken of CMNH 50238, and of the other specimens, also exhibited no significant size change between teeth in the anterior, lateral, and posterior positions in either genera (*Pearson's* P > 0.5; figure 5).

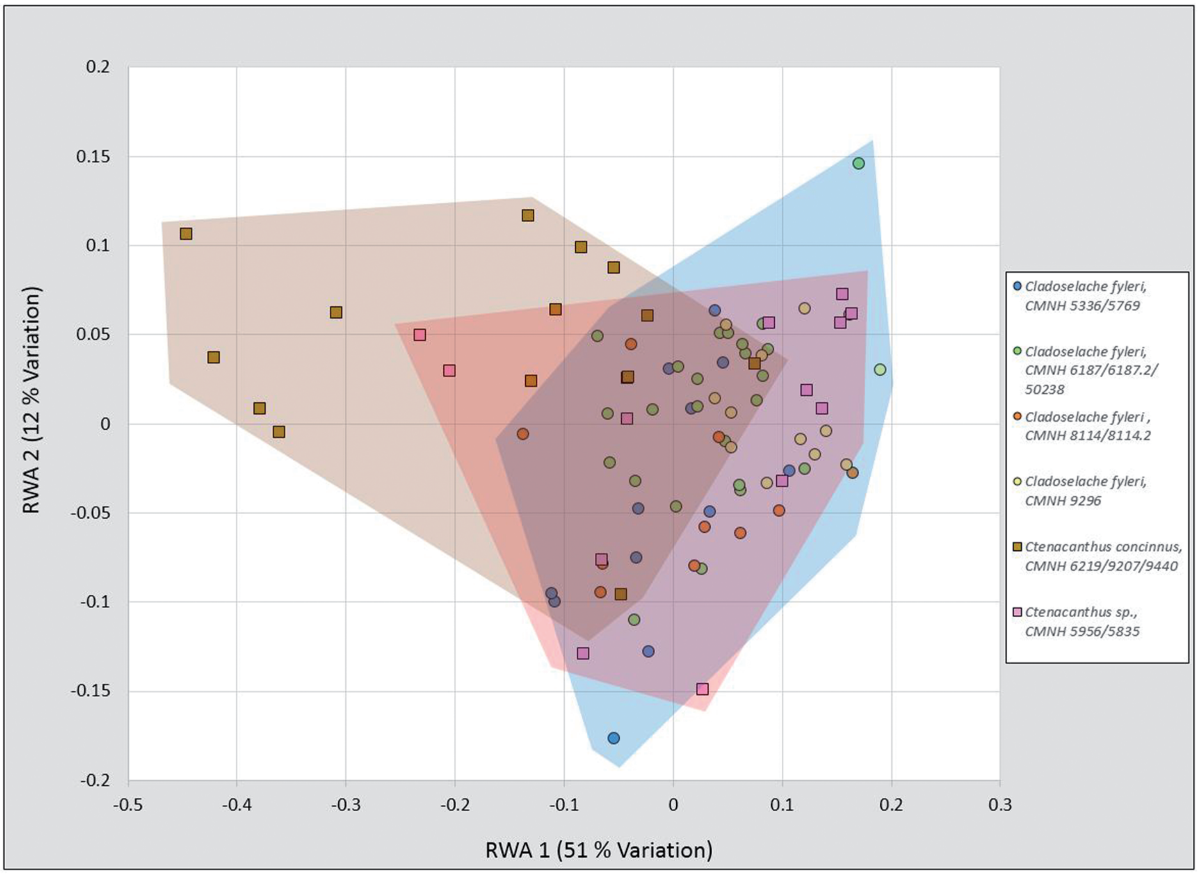

Figure 2. Relative warp analysis ordination scatterplot of two primary axes (63% variation explained) with individual taxa labeled.

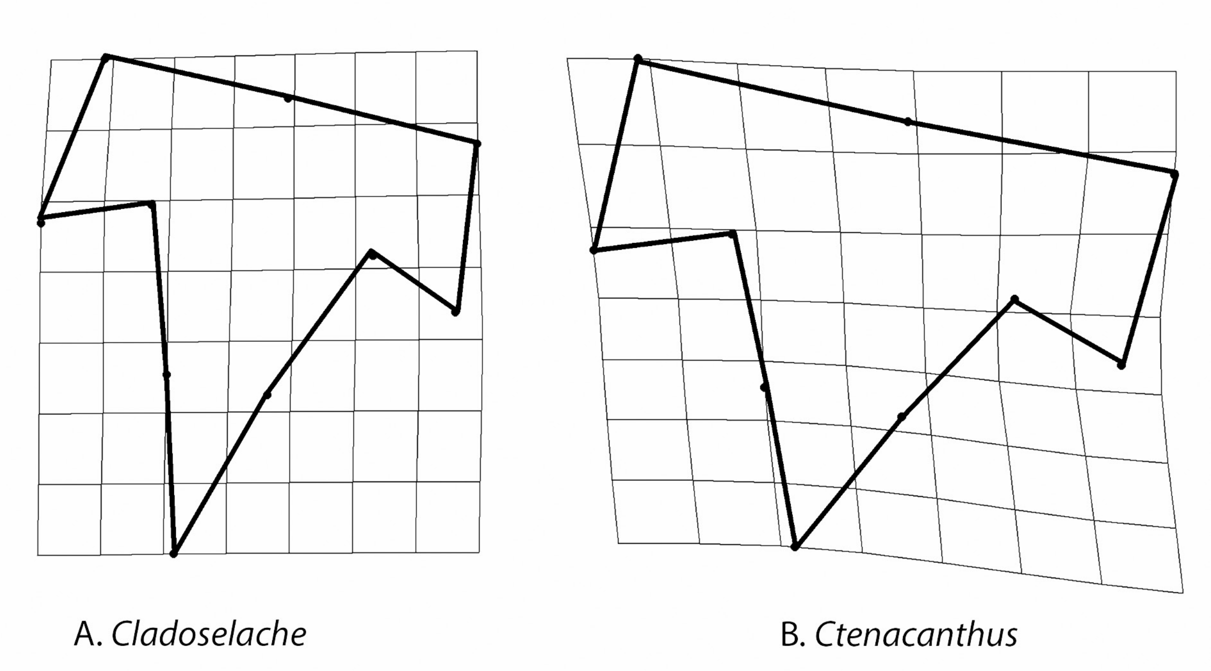

Figure 3. Consensus shapes of inter genera tooth outline differences between *Ctenacanthus* and *Cladoselache*. Deformation grids generated in tpsRelw.

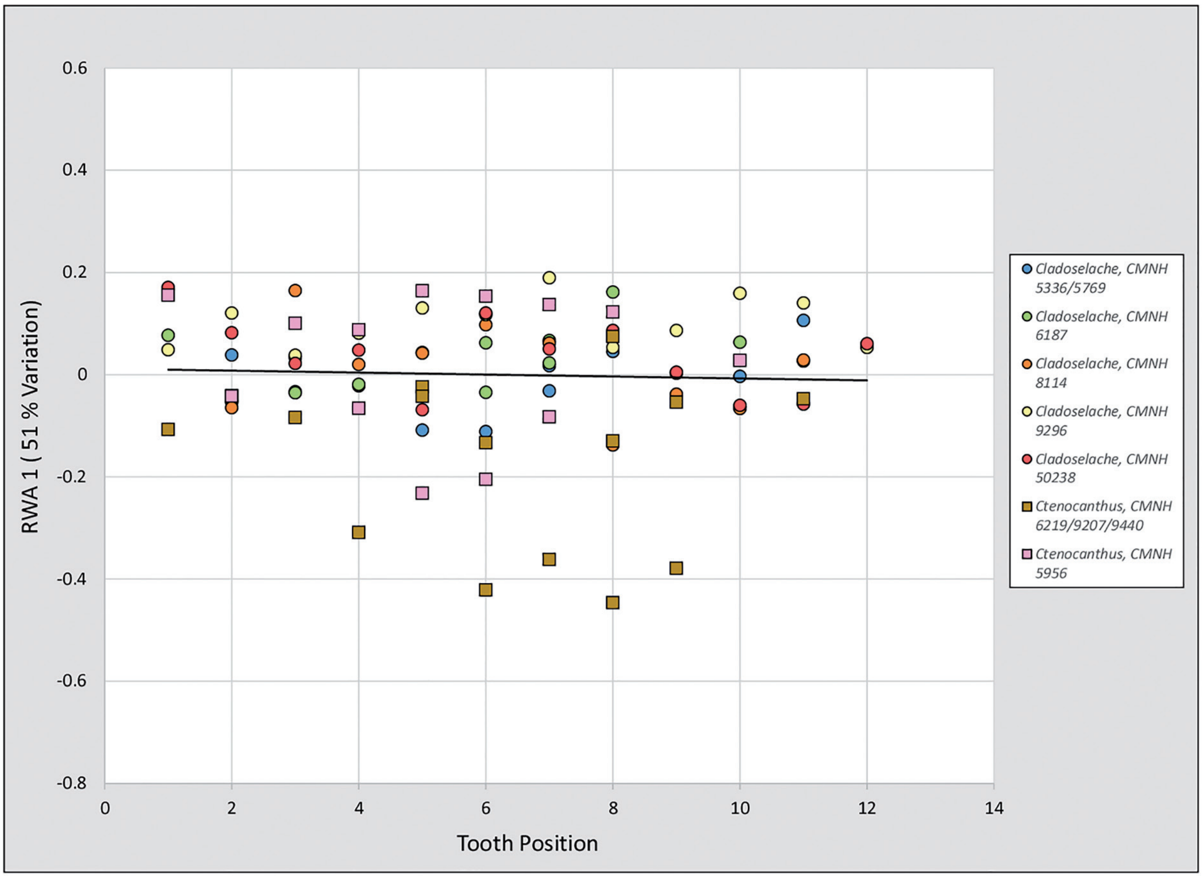

Figure 4. Scatterplot of primary shape axis (RWA1) vs. tooth position with individual taxa labeled.

Dignathic heterodonty was evaluated using the only specimen (CMNH 50238) that displays preserved and articulated sets of both upper and lower tooth files. Despite the single specimen, morphometric analysis and measurements indicate there is little or no variation in tooth morphology that delineates upper from lower dentitions (*Paired t test* upper and lower R2, R3, R4; P > 0.5). Linear measurements of visible root width, root height, and crown height also indicated little or no variation in tooth morphology that delineates upper from lower dentitions (*Paired t test* upper and lower R2, R3, R4; P > 0.5). However, the presence of symphyseal teeth in CMNH 50238 (plate 2) and CMNH 5956 (plate 1) indicate that although tooth size and shape may not differ between upper and lower jaws, there are differences in the tooth file occurrences of the anterior-most tooth files. Unfortunately, a symphyseal tooth cannot be identified as such based on morphology and must be identified *in situ*.

Ontogenetic heterodonty was evaluated using linear measurements of four articulated tooth files (symphyseal, L3, L5, L7; plate 1) in *Ctenacanthus* (CMNH 5956). Both root height (*Pearson's* r -0.8, P < 0.001; figure 6) and root width (*Pearson's* r -0.9, P < 0.001; figure 6) were significantly smaller in the labial-most teeth within files. However, when the ratio of root height to width was compared to file number, this relationship was not significant (*Pearson's* P > 0.5; figure 6). Subsequent comparison of the individual tooth file root height to root width ratio regression slopes indicated a similar rate of change independent of tooth row (P > 0.5). Visualization of each tooth file showed an organization scheme similar to an offset stack, with youngest teeth exhibiting the largest dimensions and lingual-most position in each file (figure 7). Individual teeth appear to have maintained separation and functional angle as a result of a spacing gap maintained by 'protuberances' on the underside of each tooth root base. Smaller, worn down, older teeth were maintained within a file as younger and larger teeth continued to erupt from tissue layers between tooth stacks. We did not observe any teeth with underdeveloped roots and/crowns in the study specimens. Interestingly, this seems to contrast with the 'conveyor

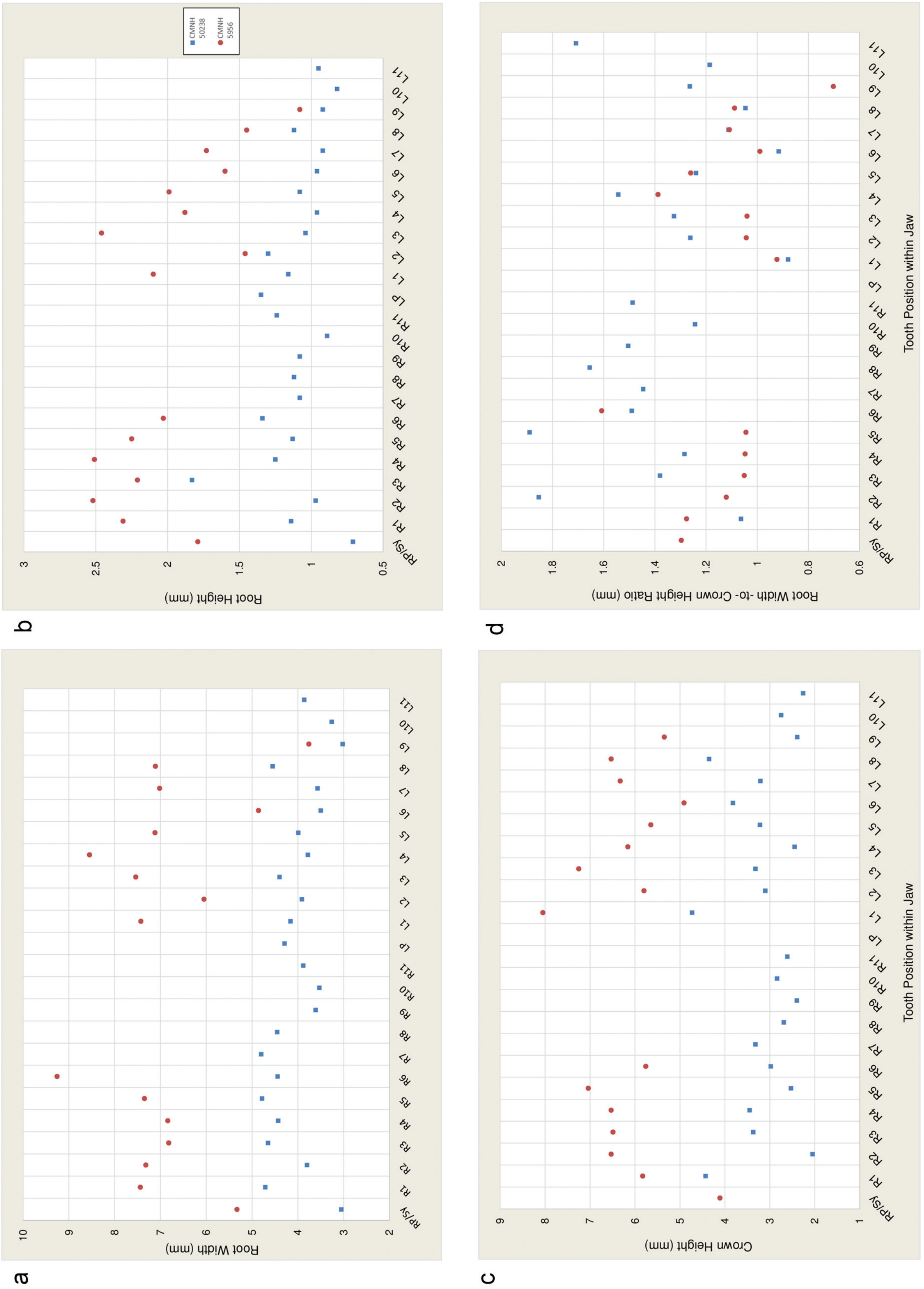

Figure 5. Scatterplot of a) Root width; b) Root height; c) Crown height; d) Ratio of root width to crown height vs. tooth position with individual taxa labeled.

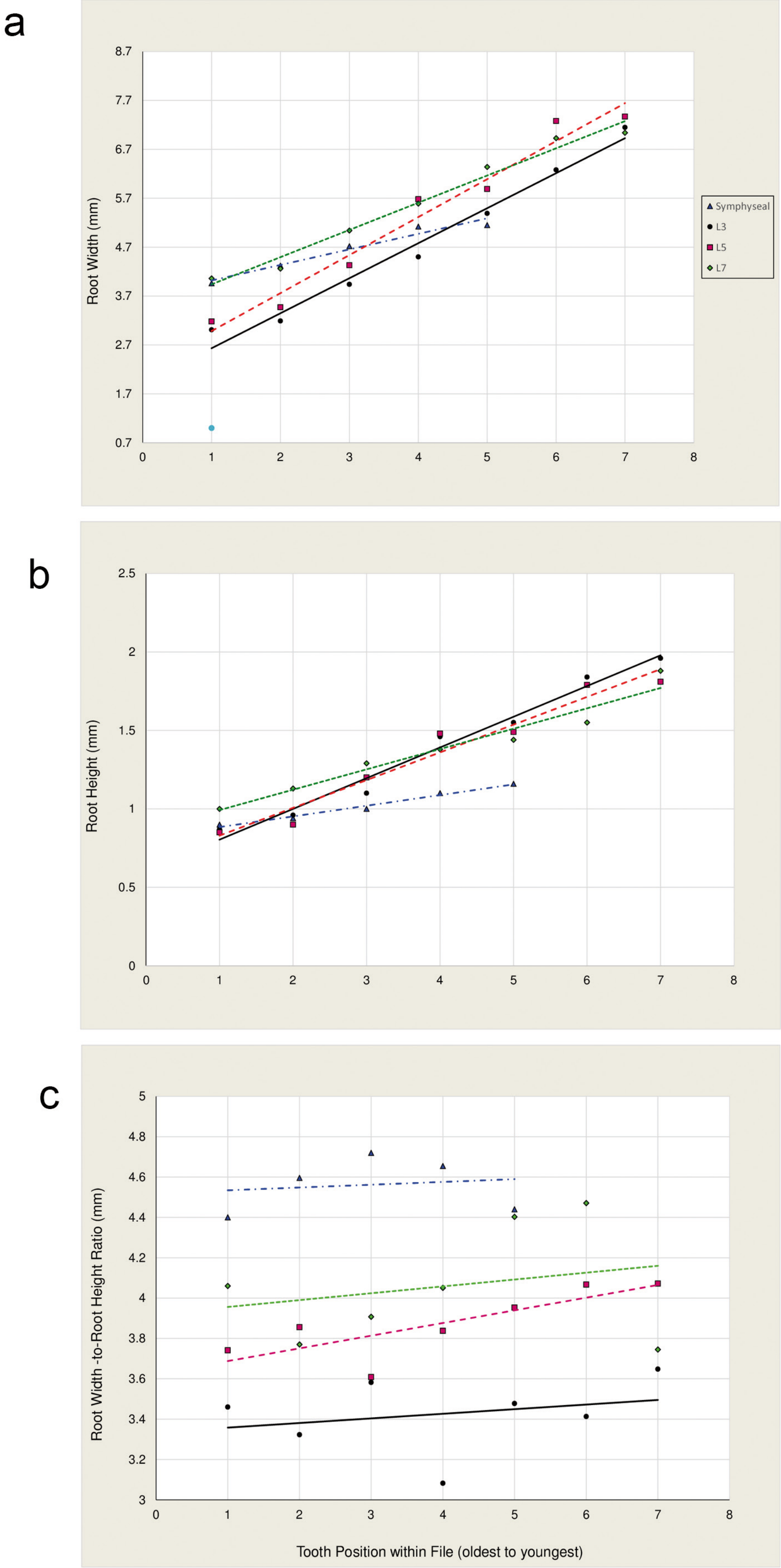

Figure 6. Scatterplot of a) Root width; b) Root height; c) Ratio of root width to root height vs. tooth position with individual tooth file position labeled.

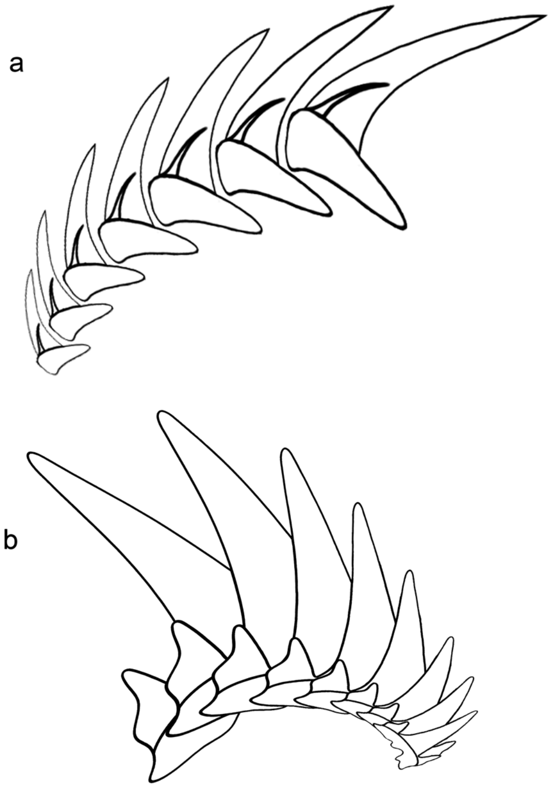

Figure 7. Hypothetical reconstruction of a Ctenacanthiformes tooth file in a) Lateral; b) Oblique labial views.

belt' arrangement found in most neoselachians whereby developing replacement teeth are not fully formed until the functional position, and are eventually shed from the jaw margin.

Discussion

These results suggest there is no statistically significant change in tooth shape within a tooth row, tooth file, or between upper and lower jaws, of either genera (*i.e.*, monognathic, dignathic, or ontogenetic heterodonty, respectively). Similarly, as where one might expect the overall physical tooth size, irrespective of shape, to gradually decrease along the tooth row from the anterior to posterior positions, this was also not observed on the measured specimens. However, predictable differences in tooth size were observed within each of the tooth files measured and the presence of symphyseal teeth on the right and left Meckel's cartilage (also Williams, 2001) that differs significantly in size from the succeeding tooth file supported mild ontogenetic and dignathic heterodonty. The most conspicuous form of heterodonty is ontogenetic and is seen in each file as a marked increase in size between the oldest tooth (at the labial-most end) and succeeding younger teeth (towards the lingual side of the jaw). These two forms of heterodonty are discussed in more detail below.

Dignathic Heterodonty and Symphyseal/Parasymphyseal Teeth

Although there is an overall lack of dignathic heterodonty between the upper and lower anterior through posterior teeth of either genera, Williams (2001) noted the presence of symphyseal teeth in the lower jaws of both *Ctenacanthus* and *Cladoselache*. Symphyseal teeth were preserved on two specimens in our sample (CMNH 5956 [plate 1] and CMNH 50238 [plate 2]), with specimen CMNH 50238 preserving what appears to be two symphyseal tooth files. If so, these teeth might more appropriately be called parasymphyseals, as they are not directly on the symphysis but positioned laterally to each side (Cappetta, 2012). Interestingly, symphyseal/parasymphyseal teeth are absent in the upper jaws of these taxa, but there is a corresponding space in the upper jaws into which the symphyseal teeth likely nestled when the jaws were closed. These symphyseal teeth cannot be differentiated from the other teeth in the row based on shape alone, and their position within the jaw is only apparent as a file of teeth that are nearly uniform in size (see below for additional discussion).

As observed in specimen CMNH 5956, the maximum mesiodistal root width and crown height of the exposed symphyseal tooth measured 5.33 mm and 4.11 mm, respectively. In contrast, the other exposed teeth in the row, from the immediately distal to the posterior end of the jaw, measured (R1) 7.44/5.83 mm, (R2) 7.32/6.53 mm, (R3) 6.82/6.49 mm, (R4) 6.84/6.53 mm, (R5) 7.35/7.04 mm, and (R6) 9.26/5.76 mm. Unfortunately the crowns of the exposed symphyseal teeth were not preserved on specimen CMNH 50238, but the preserved roots on these symphyseal files exhibit a similar trend of rather uniform size and being smaller compared to the more distal files. The largest root preserved on the right symphyseal file, interpreted to be the youngest exposed tooth, has a maximum mesiodistal root width of 3.05 mm. This is in sharp contrast to the other teeth in the row which range between 3.53 and 4.78 mm in mesiodistal root width. This size difference between the symphyseal teeth and other teeth in the row, and the lack of such teeth in the upper dentitions, suggest that degrees of monognathic and dignathic heterodonty are indeed present in both *Ctenacanthus* and *Cladoselache*. However, because teeth are essentially the same shape, assigning isolated specimens to jaw position is virtually impossible.

Ontogenetic Heterodonty

As discussed by Williams (2001) and Ginter *et al.* (2010), both *Ctenacanthus* and *Cladoselache* have unique mechanisms of tooth replacement and retention, as their teeth were not shed at the rates seen in modern lamniform sharks. Rather, these sharks retained their teeth for long periods of time, and older teeth appear to have remained functional despite the addition of multiple replacement teeth to the file. The appearance of multiple functional teeth within each file is contrary to discussions in Ginter *et al.* (2010). Of the examined specimens, as many as eight teeth have been observed within a single non-symphyseal file (see CMNH 5956, plate 1 L3). Most of the articulated files examined are preserved in lingual view and have an appearance of a 'stack' of tooth roots that incrementally increase in size from the labial to lingual positions. As a result, the tooth files seen in many of the examined specimens preserve a record of the tooth ontogeny, with the smallest, labial-most tooth in the file representing the oldest tooth, and the largest exposed lingual-most tooth representing the newest replacement tooth (figure 7).

This mechanism of long tooth retention preserves a unique record of ontogeny and gives clues to the growth rate of the animal. For example, in tooth file R2 of specimen CMNH 5956 (plate 1), the mesiodistal width of the labial-most (oldest) tooth measures 4.43 mm, with the width incrementally increasing to the lingual-most (youngest) exposed tooth which measures 7.32 mm in greatest width. Although it is beyond the scope of this study to speculate on the ratio of tooth size to body length in these taxa, the measurements of the root width in this particular file might suggests the animal nearly doubled in size over its lifetime. At the same time, several observed tooth files, like many of those preserved on CMNH 5956, show that the youngest tooth in a particular file has a nearly identical mesiodistal root width as the one or two teeth located just labial to it within the file. This suggests the animal may have reached a state of maturity and overall growth had slowed.

In contrast to the other files observed on CMNH 5956 and CMNH 50238, the symphyseal teeth appear to have remained a relatively constant size throughout the lifespan of the animals. On specimen CMNH 5965, for example, the mesiodistal width of the labial-most root of the symphyseal file measures 4.03 mm, while the lingual-most (youngest) exposed root measures 5.33 mm in width (an increase of 24%). This is in stark contrast to the previously described R2 file in the same specimen, where the teeth almost double in size. Only five teeth are preserved in the symphyseal file on CMNH 5956, suggesting several older teeth in the file may have shed, are not exposed, or were not preserved. However, a more complete growth history can be seen in the right symphyseal file of specimen CMNH 50238. Within this file, as many as ten roots appear to be preserved. The oldest measurable root (with several older that could not be measured because they are not fully exposed) has a mesiodistal width of 2.01 mm, with the top (youngest) exposed root measuring 2.70 mm in width (for an increase of 26%). While the roots of other tooth files appear to incrementally taper almost to a point in this specimen (CMNH 50238), the rapid increase in mesiodistal root width of these files suggest a much faster growth rate of teeth in the anterior, lateral, and posterior positions than those in the symphyseal or parasymphseal positions (plate 2).

Morphological Implications

Monognathic heterodonty within many extant selachians is seen as variations in tooth shape within the upper and lower dentitions, which generally allows for the distinction of symphyseal, anterior, intermediate, lateral, and posterior files in each jaw (Cappetta, 2012). These variations include overall width and thickness of the main cusp, inclination and/or curvature of the main cusp, development of crown ornamentation, development of serrations, development of lateral cusplets, and root shape. These same variations in tooth shape also characterize dignathic heterodonty, where teeth in the upper dentition differ from those in the lower dentition, and this phenomenon is quite distinctive in hexanchids and many carcharhiniform and squaliform sharks. Ontogenetic heterodonty in extant selachians is poorly understood, but at least for some species tooth shape can change drastically as an individual grows from juvenile to adult stages (Purdy & Francis, 2007). Due to the phenomenon of heterodonty, isolated teeth of some extant species of shark can not only be identified to a particular position within the upper and/or lower jaws, teeth of males/females and juvenile/adult sharks can sometimes be differentiated as well.

In contrast, our study of *Cladoselache* and *Ctenacanthus* dentitions reveals that tooth shape within a row (monognathic) on the palatoquadrate did not significantly vary, and although a symphyseal file is present in the lower dentition, the teeth are identical in shape to those in post-symphyseal positions. Thus, individual tooth positions like anterior, lateral, and posterior cannot be morphologically discerned, and any such determinations would be arbitrary. Therefore, isolated teeth cannot be confidently assigned to any particular location within a dentition, including the symphyseal files of the lower jaw. Furthermore, even though there is a significant increase in tooth size within each file (*i.e.*, ontogeny), there is no significant variation in shape. It may therefore also be impossible to determine if an isolated tooth: 1) represents a functional tooth from a more medial position in the mouth of a young shark; 2) came from a functional position closer to the jaw commissure of an adult shark: 3) was an older, non-functional tooth (younger growth stage) from a more medial position within the jaws of an adult animal. We cannot comment on the presence of gynandric heterodonty within these sharks based on the sample we examined, but it seems unlikely to have existed.

Taxonomic Implications and Conclusions

Three species of *Ctenacanthus* and one species of *Cladoselache* are currently recognized as occurring within the Ohio Shale, and gross morphological differences in tooth shape have been used to distinguish the two genera, with more subtle variations utilized to identify the three species of *Ctenacanthus* (Ginter *et al.*, 2010). However, because the material examined by us and other researchers (*i.e.*, Ginter & Williams), as well as many other specimens within the CMNH holdings, were collected from the same stratigraphic horizon, the possibility that the specimens preserve variation (heterodonty) within a population of fewer than four taxa must be considered.

Our study has shown that there is no significant variation in tooth shape within the upper and lower dentitions, and observed differences between isolated *Cladoselache* or *Ctenacanthus* morphotypes (*i.e.*, the development of crown ornamentation and lateral cusplets, nature of the tooth root) are therefore not related to heterodonty within a single species. Additionally, overall tooth shape, including development of crown ornamentation and lateral cusplets, apparently remained constant throughout the life of these sharks, as there is no significant variation in teeth within a given file except for the increase in tooth size from the labial (oldest tooth = youngest growth stage) to lingual positions (youngest tooth = oldest growth stage at time of death). This analysis supports the monospecific synonymy of the once recognized numerous *Cladoselache* taxa and the delineation of the currently recognized *Ctenacanthus* taxa. The possibility that *Ctenacanthus terrelli* (small tooth size, coarse but less extensive ornamentation, two pairs of cusplets) is conspecific with *Ctenacanthus tumidus* (large tooth size, fine but more extensive ornamentation, one pair of lateral cusplets) and represents a younger growth stage seems unlikely because no such transition was observed within the individual tooth files examined. The clustering of all the *Ctenacanthus* specimens on the negative aspect of the morphometric ordination, however, indicates that further study is necessary as the teeth representing *Ctenacanthus terrelli* could potentially represent a distinct genus. Furthermore, the clustering of *Ctenacanthus tumidus* with the *Cladoselache* teeth may indicate the synonymy of these with the genus *Cladoselache*, however further analysis with additional specimens is warranted. Overall, we must conclude that isolated teeth representing the *Cladoselache fyleri* (and all synonyms), *Ctenacanthus terrelli*, *Ctenacanthus concinnus* (including synonym *Ctenacanthus compressus*), and *Ctenacanthus tumidus* morphotypes each represent true biological species that inhabited the Cleveland Shale paleoenvironment, and isolated teeth can be identified with confidence, regardless of size. It is outside the scope of this study to elicit any phylogenetic relationships between the various taxa studied, and the taxonomic names utilized were simply used for convenience as they were assigned to these morphologies in prior studies (see references herein). However, the results presented here strongly suggest that with the lack of variation within the dentitions of these taxa, a phylogenetic analysis could indeed help revise the alpha taxonomy of this group as a whole and ultimately shed light upon their phylogenetic relationships.

Acknowledgments

We are grateful to Mike Taylor (Wright State University – Lake Campus) for assistance in preparation of several *Cladoselache* fossils and Austin Smith (Wright State University – Lake Campus) for assistance with specimen photography. We thank the staff of the Cleveland Museum of Natural History for access to the study specimens. We also thank two anonymous reviewers and one editor who provided insightful comments on an earlier draft of this study.

Cited Literature

Applegate, S.P. 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. – Contributions to Science, Los Angeles County Museum 86: 1-18.

Cappetta, 2012. Chondrichthyes: Mesozoic and Cenozoic Elasmobranchii: Teeth. Handbook of Paleoichthyology; v. 3E. – München, Verlag Dr. Friedrich Pfeil.

Claypole, E.W. 1893. The cladodont sharks of the Cleveland Shale. – The American Geologist 11: 325-331.

Claypole, E.W. 1895. On the structure of the teeth of the Devonian cladodont sharks. – Proceedings of the American Microscopical Society 16(3): 191-195.

Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires.) – American Museum of Natural History Memoir 9: 209-287.

Duffin, C.J. & M. Ginter. 2006. Comments on the selachian genus *Cladodus* Agassiz, 1843. – Journal of Vertebrate Paleontology 26(2): 253-266.

Feduccia, A. & B.H. Slaughter. 1974. Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. – Evolution 28: 164-168.

Frazzetta, T.H. 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). – Zoomorphology 108: 93-107.

Ginter, M. 2010. Teeth of Late Famennian ctenacanth sharks from the Cleveland Shale. In: Elliott, D.K., J.G. Maisey, X. Yu. & D. Miao. Eds. Morphology, Phylogeny and Paleobiogeography of Fossil Fishes. – München, Verlag Dr. Friedrich Pfeil: 145-158.

Ginter, M. & J.G. Maisey. 2008. The braincase and jaws of *Cladodus* from the lower Carboniferous of Scotland. – Palaeontology 50(2): 305-322.

Ginter, M., A. Ivanov & O. Lebedev. 2005. The revision of *"Cladodus" occidentalis*, a Late Paleozoic ctenacanthiform shark. – Acta Palaeontologica Polonica 50: 623-631.

Ginter, M., O. Hampe & C. Duffin. 2010. Chondrichthyes: Paleozoic Elasmobranchii: Teeth. Handbook of Paleoichthyology; v. 3D. – München, Verlag Dr. Friedrich Pfeil.

Herman, J., M. Hovestadt-Euler & D.C. Hovestadt. 1989. Part A: Selachii. No. 3: Order: Squaliformes. Families: Echinorhinidae, Oxynotidae and Squalidae. In: Stehman, M. Ed. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. – Bruxelles, Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: 101-157.

Herman, J., M. Hovestadt-Euler & D.C. Hovestadt. 1990. Part A: Selachii. No. 2b: Order: Carcharhiniformes – Family: Scyliorhinidae. In: Stehman, M. Ed. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. – Bruxelles, Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: 181-230.

Herman, J., M. Hovestadt-Euler & D.C. Hovestadt. 1991. Part A: Selachii. No. 2c: Order: Carcharhiniformes. Families: Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. In: Stehman, M. Ed. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. – Bruxelles, Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: 73-120.

Herman, J., M. Hovestadt-Euler & D.C. Hovestadt. 1992. Part A: Selachii. No. 4: Order: Orectolobiformes. Families: Brachaeluridae, Ginglymostomatidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomatidae. Order: Pristiophoriformes. Family: Pristiophoridae. Order: Squatiniformes. Family: Squatinidae. In: Stehman, M. Ed. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. – Bruxelles, Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: 193-254.

Herman, J., M. Hovestadt-Euler & D.C. Hovestadt. 1993. Part A: Selachii. No. 1b: Order: Hexanchiformes. Family: Heterodontidae; No. 6: Order: Lamniformes. Families: Cetorhinidae, Megachasmidae; Addendum 1 to No. 3: Order Squaliformes; Adddendum 1 to No. 4: Order: Orectolobiformes; General glossary; Summary Part A. In: Stehman, M. Ed. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. – Bruxelles, Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: 185-256.

Kajiura, S.M. & T.C. Tricas. 1996. Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray *Dasyatis sabina*. – Journal of Experimental Biology 199: 2297-2306.

Motta, P.J. & C.D. Wilga. 2001. Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. – Environmental Biology of Fishes 60:131-156.

Naylor, G.J.P. 1990. A morphometric approach to distinguish between upper dentitions of *Carcharhinus limbatus* and *C. brevipinna* with comments on its application to tracing shark phylogenies through their fossil teeth. In: Pratt, H.L., Jr., S.H. Gruber & T. Taniuchi. Eds. Elasmobranchs as resources: advances in the biology, ecology, systematic of the fisheries. – NOAA Technical Report NMFS 90: 381-387.

Naylor, G.J.P. & L.F. Marcus. 1994. Identifying isolated teeth of the genus *Carcharhinus* to species: relevance for tracking phyletic changes through the fossil record. – American Museum Novitates 3109.

Newberry, J.S. 1889. The Paleozoic fishes of North America. – United States Geological Survey Monograph 16.

Purdy, R.W. & M.P. Francis. 2007. Ontogenetic development of teeth in *Lamna nasus* (Bonnaterre, 1758) (Chondrichthyes: Lamnidae) and its implications for the study of fossil shark teeth. – Journal of Vertebrate Paleontology 27(4): 798-810.

Rohlf, F.J. 2007. tpsRelw version 1.45. State University of New York, Stony Brook.

Rohlf, F. J. 2008. tpsDig version 2.11. State University of New York, Stony Brook.

Rohlf, F. J. 2011. tpsRegr version 1.38. State University of New York, Stony Brook.

Shimada, K. 2002. Teeth of embryos in lamniform sharks (Chondrichthyes: Elasmobranchii). – Environmental Biology of Fishes 63:309-319.

St. John, O. & A.H. Worthen. 1875. Description of fossil fishes. – Geological Survey of Illinois 6: 245-488.

St. John, O. & A.H. Worthen. 1883. Descriptions of fossil vertebrates. – Geological Survey of Illinois 7:57-264.

Williams, M.E. 1990. Feeding behavior in Cleveland Shale Fishes. In: Boucot, A.J. Ed. Evolutionary Paleobiology of Behavior and Coevolution. – Amsterdam, Elsevier Press: 237-287.

Williams, M.E. 1998. A new specimen of *Tamiobatis vetustus* (Chondrichthyes, Ctenacanthoidea) from the Late Devonian Cleveland Shale of Ohio. – Journal of Vertebrate Paleontology 18(2): 251-260.

Williams, M. E. 2001. Tooth retention in cladodont sharks: with a comparison between primitive grasping and swallowing, and modern cutting and gouging feeding mechanisms. – Journal of Vertebrate Paleontology 21(2): 214-226.

Zelditch, M.L., D.L. Swiderski, H.D. Sheets, & W.L. Fink. 2004. Geometric Morphometrics for Biologists: A Primer. – London, Elsevier Academic Press.

Submitted: 19 May 2015
Published: 18 January 2016

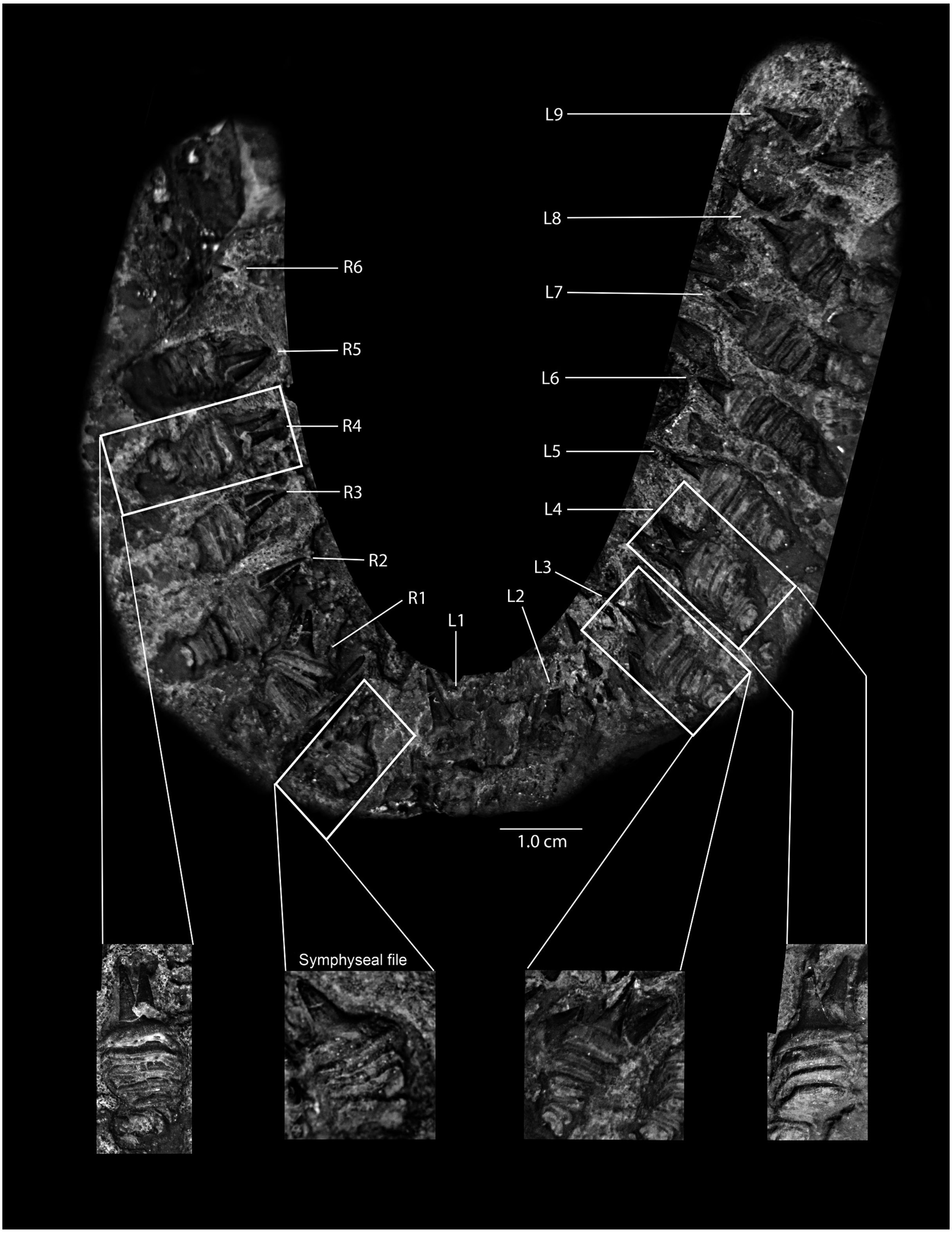

Plate 1. Dentition of *Ctenacanthus* (CMNH 5956) with closeup of several tooth files. Specimen courtesy of the Cleveland Museum of Natural History.

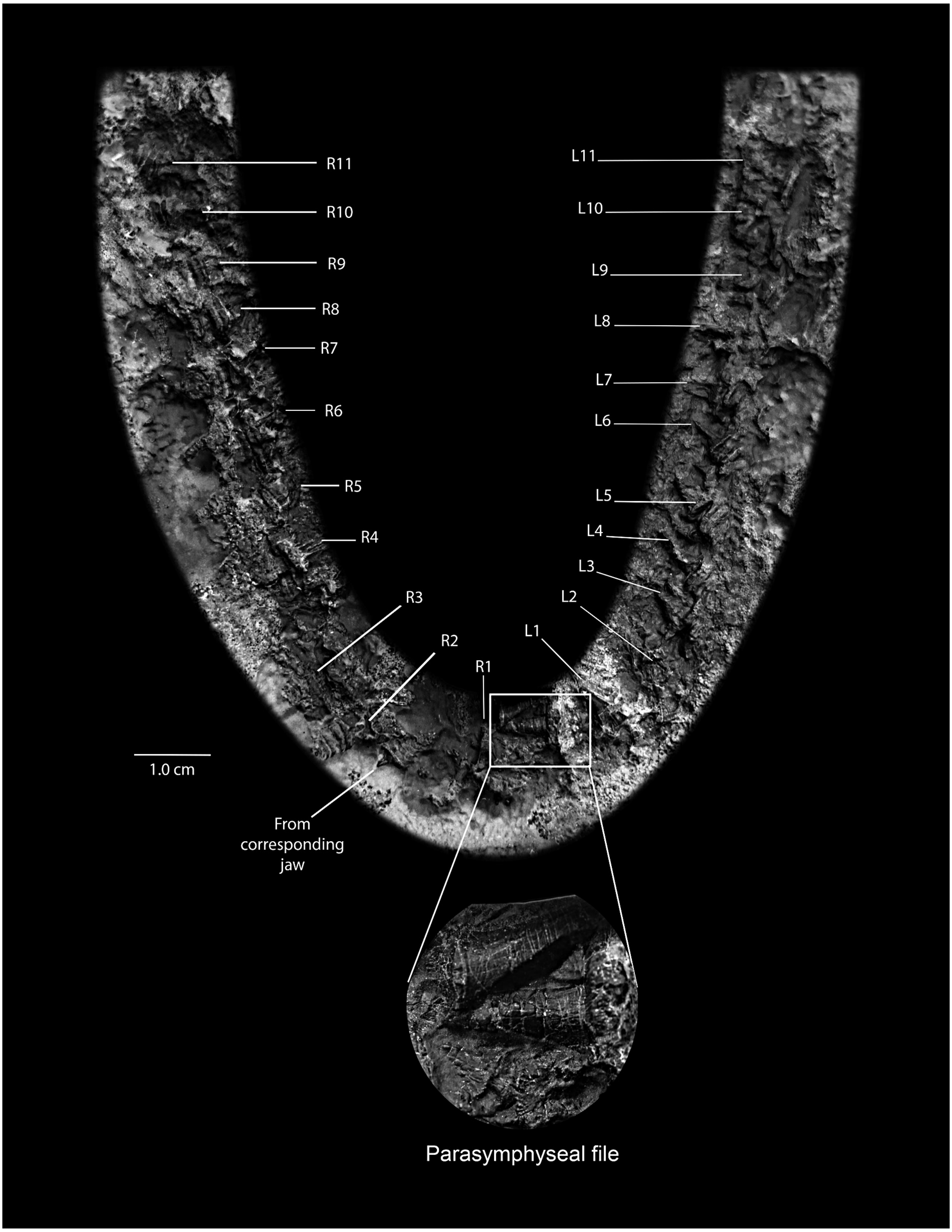

Plate 2. Dentition of *Cladoselache* (CMNH 50238) with closeup of single tooth file. Specimen courtesy of the Cleveland Museum of Natural History.

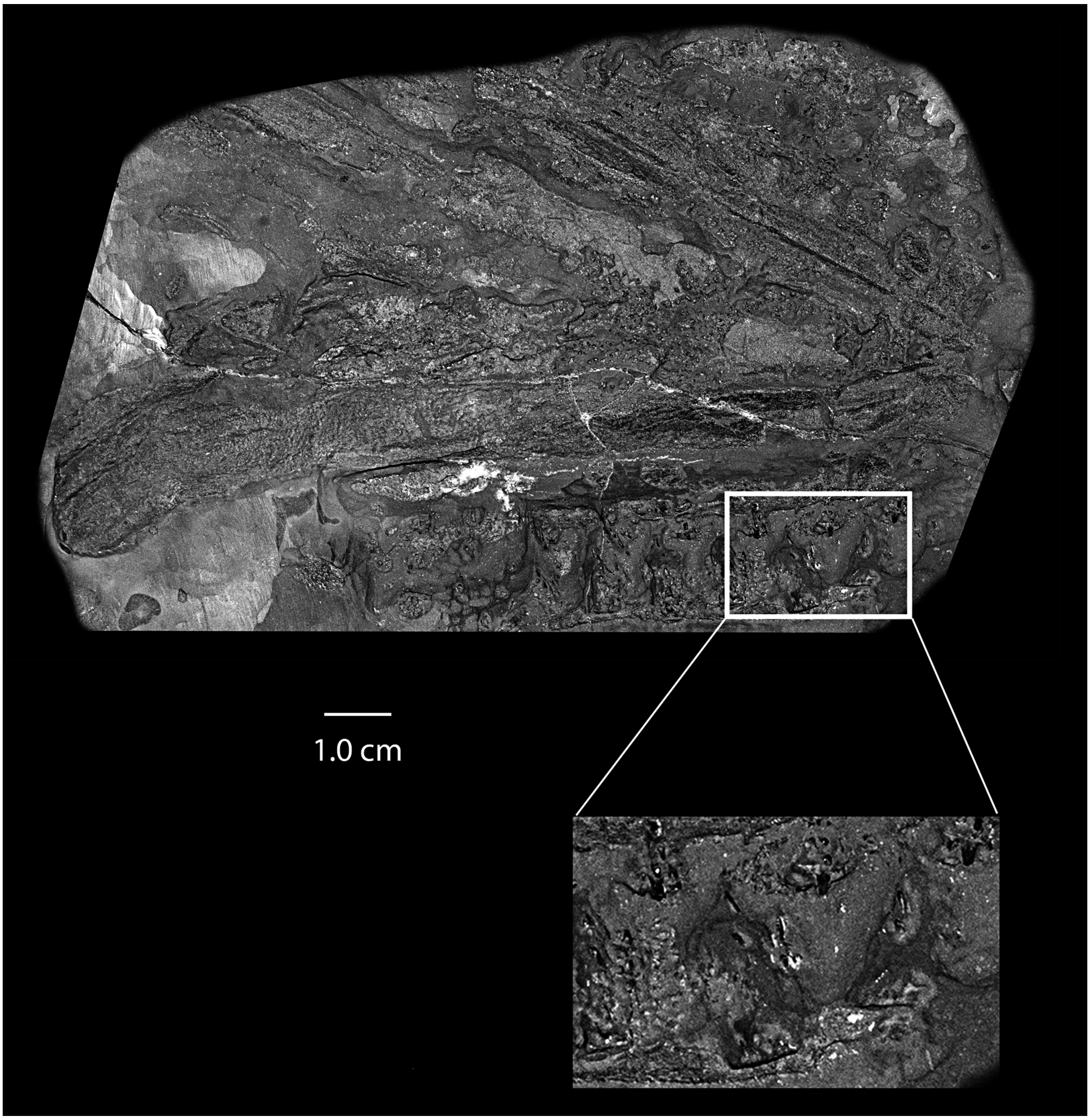

Plate 3. Dentition of *Cladoselache* (CMNH 8114) with closeup of several tooth files. Specimen courtesy of the Cleveland Museum of Natural History.

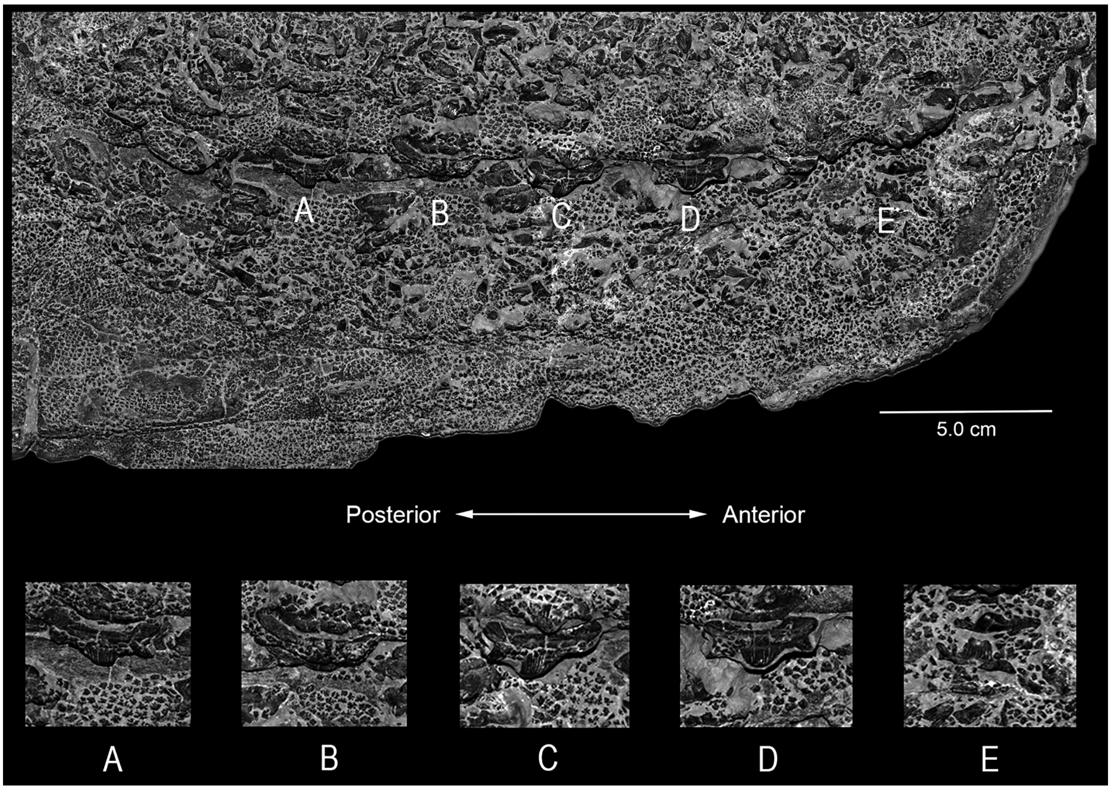

Plate 4. Dentition of *Ctenacanthus* (CMNH 9440) with closeup of several tooth files. Specimen courtesy of the Cleveland Museum of Natural History.

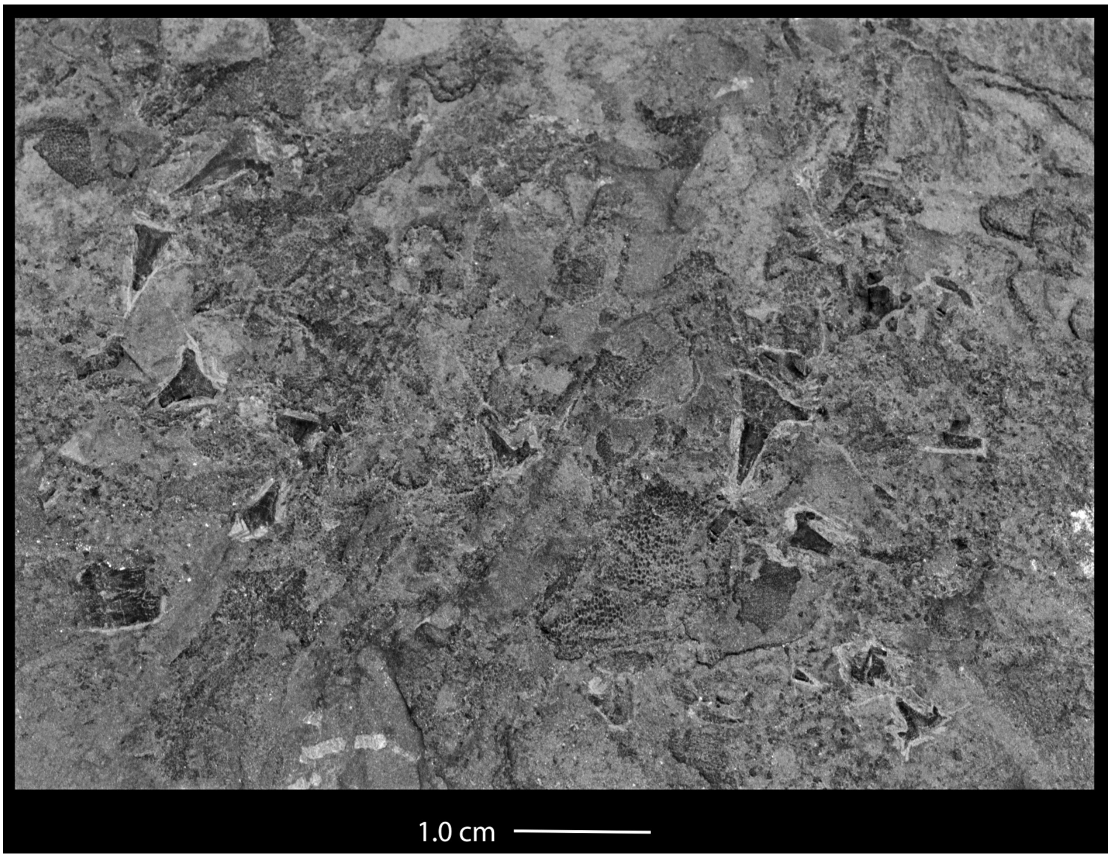

Plate 5. Closeup of scattered teeth associated with *Cladoselache* (CMNH 6187). Specimen courtesy of the Cleveland Museum of Natural History.

This publication is deposited as hard copy in four archival libraries and the archive of the PalArch Foundation. All of PalArch's publications are stored in the e-depot of The National Library, The Hague, The Netherlands (www.kb.nl).

Het Natuurhistorisch
Westzeedijk 345
3015 AA Rotterdam
The Netherlands

Royal Belgian Institute of Natural Sciences Library
rue Vautier 29 B- 1000
Brussels
Belgium

Library Naturalis
National Museum of Natural History
P.O. Box 9517
2300 RA Leiden
The Netherlands

PalArch Foundation
Spieregerweg 1
7991 NE Dwingeloo
The Netherlands

Vrije Universiteit
UBVU-Library of Earth Sciences
De Boelelaan 1079
1081 HV Amsterdam
The Netherlands