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Ontogenetic Trends of Sutural Complexity in Jurassic Ammonites

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Abstract: Ontogenetic sequencing of suture fractal dimensions from a single ammonite specimen was not previously accessible without extreme measures. The necessity for destruction of the full conch due to whorl overlap or, alternatively, the prohibitively expensive or inaccessible imaging equipment for use by paleontologists has led to this rich source of data remaining elusive. Tracings of ontogenetic sequences of sutures have rarely been published since the middle of the last century. These studies only focused on the outermost whorl of a given specimen or composited several specimens. Oftentimes, they focused only on the umbilical and juvenile stages of shell growth. Complete or multi-whorled ontogenetic sequences, including those of subadult and mature specimens, are especially uncommon. Using methods published in 2021 to address the accessibility problem in sutural ontogenies, our paper represents the first comparisons of the fractal trajectories of ammonoids and includes several significant Jurassic ammonite families. We found that ammonite sutures did not steadily increase in complexity, as was previously suggested. Instead, juvenile ammonoids were more likely to exhibit ups and downs in their fractal ontogeny. We also found that pathologies must be considered as extremely common phenomena for ammonoids. Finally, we explored the ways that the unsteady ontogenetic trends of fractal complexity in ammonoids offer insights into the formation mechanism of ammonoid septa.

Keywords: ammonites; ammonoid; ammonite sutures; ontogeny; evolution; functional morphology

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1. Introduction

Ontogenetic sequences of ammonite sutures have rarely been published. Consequently, the biological implications for differences in the rate of complexification over a life cycle have hardly been examined. Throughout the middle of the 20th century, tracings of sutures which illustrate the trend for sutures to become more complex over ontogeny were somewhat common, such as those by Schindewolf [1–3] or Schlegelmilch [4–6]. The highly irregular patterns of ammonite sutures mimic the mathematical phenomenon of fractal self-similarity [7]. Fractal geometry is used to measure the positive space of such forms, and it became a popular metric for sutural complexity in the 1980s and 1990s (Garcia-Ruiz et al., 1990) [8]. However, in 1995, Lutz and Boyajian [9] lamented the lack of ontogenetic sequences, which are commonly expressed as fractal dimensions. Hoffmann and Maisch [10] plotted the ontogenetic trajectories of other aspects of shell growth, such as changes in the width and rate of accretion away from the generating curve. Similar plots for the complexity of the ammonite suture over ontogeny have been difficult to procure in large part due to the phenomenon of whorl overlap, by which the marginal portions of the suture are covered up by new revolutions of shell growth, and only the medial portions

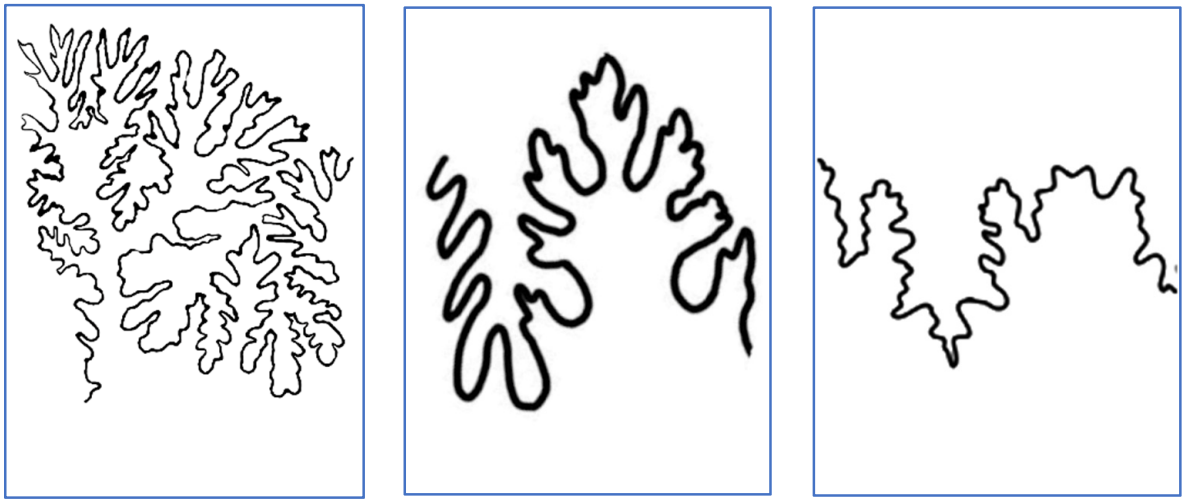
of the hemisuture are easily accessible. In 2021, Marriott and Chamberlain [11] devised a mathematical modification to normalize data taken from the medial part of the hemisuture, namely the lateral lobe (L) and second saddle (S_2), or LLS, which is visible and uncovered by successive whorls in most sutured ammonites. The LLS data greatly elongated the portion of a single shell that can be used to plot the fractal dimensions of sutures within a single specimen's ontogenetic sequence. Here, we compare the ontogenetic trajectories of suture complexity in several Jurassic and Cretaceous ammonite families: Hildoceratidae, Lytoceratidae, Perisphinctidae, and Phylloceratidae.

Complexity expressed as a fractal dimension is driven by several factors. The number of subdivisions, including lobelets and saddlets, is one factor. The other more abstract driver of complexity appears to be the shape and configuration of the suture pattern itself. For example, in baculitids measured in [11], more geometrically orthogonal saddles and lobes offered lower complexity, and with it, lower conversion values. The saddles and lobes of the more complex baculitids had narrow bases and wide, branching septal fluting configurations. Yacobucci and Manship [12] described these narrow bases as "waists".

2. Materials and Methods

In the 1990s, size-independent metrics for fractal dimensions of sutures became popular, including the box method and the Richardson step method [7,13–15]. Because the degree of accuracy changes based on the rule size, size-independent applications of fractal geometry are especially useful for ammonite shells or any fractal-mimicking object that is subject to growth. The LLS method described in [11] addresses the process by which partial ammonite sutures can be used to collect ontogenetic data from a single specimen. When taking a fractal dimension of a portion of the suture, the fractal dimensions are higher than they would be for the full suture. Because ammonite genera have distinct ranges of fractal values [9], factors that are consistent across genera can be used to normalize the partial suture's data in order to obtain the full suture's fractal dimension. These values were calculated for incomplete sutures using only the lateral lobe (L) and second saddle (S_2), or LLS. However, Marriott and Chamberlain [11] noted the separate value of leaving fractal values unconverted. Because of the wider range of "natural fractal" values required for unconverted LLS data, a more nuanced examination of the differences between ontogenetic data points is possible. Unconverted LLS data are consistent with one another.

We measured the ontogenetic trajectories for suture complexity, expressed as a fractal dimension, for the photographed ammonite specimens used in this study. The Kruskal–Wallis analyses from [11] indicated that LLS tracings from the photographs could be used for the analysis of suture complexity without significant distortion. Photographs were shared from the research collection of Rene Hoffmann and were also taken from the Museum National d'Histoire Naturelle in Paris and the online repository JSD Ammonites, the private collection of Jean-Stephane David, which is based in France (File S2 in the Supplementary Materials). The LLS portions of each ammonite suture were traced in black in GIMP and Photoshop and placed on a solid white background to a create size-independent rasterized image of 3″ × 4″ (Figure 1). The tracings were standardized by DPI at this stage. The sutures were fit to the same background, and their exposure levels were adjusted to solid black on white. The thickness of the ammonite sutures always decreases as complexity increases according to Saunders [16,17], so the tracings from the suture lines showed differences in line quality when placed on the same standardized digital format (Figure 1). The sequences of the ammonite sutures in the LLS were then entered into FDEstimator [18], a type of open-source fractal dimension software, for the unconverted fractal dimension of the LLS portion of the suture. As per [11], unconverted data were more sensitive to differences in fractal dimensions and more clearly illustrated the nuance between consecutive sutures. These values were then plotted in their natural sequence using the open-source quantitative paleontology software PAST [19].



(**a**) (**b**) (**c**)

Figure 1. (**a**) Second *Hemilytoceras fraasi*, (number 15 its ontogenetic sequence). (**b**) *Phylloceras* sp., number 6 in its sequence. (**c**) *Strajevskya strajevskyi*, number 10 in its sequence.

FDEstimator is based on the fractal box-counting method. This method measures the ability of a fractal surface to fill a space [8,13,14,20,21] by measuring the number of units in a box (number of magnification) to solve for the fractal dimension:

$$N(M) = a \cdot M^{-D} \quad (1)$$

where N(M) is the amount of magnification, D is the fractal dimension, and a is a constant (from [13]).

The box method is useful when determining that the fractal dimension does not significantly vary when M is increased or decreased. However, we chose not to adhere to the conventional types of graphs for this type of data because of the purely comparative and ontogenetic focus of this study. Both the box-counting method and other methods could be used to acquire single fractal data points.

The fractal method used to describe the LLS was the Richardson method, which chooses a rule size and counts the number of times the ruler can be fit to the curve of the ammonite suture. The fractal dimension is then the log of the number of times divided by the log of the rule size units. In [13], the equation for this is shown to be

$$D = \log(N)/\log(r) \quad (2)$$

in which N is the number of times the ruler was applied and r is the rule size. Marriott and Chamberlain [11] determined that applying Richardson's method to only an isolated portion of the suture—the lateral lobe L and second saddle S_2, or LLS (boundaries of LLS portion of suture in Figure 2)—enabled ontogenetic data to be accessed from single shells exhibiting whorl overlap. They concluded that when left non-normalized, the fractal dimensions of the LLS more clearly showed differences in the fractal dimensions between the sutures in an ontogenetic sequence.

Instead of manually calculating the fractal dimensions of the sutures in this study, we traced them from the shells in black vectors and then pasted them onto 3″ × 4″ solid white backgrounds. Each suture was fit to the 3″ × 4″ rectangle so that size would not become a factor. We then saved each 3″ × 4″ rectangle in sequence, beginning with the first suture that was visible, and ran them through the FDEstimator software [18]. Examples of the 3″ × 4″ rectangles can be seen in Figure 1.

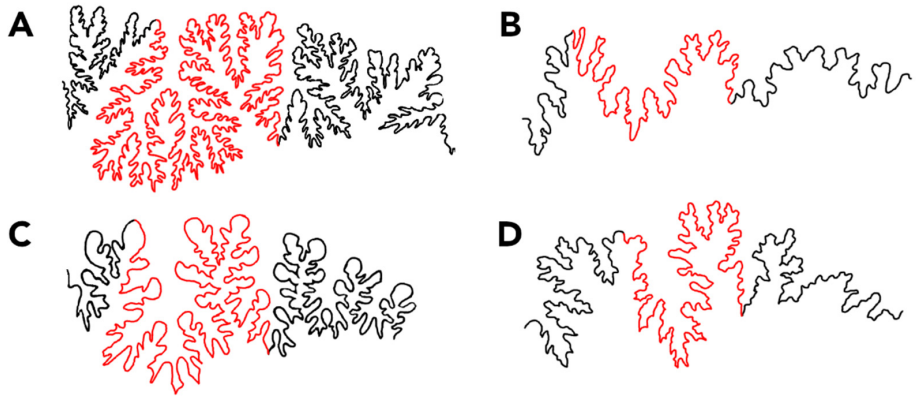


Figure 2. LLS portion of suture with cutoff points determined by Marriott and Chamberlain [1] highlighted in red, with L_{max} values representing the distance between the lateral lobe (L) and second saddle (S_2) for (**A**) *Lytoceras* (retracted from [22]) (**B**) *Cadoceras* (retraced from [23]) (**C**) *Phylloceras* (retraced from [24], and (**D**) *Perisphinctes* (retraced from [4]).

We then plotted the fractal values for each ontogenetic sequence in PAST, and estimations of the positions of each specimen's ontogeny began on the *x*-axis based on the whorl number.

3. Results

3.1. Lytoceratids

Overall, the ammonite sutures examined showed increased complexity throughout ontogeny [8,9] (Figures 3 and 4), but the increments between consecutive sutures can be irregular and can also decrease [13,20]. Peterman et al. [20] calculated fractal dimensions for the baculitids over ontogeny, but Jurassic lytoceratids, as planispirals, require use of the LLS method to plot ontogenetic change. The LLS fractal values were left unconverted and only reflected the fractal values of the lateral lobe (L) and second saddle (S_2). Lytoceratidae exhibited high degrees of irregularity with regard to the complexity in the early life stages between the immature stages and subadulthood. Juvenile lytoceratids had significant increases and decreases in complexity from one suture to the next. However, subadult and mature lytoceratids nearly stabilize their complexity, with near-constant ranges for fractal complexity and nearly horizontal slopes between consecutive sutures. This trend continued into the Cretaceous family Gaudryceratidae (Figure 4).

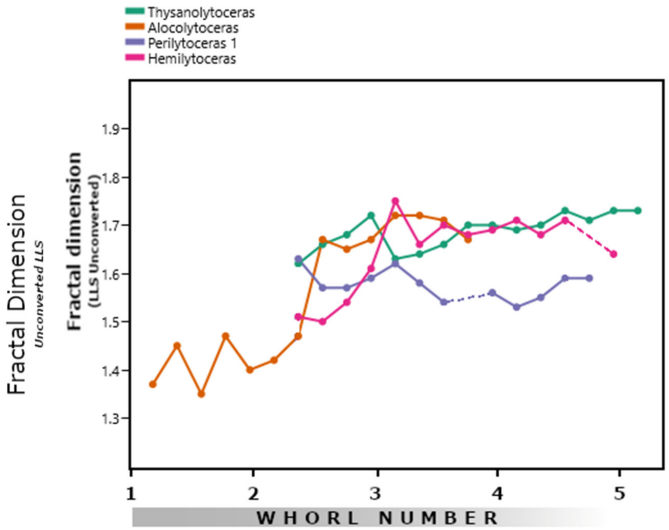


Figure 3. Ontogenetic sequences of lytoceratids. The dashed lines indicate unusable sutures within the ontogenetic sequence. The fractal dimensions can be found in File S1 in the Supplementary Materials.

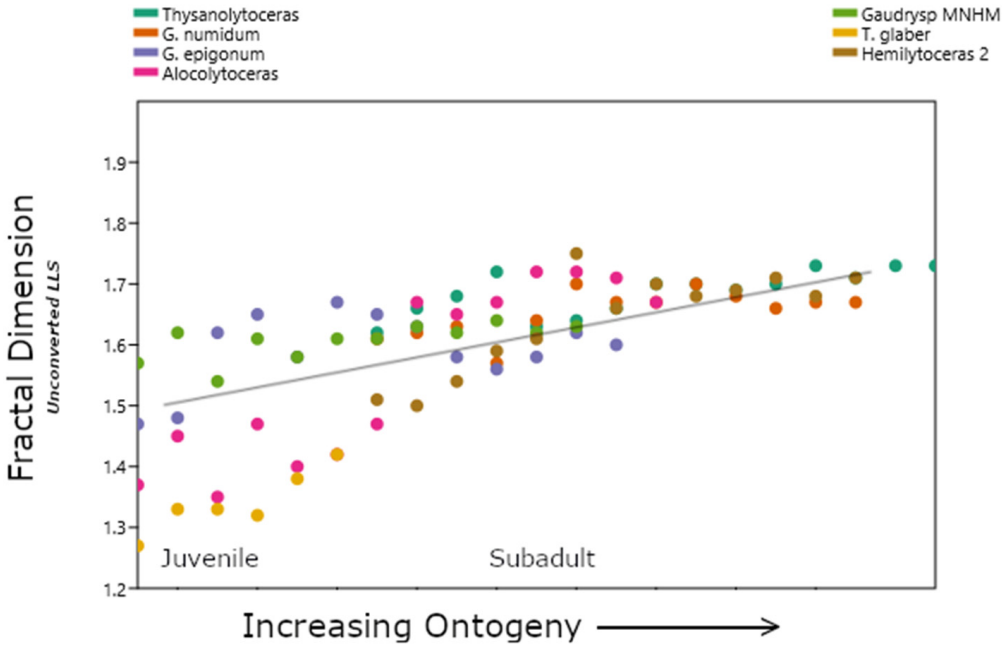


Figure 4. Decrease in variance in suture complexity over ontogeny for Lytoceratoidea, including Jurassic lytoceratids and Cretaceous gaudryceratids.

3.2. Hildoceratids

Some hildoceratids, including members of *Hildoceras* and *Harpoceras*, exhibited tight whorl overlap such that the LLS data were not available from the photographed specimens. The LLS method is effective for these ammonites in the adult stage and in steinkerns, but whorl overlap limits its ability to procure multi-whorled ontogenetic sequences. For this reason, new conversion values needed to be devised that encompassed the next available saddle–lobe pair. The second saddle (S_2) and third umbilical lobe (U_3) were chosen for this purpose, which we designated as a "secondary conversion value", or V′. The secondary conversion value was calculated in exactly the same way as the primary conversion values described by Marriott and Chamberlain [11] with comparable sample sizes, but instead the focus was on S_2 and U_3. Table 1 shows the secondary conversion values for *Hildoceras*, *Harpoceras*, and *Esericeras*, as well as the conversion from V′ to V for *Hildoceras*. Because secondary conversion values for the hildoceratids are consistent, it is possible that secondary conversion values are consistent at the genus level rather than the family level, but this needs to be confirmed.

Table 1. Fractal data for hildoceratids based on average fractal dimensions of *Hildoceras* and *Harpoceras* from File S1 in the Supplementary Materials of Marriott and Chamberlain [11], LLS conversion value (V), and secondary (S_3U_3) conversion value. Estimated fractal range and conversion values determined for *Esericeras* by the authors of this paper in the same methods laid out by Marriott and Chamberlain [11].

Genus	Average Df	LLS V	S_2U_3 V	V′ to V
Hildoceras	1.227	1.4	1	×1.1
Harpoceras	1.299	1.144	1	N/A

The secondary conversion value V′ of *Hildoceras* and *Harpoceras* was one, meaning that there was no significant difference in *N* from Equation (1) whether taking the fractal dimension of the full hemisuture, as in the Richardson method, or the distance from the second saddle to the last umbilical lobe. We needed to scale this to the same fractal value as the unconverted LLS. We found we could do this by multiplying the V′ value by 1.1, as seen in Table 1. Hildoceratids did not clearly show a gradual overall increase in fractal

complexity when using a size-independent ruler. Ontogenetic sequences for hildoceratids can be seen in Figure 5.

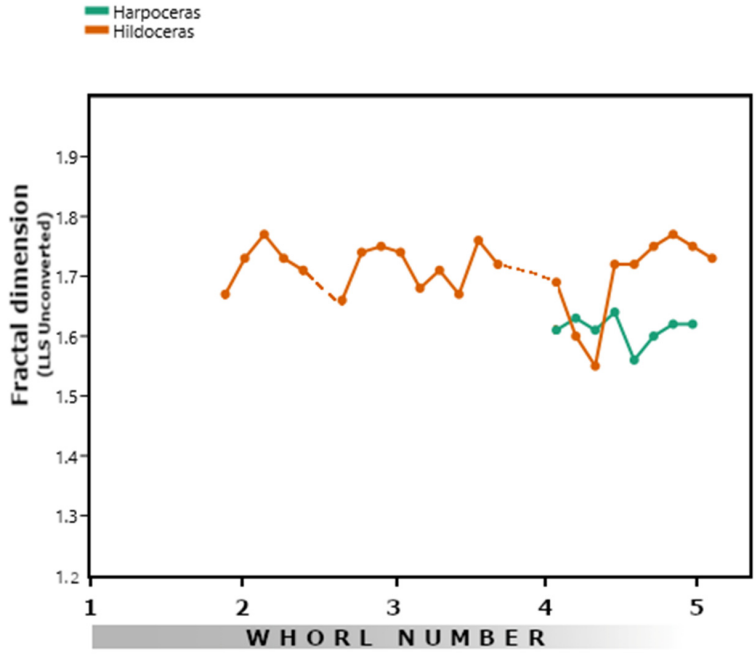


Figure 5. Ontogenetic sequences of hildoceratid suture complexity. The dashed lines indicate an unusable suture in the sequence. The fractal dimensions can be found in File S1 in the Supplementary Materials.

3.3. Perisphinctids

Perisphinctids (Figure 6) showed no plateauing of their irregular ontogenetic trends between the ontogenetically younger and older specimens and were found to be ontogenetically erratic in both their juvenile and mature stages.

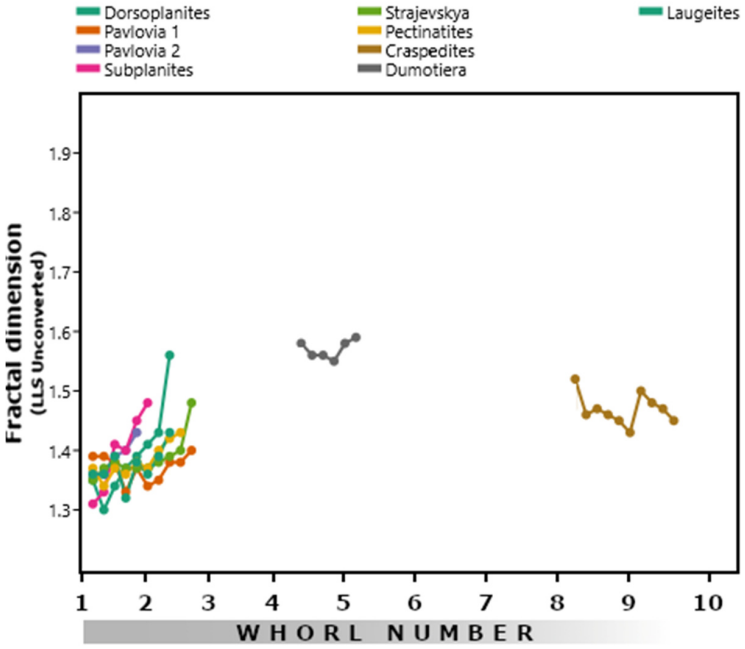


Figure 6. Ontogenetic sequences of perisphinctid suture complexity. The fractal dimensions can be found in File S1 in the Supplementary Materials.

3.4. Phylloceratids

Phylloceratidae are the most distantly related of the ammonite families included in this study [25]. They have distinct morphological traits. Ontogenetically, they appear to be more gradual in their increase and less erratic in their sudden increases and decreases in complexity than lytoceratid-derived taxa. However, more data are needed for phylloceratid-derived taxa to confirm these ontogenetic differences (Figure 7).

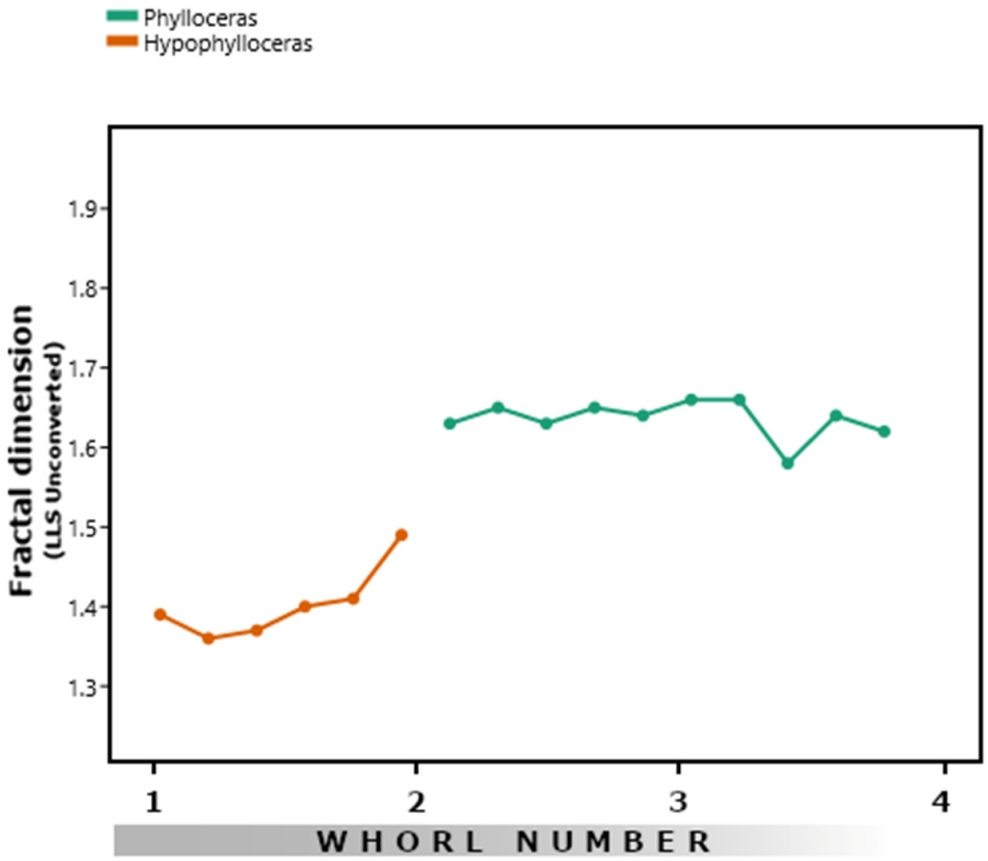


Figure 7. Ontogenetic sequences of phylloceratid suture complexity. The fractal dimensions can be found in File S1 in the Supplementary Materials.

4. Conclusions

4.1. Discussion

Ammonite sutures do not steadily increase in complexity from one suture to the next [20] (Figure 8). However, the constantly shifting rates of change in complexity are somewhat endemic to the genera of Jurassic ammonites. It may be interesting to carry out additional research on the developmental biology underlying these differences in the future. Lytoceratids show much more variation in the fractal dimensions between consecutive sutures than phylloceratids but eventually taper off after they reach a certain point in their ontogeny, that being around the fifth or sixth whorl. It is unclear whether this tapering is due to the upper limits of fractal complexity for the septal wall or if it is truly ontogenetic. Perisphinctids showed the least predictability in their ontogenetic sequences, and they may exhibit the most significant ontogenetic eccentricity of all. It is important to note that increased complexity alone is not a factor for unsteady rates of complexification. Perisphinctids and hildoceratids show greater hills and valleys in the later stages of ontogeny, where suture complexity should be higher overall than in their younger phases.

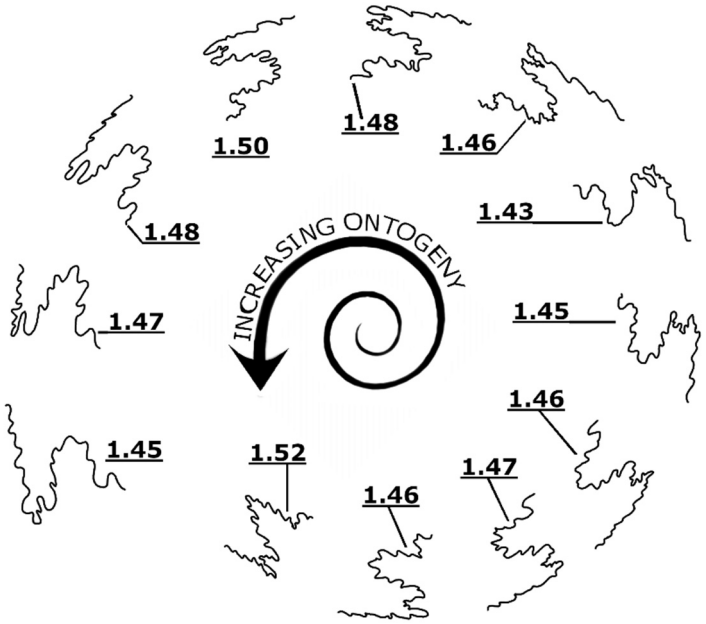


Figure 8. Ontogenetic sequences of perisphinctoid *Craspedites nodiger*.

4.2. Implication for the Formation Mechanism of Sutures

The growing number of examples for unsteady rates of complexification in an ammonite suture may offer insights into the way that sutures form in the first place. Despite this recent evidence, it is still commonly generalized (incorrectly) that ammonite sutures grow steadily more complex with each new suture that is deposited. All ammonoids exhibited considerable ontogenetic instability in their juvenile stages. Lytoceratidae exhibited high degrees of irregularity in their complexity in the early life stages between the paralarval or umbilical stage and maturity.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/geosciences12020066/s1. The ontogenetic sequences of fractal dimensions for each family are available in the supplementary zip file.

Author Contributions: K.M., S.O., D.B., C.C., R.J.L., R.O. and K.I.W. collected and curated data; K.M. wrote the body text of the first draft; D.R.P. supervised throughout and edited the revised manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The supplementary file for this paper contains all of the ontogenetic sequences included in the study.

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Conflicts of Interest: The authors declare no conflict of interest.

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