



## Size Classes in Ammonoids from the Middle Devonian Cherry Valley Limestone of New York State, U.S.A.

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7 Text-Figures, 1 Table and 3 Plates

USA  
Devonian  
Cephalopods  
Ammonoidea

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## Größenklassen von Ammonoideen aus dem mitteldevonischen Cherry Valley Limestone in New York State, U.S.A.

### Zusammenfassung

Im Cherry Valley Limestone (Mitteldevon; New York State, U.S.A.) treten Agoniatiten während ihrer gesamten Reichweite in getrennten Lagen auf. Sie stellen periodische Einwanderer in das Gebiet in Transgressionszeiten dar.

An einer kleinen Gesteinsplatte, die im Museum von Albany (New York State Museum) erhalten ist, wurde versucht, eine Population von *Agoniatites vanuxemi* (HALL, 1897) zu untersuchen. Die Unterfläche einer Platte von ca. 1,6 m x 2,0 m enthält 43 Stück von *Agoniatites vanuxemi* in Seitenansicht, 39 davon messbar. Folgende Messungen wurden gemacht: maximaler Durchmesser, maximale Windungshöhe, Phragmokondurchmesser. Windungshöhe am Ende des Phragmokons und der Winkel der Wohnkammer. Die Septalwinkel wurden ebenfalls gemessen, wo es möglich war.

Der Phragmokondurchmesser wurde als Größenmaßstab genommen, weil die Wohnkammern nicht messbar waren. Ein Diagramm der Größenverteilung (N = 25) ergab das Vorhandensein von drei deutlich erkennbaren Größenklassen. Diese wurden verwendet, um Sexualdimorphismus und das Vorhandensein verschiedener Altersklassen nachzuweisen. Sexualdimorphismus kann hier wegen des Fehlens eines Nachweises der Maturität ausgeschlossen werden, insbesondere wegen des Fehlens von Kammerdrängung.

Die drei Größenklassen stellen drei Alterskategorien in der Population von *Agoniatites vanuxemi* dar, möglicherweise drei Jahrgänge. Die kleinsten und jüngsten Individuen waren subadult, Die größten und vermutlich ältesten waren wahrscheinlich kurz vor der Geschlechtsreife, weil erst einige aus dieser Gruppe Septendrängung zeigten. Kleine Jungtiere lebten vermutlich in anderen Bereichen. Erst ab einer gewissen Größe und einem gewissen Alter suchten sie den Lebensraum der Adulten auf.

### Abstract

The agoniatites in the Cherry Valley Limestone (Middle Devonian) of New York State, U.S.A. occur in discrete beds throughout their range. The agoniatites represent periodic immigrants into the area during times of transgression.

A population study of *Agoniatites vanuxemi* (HALL, 1879) was attempted using a small bed that is preserved in the New York State Museum, Albany. It is the lower surface of a slab of Cherry Valley Limestone, measuring about 1.6 m x 2.0 m and contains 43 specimens of *Agoniatites vanuxemi* in lateral view, of which 39 were measurable. The following measurements were made: maximum diameter, maximum whorl height, phragmocone diameter, whorl height at the end of the phragmocone, and body chamber angle. Septal angles were also measured where possible.

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Phragmocone diameter was used as a measure of size because the body chambers were not measureable. A size frequency histogram of phragmocone diameter ( $N = 25$ ) indicated the presence of three discrete size classes. Size classes in ammonoids have been used to suggest sexual dimorphism and the presence of different age groups in a population. Sexual dimorphism is discounted here based on the lack of evidence of maturity, i.e., the absence of septal approximation.

The three size classes in this sample represent different age classes in the population of *Agoniatites vanuxemi* (HALL), possibly three annual cohorts. The smallest and youngest individuals were subadults. The largest and presumably oldest were probably near maturity because only a few of them exhibited septal approximation. Smaller juveniles probably lived elsewhere, as suggested by their absence. Only upon reaching a certain size and age did they enter the adult habitat.

## 1. Introduction

As paleontologists one of the things we try to do is to treat the fossils we study, in this case ammonoids, as biological entities that in life possessed all of the characteristics that modern organisms do. Such characteristics include growth parameters, feeding habits, biological interactions with other organisms, reproductive habits and life history strategies. In other words all aspects of biology and ecology.

Documenting these phenomena in fossil organisms is not always easy and in fact is sometimes impossible. Attempting such a study requires that certain conditions of preservation and taphonomy occur. These requirements depend upon the nature of the study undertaken. For example, while the study of shell microstructure requires the original aragonite be preserved, a study of any organic tissue requires that the fossil be deposited in a reducing environment, not necessarily conducive for shell preservation.

Studies on fossil communities and populations are commonly done (LEVINTON & BAMBACH, 1969; SURLYK, 1972; RICHARDS & BAMBACH, 1975). Once the organisms present can be determined to have lived at the same time and represent a true community or biological population (generally done by studying the sedimentology and

taphonomic history) (HALLAM, 1967; NOBLE & LOGAN, 1981; KIDWELL, 1991; KIDWELL & JABLONSKI, 1983; KIDWELL & BONSENCE, 1991; KIDWELL & FLESSA, 1996), they are analyzed in much the same way as living populations (DEEVEY, 1947; HALLAM, 1972). Most of these studies are done on benthic organisms because it is easier to determine an in situ population.

One type of study done is the use of size frequency to analyze a population of a single species (RICHARDS & BAMBACH, 1975; NOBLE & LOGAN, 1981; MANCINI, 1978). All specimens of a given species are measured using some homologous measurement. They are then ordered and grouped according to size. The structure of the population is then analyzed based on the resultant distribution.

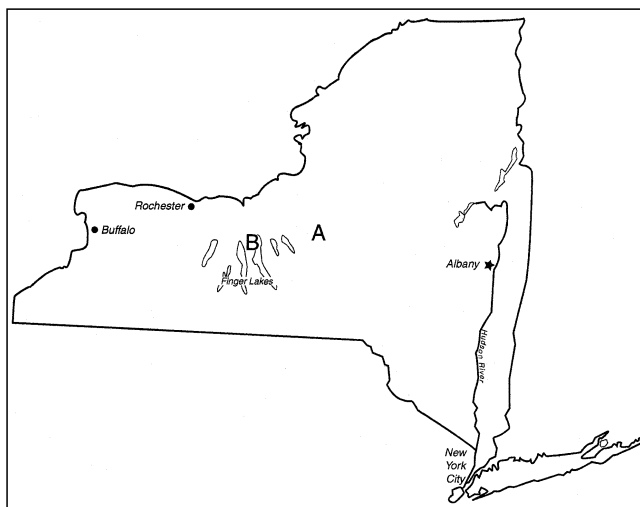
In this study a small population of Devonian ammonoids is analyzed in this way and an attempt is made to place the size classes found there in a biological context. Since ammonoids are nektonic, i.e., mobile organisms, demonstrating that a true population is present is particularly difficult. In rare cases where death of the organisms was sudden, followed by rapid burial, this problem can be overcome. Such is the case in the lagerstätten deposits of the Middle Devonian Cherry Valley Limestone.

## 2. Materials

Devonian rocks are well exposed in New York State, covering an area of almost one-half the state. The Cherry Valley Limestone is part of the Marcellus shale (upper Eifelian to lower Givetian), the lowermost formation in the Hamilton Series (GRIFFING & VER STRAETEN, 1991). The Cherry Valley Limestone occurs as the topmost member in the lower part of the Marcellus Formation (RICKARD, 1952). It is composed of skeletal limestones and shales and outcrops eastward from just south of Rochester, New York, to southwest of Albany, New York. It is primarily a dark argillaceous massive-nodular stylolinitid-cephalopod packstone. The fauna is primarily pelagic, with rare benthic elements (GRIFFING & VER STRAETEN, 1991). It has been compared to the red and black cephalopod limestones of the Middle Devonian to the Lower Carboniferous of Europe and North Africa (TUCKER, 1974; BANDEL, 1974; WENDT & AIGNER, 1982, 1985; GRIFFING & VER STRAETEN, 1991).

The characteristic cephalopod fauna occurs in the lower half of the upper layer (FLOWER, 1936). In places it has been recorded as a fossil lagerstätten containing many exceptionally well preserved cephalopods of the genus *Agoniatites* and diverse orthoconic nautiloids (WHITELEY & KLOC, 1999). These lagerstätten deposits contain no juveniles and this has led workers to believe that the cephalopods present represent immigrants that entered the area during times of transgression and then suffered a mass mortality before a viable reproducing population could become established (KLOC, 1983; ANDERSON et al., 1988). One hy-

pothesis to explain this mass mortality is that a storm churned up the sediments in the Paleozoic sea rapidly, but incompletely, burying the fauna (WHITELEY & KLOC, 1999). The type of mass mortality present in the Cherry Valley Limestone is essentially like freezing a moment in time and is ideal for a study of fossil populations.



Text-Fig. 1.  
Map of New York State showing the localities of the Seneca Stone Quarry near Seneca Falls, New York (B) and the area near Manlius, New York where the bed of *Agoniatites vanuxemi* (HALL) had been quarried (A).

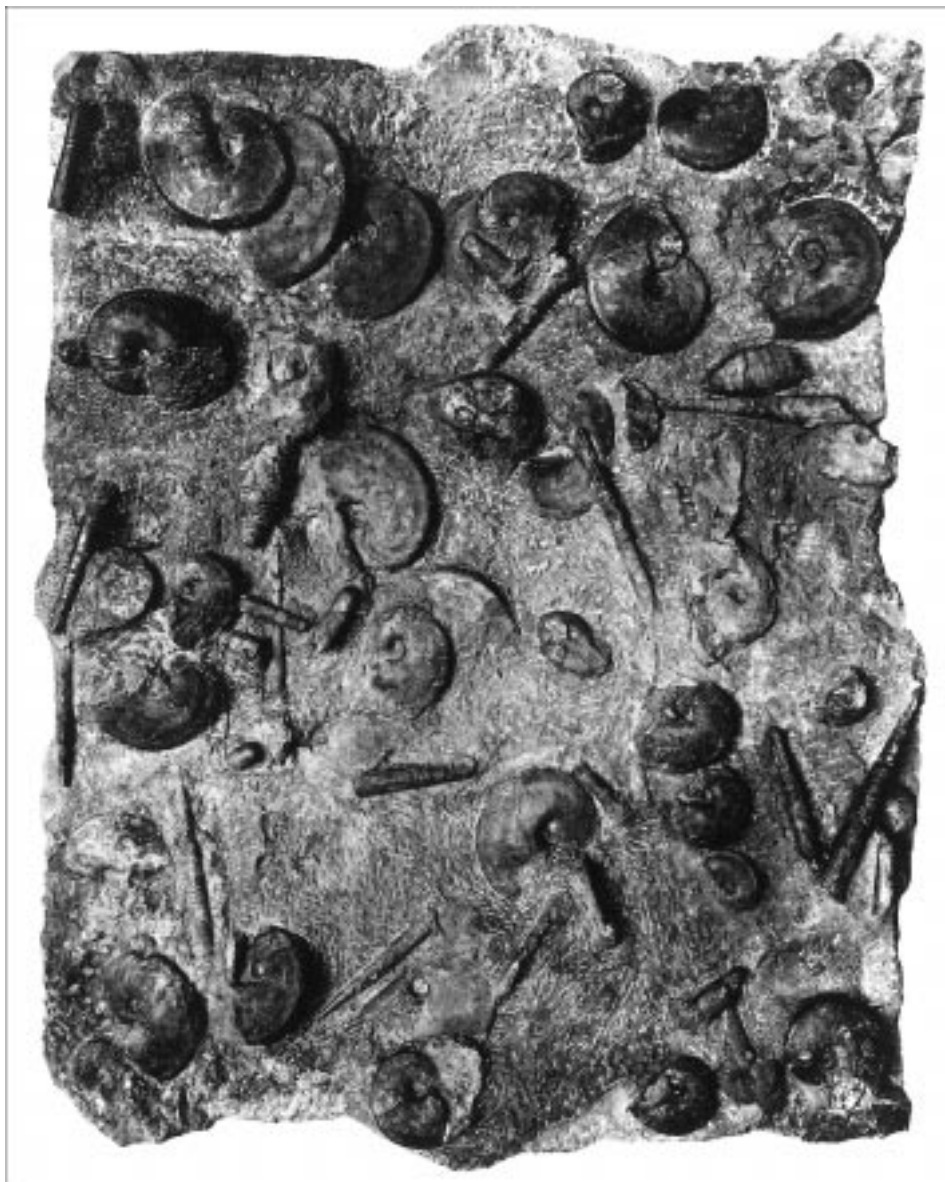
Text-Fig. 2.

Top view of the bed from the Cherry Valley Limestone on display in the New York State Museum, Albany, New York. The bed measures 1.6 meters X 2.0 meters and contains 43 specimens of *Agoniatites vanuxemi* (HALL) and a variety of orthoconic nautiloids. Frontispiece (Plate 1) from MILLER (1938).

One of the most extensive lagerstätten beds is found in the Seneca Stone Quarry located near Seneca Falls, New York (B, Text-Fig. 1). At the top of the south end of the quarry pit, there is a bed (9.14 m X 24.38 m) literally covered with cephalopods, most of which are preserved as median cross sections (VAN DYK, 1988) (Pl. 1, Fig. 1). Most abundant are specimens of the species *Agoniatites vanuxemi* (HALL, 1879) (Pl. 2). Orthoconic nautiloids are also present. While several species of *Agoniatites* occur in the Marcellus shale, these lagerstätten accumulations have generally been described as monospecific. In the case of the Seneca Stone Quarry, the systematic designation is based on the few specimens which could be described.

It was the original intent of this study to use the exposed cross sections in a population study based primarily on size. Unfortunately most of the exposed specimens were lying oblique to the bedding plane (Pl. 2, Fig. 2) or were weathered in such a way as to make accurate and consistent measurements impossible (Pl. 2, Fig. 3).

A second option presented itself in the form of a preserved bed on display in the New York State Museum in Albany, New York (Pl. 1, Fig. 2). The bed, similar in type to that exposed in the Seneca Stone Quarry, was collected approximately 2 miles west of Manlius, New York (A, Text-Fig. 1). It measures approximately 1.6 m X 2.0 m and contains 43 specimens of *Agoniatites vanuxemi* (HALL) and numerous orthoconic nautiloids, generally in lateral view (Text-Fig. 2). Unlike those found in the Seneca Stone Quarry bed, the specimens are in three dimensions. All of the specimens on the bed are morphologically similar and are regarded as the same species. What variation may occur is consistent with what would be expected in a normal population. The covered portions of the specimens (that which is embedded in the sediment) are largely not preserved. The bed is viewed stratigraphically inverted with the lower surface facing up and therefore represents a 3-dimensional mirror of the bed in the Seneca Stone Quarry. As noted by FLOWER (1936) the uppermost portion of most fossils was rarely preserved in the Cherry Valley



Limestone. This led him to the conclusion that the animals were only partially buried. So while death was instantaneous and burial rapid, the animals were partly exposed and the tops were destroyed before more sediment was deposited on them. ANDERSON et al. (1988) and MAEDA & SEILACHER (1996) have further elaborated on the processes which produced half ammonoids like those in the Cherry Valley limestone. This is what we see in the specimens from the bed on display in Albany. In fact, most ammonoids found in the Cherry Valley limestone, while exhibiting excellent preservation are missing one side. We do not see them in the Seneca Stone Quarry because the eroded portions have been further planed off.

### 3. Methods

In July of 1993, Dr. Ed LANDING of the New York State Geological Survey granted me access to the bed on display in the State Museum in Albany in order to measure the specimens. Before measurements were taken, the photograph of the bed published by MILLER (1938) (Text-Fig. 2) was used as a template to create a schematic of the bed. All of the specimens on it were traced and then numbered to keep track of the data (Text-Fig. 3).

Text-Fig. 3.

Schematic map of the bed of ammonoids for Text-Fig. 2.

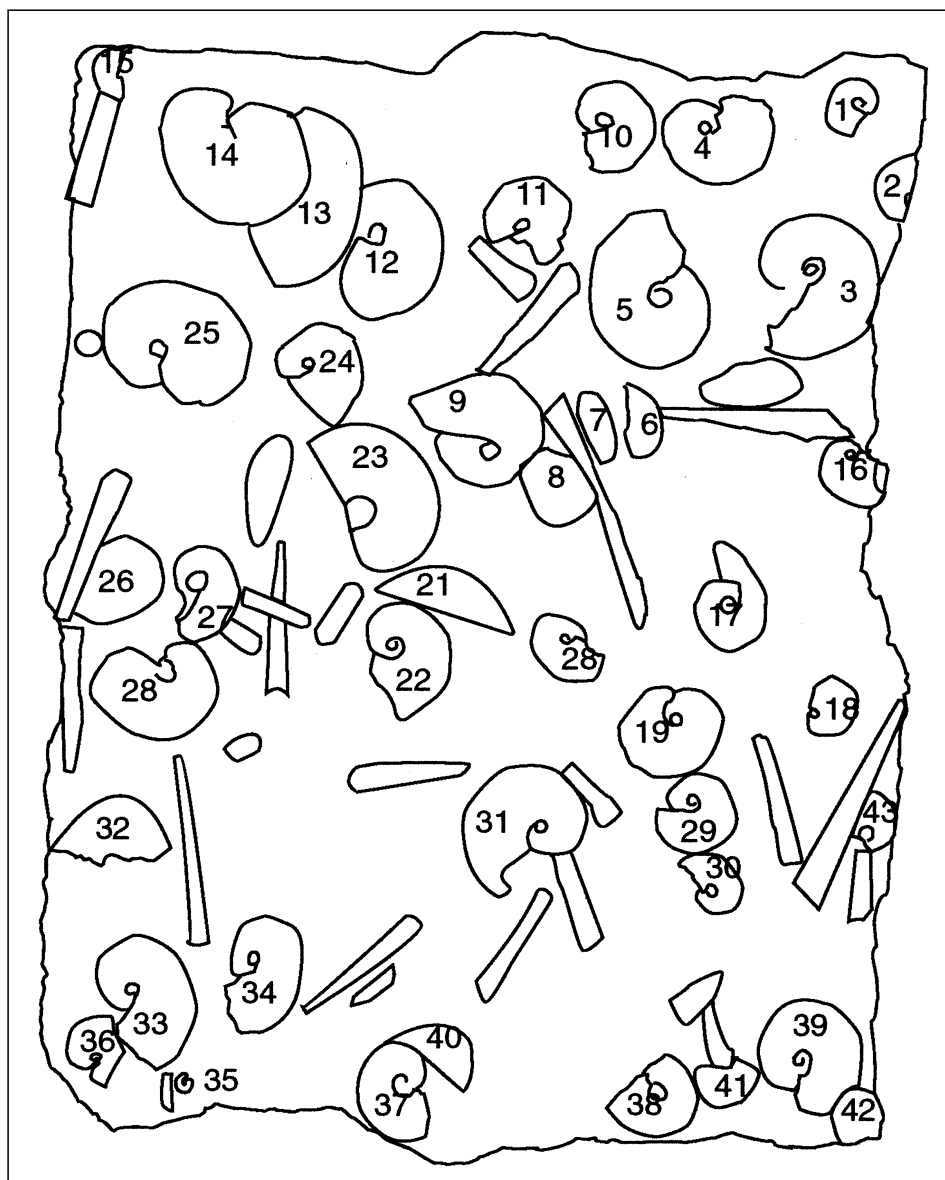
All of the specimens of *Agoniatites vanuxemi* (HALL) have been numbered. These numbers are used in this study to correlate specimens with their measurements and any photographs taken.

The following measurements were taken:

- Maximum diameter
- Whorl height at maximum diameter
- Phragmocone diameter
- Whorl height of the phragmocone
- Body chamber angle
- Septal angle

Not all specimens were measurable for any or all measurements because of varying degrees of preservation. For example on Pl. 3 there are several specimens which are excellently preserved in which the phragmocone diameters could not be measured because most of the body chambers are still present. A less complete body chamber would have allowed the phragmocone diameter to be measured. Of the 43 specimens 39 could be measured for at least one measurement (Table 1). In addition to the measurements given, body chamber angles were measured for 22 specimens. They ranged from 57°–310°, with most measurement falling in the area of 200°. Eighteen specimens had 2 or more septa visible and were measured for septal angle, i.e., the angle between successive septa.

Maximum diameter is the measurement used to define size of an ammonoid specimen. In any population study it is critical that the specimen be complete in order to accurately reflect size distribution. The variation in body chamber angle of these specimens was a clear indication that in most, if not all, of the specimens the body chambers were not complete. Therefore it cannot be established with any certainty that the measured total diameters reflect the actual size of the specimens. Phragmocone diameter has been used as an indicator of relative size in many studies. This assumes that body chamber angle in complete specimens would be statistically the same for all members of the same species. One factor which has been shown to be correlated with differences in body chamber angles is the whorl expansion rate (OKAMOTO, 1996). One indicator of differences in whorl expansion rate is the whorl height/diameter ratio (Wh/D). For the specimens used in this study the  $\bar{X}_{Wh/D} = 0.545 \pm 0.099$  ( $\bar{X}$  = mean Wh/D, N = 31). All but three points fall within the range of



variation and are therefore statistically the same. Therefore, for this study, phragmocone diameter is considered to be an accurate estimate of relative size.

Of the 39 specimens measured only 10 could be measured for phragmocone diameter, but in an additional 15 specimens the whorl height of the phragmocone had been measured. Phragmocone diameters for these specimens were estimated in the following manner.

All diameter measurements which had an accompanying whorl height measurement were regressed employing the JMP Version 3.2 program for MacIntosh using the  $\ln$  for both variables (Text-Fig. 4). The number of measurements used in this analysis is 31. The regression produced a line with the following equation:

$$\ln Wh = -0.0574 + 0.88901 \ln D \quad (SD = \pm 0.06)$$

where Wh is the whorl height and D is the diameter of the specimen and SD is the standard deviation of the regression. Three points fall outside of the standard deviation. These are the same three specimens which yielded the outliers in the Wh/D ratio. All three represent total diameter measurements. There are several factors which could account for the lack of it:

Table 1.

Measurements used in this analysis.

Specimen numbers correspond to the numbering of specimens given in Text-Fig. 3.

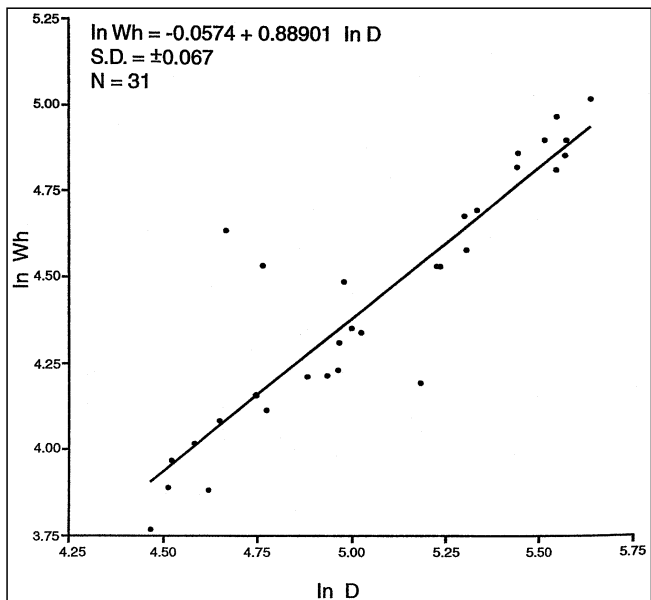
Dmax = maximum diameter; Whmax = whorl height at maximum diameter; Dphrag = phragmocone diameter; Whphrag = whorl height of the phragmocone; Dphrag measurements given in bold are those measurements estimated from the regression analysis equation given in Text-Fig. 4. All measurements are given in millimeters.

Specimen #	Dmax	Whmax	Dphrag	Whphrag
1	101.71	48.74	87.19	43.51
2	115.87	64.46	<b>76.64</b>	44.83
3	255.00	124.04	145.00	89.35
4	201.00	98.19	131.74	67.77
5	262.00	129.94	175.00	91.32
10	147.95	78.13	104.55	59.39
11	155.05		126.27	65.25
12	256.00	144.98	<b>159.70</b>	86.10
14	263.00	135.14	<b>140.49</b>	76.83
15	232.00	100.12	<b>141.56</b>	77.35
16	143.39	74.77		
17	178.00	66.56	<b>88.25</b>	50.82
18	99.98		92.31	53.06
19	107.00	103.37	<b>121.09</b>	67.32
20	133.12		<b>75.53</b>	44.25
22	200.00	108.11	130.91	70.16
23	280.00	152.80	<b>212.13</b>	110.82
25	231.00	125.23	<b>134.30</b>	73.81
27	139.19	68.09	<b>85.06</b>	49.18
29	142.88	69.21	97.99	55.76
30	118.36	61.56	91.42	49.02
31	248.00	135.40		
33	231.00	129.92	<b>164.38</b>	88.34
34	207.00	109.67	<b>130.00</b>	71.71
36	117.91	93.51	<b>87.96</b>	50.67
37	187.00	93.51	<b>73.99</b>	43.45
38	152.37	77.29		
39	188.00	93.52	<b>112.30</b>	62.96

- 1) taphonomy or some form of preservational bias,
- 2) measurement error or,
- 3) there are biologically real differences.

At this time it is not possible to choose with any certainty among these factors, but it is more likely that some combination of taphonomy and/or measurement error is responsible. Looking at the slab (Text-Fig. 2) it is easy to see that while generally flat lying, specimens were not always exposed in an optimal position for measurements (see for example No. 12, 13, 14, Text-Figs. 2, 3).

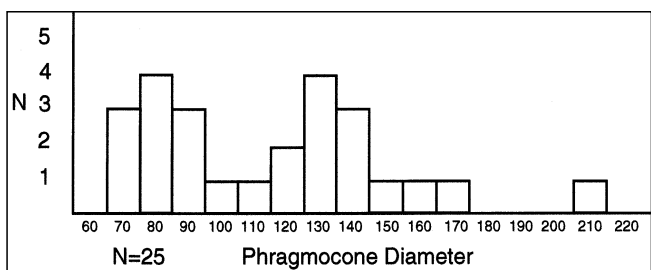
Using the above equation based on whorl height at the adoral end of the phragmocone, phragmocone diameters were estimated. The new N for this analysis is 25 (the estimated phragmocone diameter values are given in bold in Table 1) Using these data a size frequency histogram was produced. The resultant histogram is shown on Text-Fig. 5. The distribution shows two well defined peaks at 80 mm and at 130–140 mm and possibly a third at the uppermost end around 210 mm, but this is questionable as it is based on only one specimen. The mean of the distribution is  $119.67 \pm 10.9$  mm. A range which barely touches either of the well defined peaks.



Text-Fig. 4.

Graph of the regression analysis done using the ln of the whorl height (ln Wh) against the ln of diameter (ln D).

N = 31, data is given on Table 1. The resultant equation:  $\ln Wh = -0.0574 + 0.88901 \ln D$  was used to estimate Dphrag values where they were not directly measurable on the specimens. The estimated Dphrag values are given in Table 1 in bold.



Text-Fig. 5.

Size frequency histogram of the phragmocone diameters from Table 1 (N = 25).

The size intervals are 10 millimeters. The number given for each interval represents the lower limit. The interval extends to that number + 9.99 mm. (eg., interval 70 ranges from 70.0 mm to 79.99 mm).

N (vertical axis) = number of specimens in each interval. Peaks are found in the 80 mm, 130–140 mm, and a minor one in the 210 mm intervals.

#### 4. Discussion

Ignoring for now the third, somewhat questionable peak and focusing on the two well defined peaks, the distribution is clearly bimodal. Bimodal distributions in animals have been explained in several ways; sexual dimorphism is one.

In general, sexual dimorphism is a common feature in many cephalopods. Size usually plays a role in diagnosing it. In some cases it can be quite extreme, as in the case of the *Argonauta*, where the female is approximately 20 times larger than the male (LANE, 1957). In more modest examples, such as *Nautilus*, the male is slightly larger than the female (SAUNDERS & WARD, 1987).

Likewise, sexual dimorphism has been diagnosed in many ammonoid species. Here the size differences play a prominent role in the diagnosis (CALLOMON, 1955, 1963, 1981; MAKOWSKI, 1962, 1971, 1991; WESTERMANN, 1964; COBBAN & KENNEDY, 1993; DAVIS et al., 1996). The microconch, or smaller shell is generally thought to be the male and the larger macroconch, the female (LEHMANN, 1981;

see DAVIS et al., 1996 for discussion). Usually the distribution will show two distinct peaks with little overlap (MAKOWSKI, 1991; LANDMAN & WAAGE, 1993). Sometimes other morphological differences are present to aid in the diagnosis, such as fewer number of whorls, the development of lappets or other apertural modifications (DAVIS et al., 1996). Very few studies exist for Devonian ammonoids. Those that do exist generally pertain to taxa from the Late Devonian and rely only on size as the defining criterion (MAKOWSKI, 1962, 1991). Modified apertures do not appear until the Carboniferous (DAVIS et al., 1996). Furthermore, there is a lack of good evidence that Early–Middle (in fact, any) Devonian ammonoids exhibited recognizable sexual dimorphism. MAKOWSKI's (1991) study, for example, fails in that it never adequately explains how he defines an adult. Furthermore, it fails to account for the lack of dimorphism in related taxa in other time equivalent localities (see BECKER, 1993). Only one vague description exists for the Anarcestina. An abstract by WALLISER (1963) suggests sexual dimorphism characterized by sculptural differences, but the data were never fully presented.

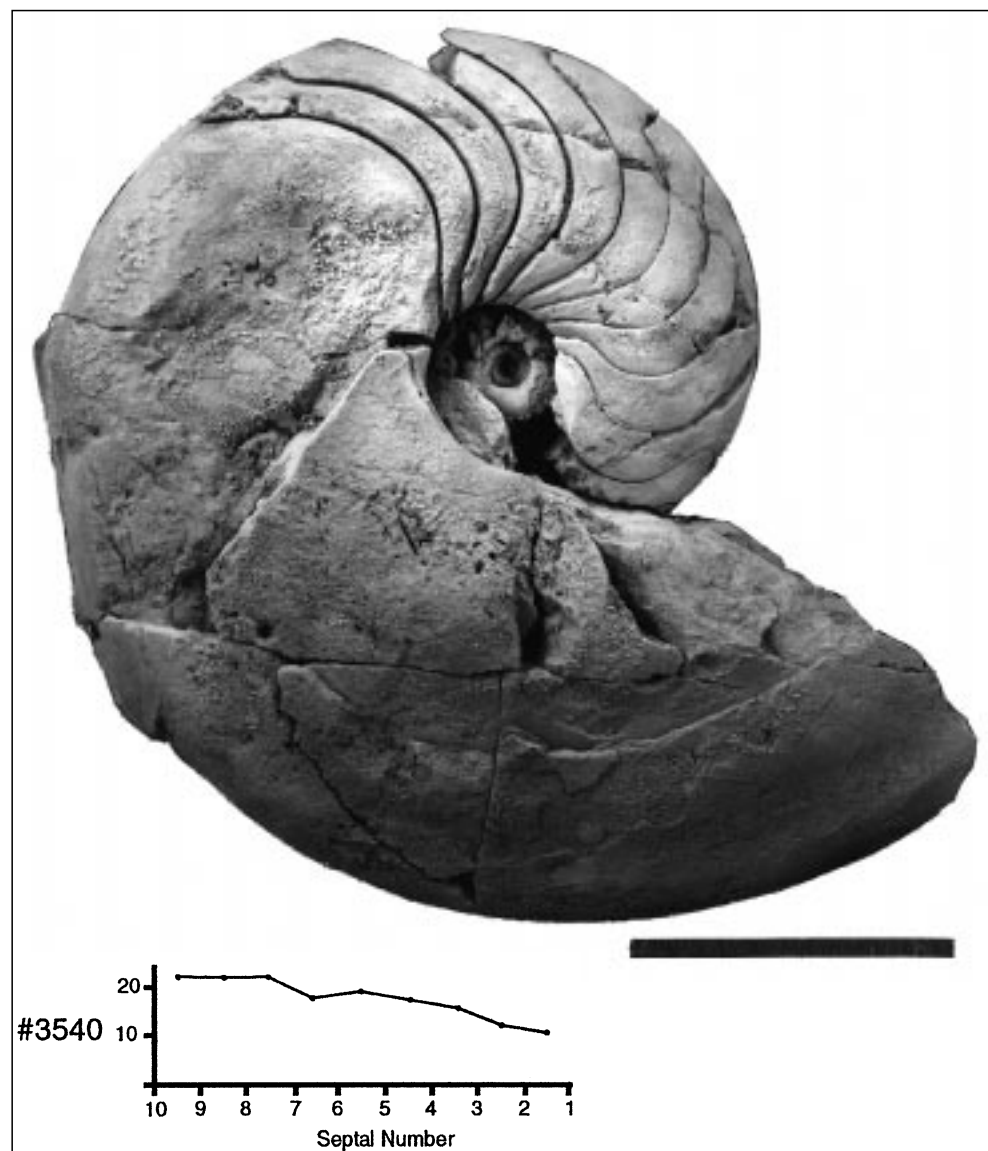
In any example where sexual dimorphism is hypothesized, the specimens studied must be fully mature adults. In some ammonoids, adults are easy to identify. Apertural modifications, such as lappets and projections occur in some forms when they reach maturity (DAVIS, 1972; DAVIS

et al., 1996; TANABE, 1977; LANDMAN, 1989). In others, like the Scaphitidae and other heteromorphs the adult has a unique coiling mode, different from the juvenile (COBBAN, 1951; COBBAN & KENNEDY, 1993; LANDMAN, 1989; LANDMAN & WAAGE, 1993). There are also some more subtle indicators such as a change in ornament, but these can be more difficult to detect.

One of the most universally accepted methods of identifying adult ammonoids is the presence of septal approximation, a reduction in the spacing of the last few septa at maturity (CALLOMON, 1963; CRICK, 1978). However, septal approximation does not always occur, and in some species it can occur iteratively throughout growth (CLAUSEN, 1968; BUCHER et al., 1996).

Unfortunately *Agoniatites vanuxemi* (HALL) and most primitive ammonoids do not show obvious adult apertural modifications. The adult does, however, have a distinct whorl profile (HALL, 1879; MILLER, 1938). In the genus *Agoniatites* there is a rapid increase in the whorl height / whorl width ratio as the individual approaches maturity, but its onset is gradual over at least one whorl, so some near adults could easily be mistaken for adults. The whorl height/whorl width ratio, therefore, is not in and of itself enough to indicate maturity. This leaves septal approximation as the only as yet reliable method of identifying adults.

Specimens of *Agoniatites vanuxemi* (HALL) from the type collections of the American Museum of Natural History and the New York State Museum in Albany previously had septal angles measured. One example is presented for illustrative purposes in Text-Fig. 6. The spacing over the course of the last 10 septa is visibly becoming smaller. Graphically (see Text-Fig. 6), the gradual reduction in spacing is readily apparent. From this we can assume that septal approximation occurs in *A. vanuxemi* (HALL).



Text-Fig. 6.  
Type specimen of *Agoniatites vanuxemi* (HALL) (NYSM 3540).  
One of the largest specimens with a  $D_{max} = 311$  mm. The spacing of the septa can be seen to decrease over the last ten septa. Below the specimen is a graph of the septal angles for the last ten septa. Each number on the horizontal axis is the number of a septum, 1 being the last septum formed. The points, plotted between them, are the measured septal angles between the two adjacent septa. Angle measurements are given in degrees on the vertical axis. The septal angle can be seen to decrease from  $22^\circ$  to  $11^\circ$  over the septa shown.  
Scale bar = 10 mm.

Text-Fig. 7.

Septal angles for 18 specimens from the bed used in this study.

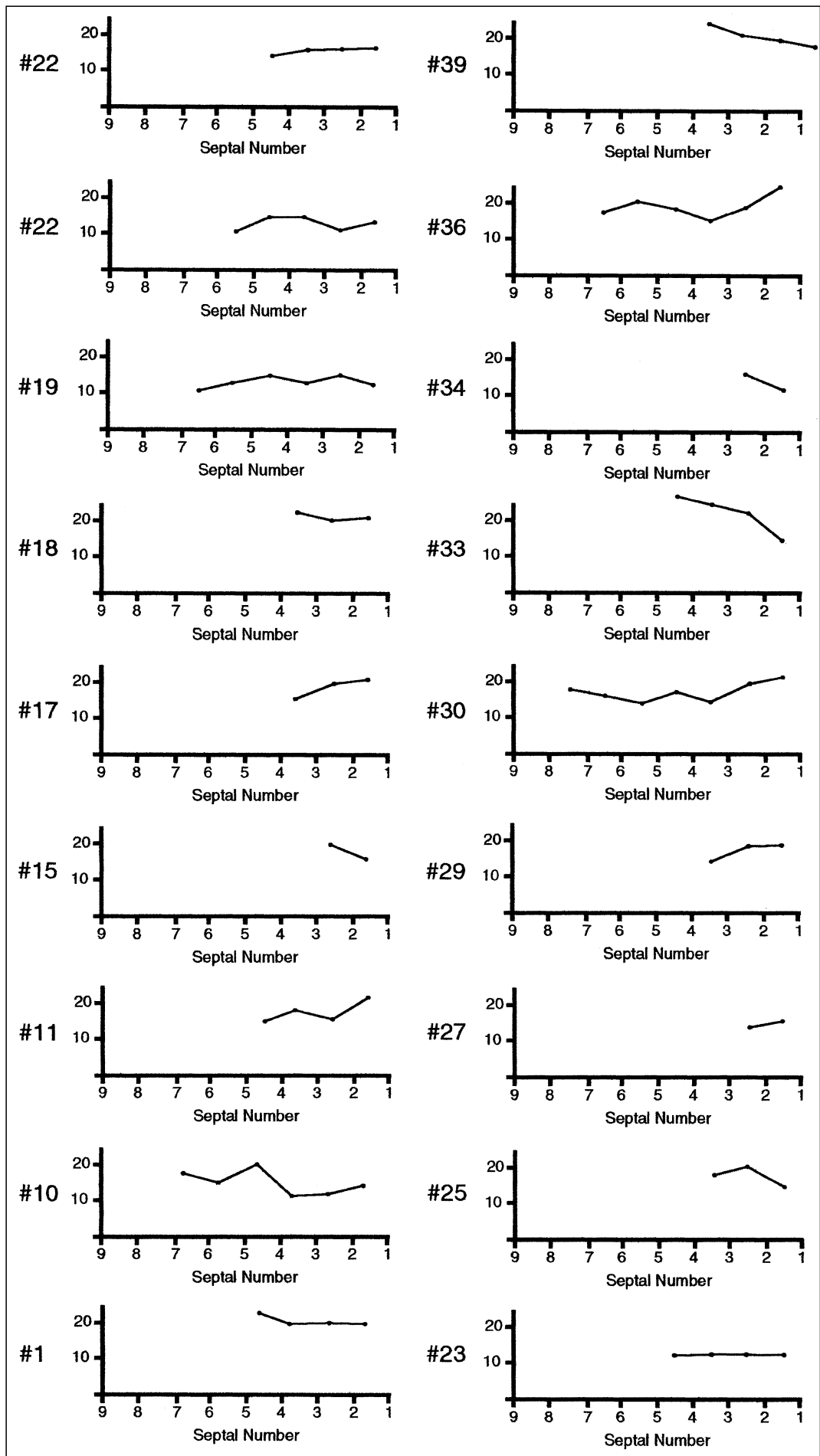
Numbers on the left correspond to specimen numbers given on Text-Fig. 3. Each number on the horizontal axis is the number of a septum, 1 being the last septum formed. The points, plotted between them, are the measured septal angles between the two adjacent septa. Angle measurements are given in degrees on the vertical axis.

Eighteen of the specimens from the bed in this study had two or more septa visible. Angles were measured from homologous points on each specimen.

Text-Fig. 7 shows the graphs of septal angles of those specimens.

From these data there is no clear evidence that septal approximation occurs in these specimens. A few of the specimen show a decrease in spacing (see No. 33, 34, 39), but it is hardly an overwhelming number. Most specimens show random fluctuations, or no change in spacing at all. Based on this it would not be possible to argue that these specimens are adults.

In view of the fact that a majority of the specimens contained on the bed used in this study cannot be taken for adults, it is not possible in this case to call upon sexual dimorphism as an explanation for the apparent size classes.



An alternative hypothesis is suggested here. The two size classes could represent distinct age classes. This model could then account for the possible third size class present in the form of one specimen. Thus, there would be three age classes.

This model assumes that reproduction occurred during a specific time period for all sexually mature individuals in the population. Each cohort would then grow at a similar enough rate so that all individuals from that cohort would be about the same size. When several of these cohorts from different times were present each one would produce a separate peak in the distribution. This is what we see here: two or three peaks at 80 mm, 130–140 mm and possibly >210 mm.

Because there is no clear evidence that any of the individuals are adults, it can be assumed that all three age classes present are all submature. If any of the specimens present were, in fact, adults, any septal approximation observed should correlate with the largest specimens present. This is clearly not the case. Since the whorl profiles closely resemble that of adults it is believed that the individuals present, while not fully mature, were close to adulthood. Even the largest specimen present (No 23) shows no change in septal spacing.

If we accept the model that the individuals present on the bed represent near adults specimens of several ages, what can this tell us about the ecology of these animals? Most obviously, that reproduction occurred during discrete time intervals resulting in the presence of distinct size classes. With no fully mature adults present the notion that these individuals were immigrants that died before reproducing is strengthened. The absence of juveniles of any size also supports this idea.

Juveniles of *Agoniatites vanuxemi* (HALL) have a different morphology than the adults/near adults. Since none of these mid-sized juveniles are found here it is possible that these morphological differences correlate with different environmental constraints and that the adults/near adults did not share the same habitat. Only when the juveniles approached maturity were they able to move into the adult habitat. The habitat in which these juveniles lived is as yet unknown.

## 5. Conclusions

Previous works which have attempted to look at the biology of ammonoids have centered upon aspects of buoyancy, depth constraints and swimming ability. These types of analyses rely upon the measureable physical parameters of individual ammonoid shells as well as analysis of the surrounding sediments. Other works, based

upon the rare soft tissue preservation, have looked at diet and feeding habits. Embryonic shell data have led to analysis of reproductive strategy (generally as a comparison to nautiloids), as well as embryonic development. Other aspects of biology, such as predation, repairing injuries and pathologies have also been studied. In most cases these studies can be accomplished using few specimens.

The analysis of population dynamics has only rarely been attempted. This is due largely to the lack of adequate samples of a type and size that allow us to infer a single population, which lived and died together.

This is one of the few studies on Paleozoic ammonoids which attempts to examine life history. The special lagerstätten nature of the deposits in this study satisfy the criterion of the ammonoids representing a living assemblage and as such supplies us with valuable information about how *Agoniatites vanuxemi* (HALL) lived. We see a pattern where juveniles and adults/near adults lived separately. The adults/near adults also possessed seemingly greater mobility.

What may be more important is what information is missing. The rich fossil deposits of North Africa (Morocco, in particular) may supply the answers. Ammonoid collections have been made containing many specimens of single species, of all sizes (ages) (KLUG, 2002). We may be able to use these to supplement the data already collected on adult/near adult specimens. Size frequency data may fill in the missing age intervals not found in this study. Facies and environmental analysis may tell us why only adults/near adults migrated to North America and if they all lived in different environments from juveniles. Much more work is needed to answer the questions opened by this study.

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## Plate 1

Fig. 1: View of the top surface of the south end of the Seneca Stone Quarry.

The bedding surface is the Cherry Valley Limestone. The surface is covered with median cross sections of *Agoniatites vanuxemi* (HALL) and a variety of orthoconic nautiloids.

Fig. 2: An overturned bed of the Cherry Valley Limestone on display in the New York State Museum in Albany, New York.

The top surface contains 43 representatives of *Agoniatites vanuxemi* (HALL) and a variety of orthoconic nautiloids.



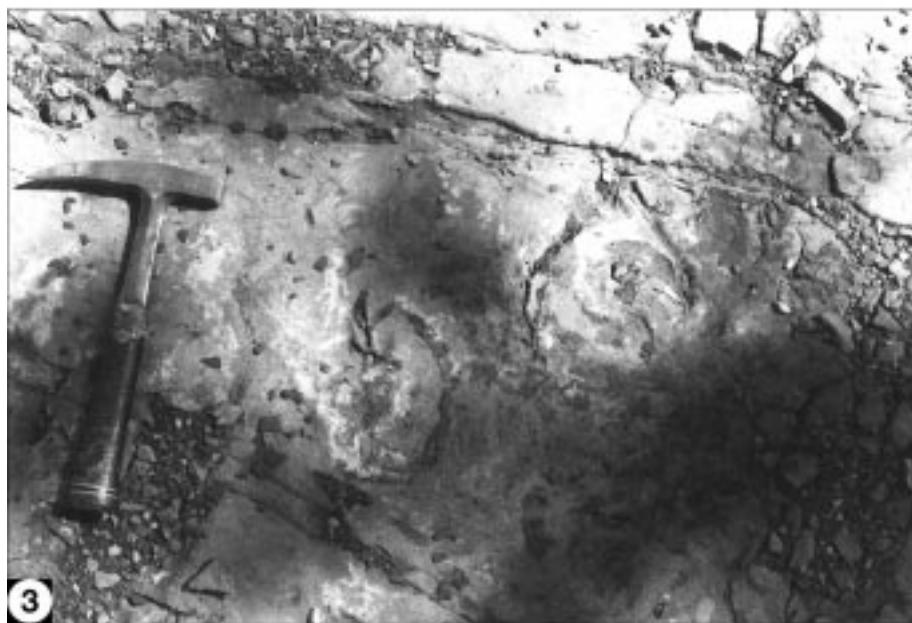


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## Plate 2

Close ups of the surface of the Seneca Stone Quarry.

- Fig. 1: Median cross section of a specimen of *Agoniatites vanuxemi* (HALL).  
Fig. 2: Oblique cross section of a specimen of *Agoniatites vanuxemi* (HALL).  
The body chamber is relatively complete, while the phragmocone is eroded away.  
Fig. 3: Two examples of *Agoniatites vanuxemi* (HALL) from the Seneca Stone Quarry.  
Both are eroded beyond the median plane.
-



## Plate 3

Some examples of *Agoniatites vanuxemi* (HALL)  
from the bed of Cherry Valley Limestone in Pl. 1, Fig. 2 and Text-Fig. 3

- Fig. 1: Specimen No. 25 from Text-Fig. 3, is nearly complete (body chamber angle =  $190^\circ$ ).  
Measurements are given in Table 1 ( $D_{\max} = 231$  mm). Septal angle measurements are graphed on Text-Fig. 7.
- Fig. 2: From top to bottom; specimens No. 12, 13 and 14 (Text-Fig. 3).  
Measurements are given in Table 1.  
Specimen No. 14 is nearly complete (body chamber angle =  $223^\circ$ ,  $D_{\max} = 263$  mm).  
Specimen No. 12, while having only about  $\frac{3}{4}$  exposed, is still measurable (body chamber angle =  $201^\circ$ ,  $D_{\max} = 256$  mm).  
Specimen No. 13 was not measurable.
- Fig. 3: Two examples of *Agoniatites vanuxemi* (HALL).  
A larger specimen on the right (No. 33,  $D_{\max} = 231$  mm), as well as the smaller on the left (No. 36,  $D_{\max} = 117.91$  mm) (see Text-Fig. 3) were both measurable (Table 1).  
Septal angle measurements are graphed on Text-Fig. 7.



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