

Intraspecific variation of *Dufrenoyia furcata* SOWERBY  
(Ammonoidea, Ancylocerataceae, Deshayesitidae) from the  
Gargasian in the Vaucluse (Southern France)

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With 10 figures

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**Abstract**

The ammonoid species *Dufrenoyia furcata* SOWERBY from the uppermost Lower Aptian and lower part of the Upper Aptian of the Vaucluse, France exhibits a considerable range of intraspecific variability. The statistical analysis, based on 277 specimens, preserved as internal pyritic moulds, shows that the morphological variation is continuous, all specimens are variants of a single biospecies.

**Zusammenfassung**

Die Ammonitenspezies *Dufrenoyia furcata* SOWERBY aus dem obersten Unterapt und tieferen Oberapt der Vaucluse, Frankreich zeigt bezüglich Gehäuseform und Berippung eine bemerkenswerte intraspezifische Variabilität. Die statistische Analyse, basierend auf 277 Exemplaren von Pyrit Steinkernen macht deutlich, dass die morphologische Variation der Gehäuse kontinuierlich ist und damit die verschiedenen Varianten einer einzigen Biospezies zuzuordnen sind.

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## I. Introduction

*Dufrenoyia furcata* SOWERBY (syn. *Dufrenoyia dufrenoyi* d'ORBIGNY) is a very common and typical ammonite species straddling the Bedoulian/Gargasian - boundary in the Vaucluse department in Southern France.

The species occurs immediately above the top of the massive Bedoulian limestone series and disappears near the top of the bluish grey marls together with a rich ammonite fauna in the transition zone to sandy grey marls containing abundant belemnites, especially *Neohibolites ewaldsimilis* STOLLEY. The stratigraphic range of the species seems to be controlled by facies changes at the base and also towards the top of the marls and is believed to be slightly more extended in regions where continuous sedimentation of bluish pyrite rich marls lasted into the uppermost Aptian (Clansayesian).

Usually *Dufrenoyia furcata* SOWERBY is associated with *Aconeceras nisum* d'ORBIGNY, which is the most common ammonite at several localities and occurs from the base to the top of the marl sequences. Biozones of both species are assumed to have similar extension. Like *Aconeceras nisum*, *Dufrenoyia furcata* serves as an index species for the lower Gargasian and also indicates the so called Provençal Faciestype which is characterized by an assemblage of heteromorph ammonite genera (*Ancyloceras*, *Hamites*, *Toxoceras*, *Parahoplites*, *Chelonicer*, *Acanthoplites*).

The collection of pyrite-phragmocones of *Dufrenoyia furcata* SOWERBY in several outcrops yielded specimens with a considerable high degree of variation, especially regarding the number of ribs, their strength, and the occurrence of elongated tubercles (clavi) on the ventrolateral shoulders. In many official and private collections, specimens with numerous fine ribs were described as *Neocomites* (*Neocomites aptiensis*), specimens with fewer but more pronounced ribs were attributed to *Hoplites* (*Hoplites furcatus*). To a certain extent the variability of *D. furcata* and the regular shell geometry was an obstacle in the correct attribution to the heteromorph *Deshayesitidae*.

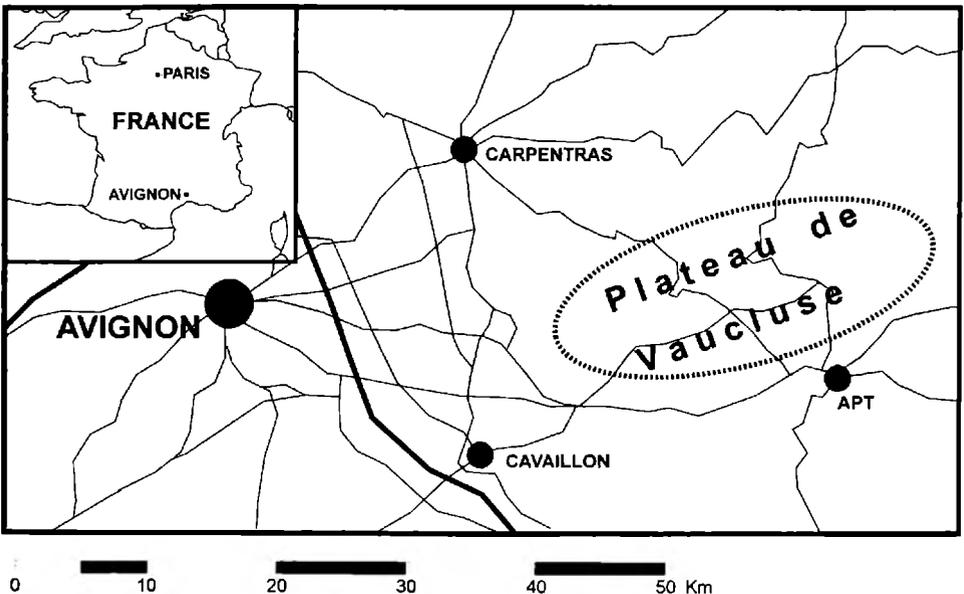


Fig. 1: The fossil locality in Southern France.

The wide range of variability in density and strength of the ribs suggests a splitting in several subspecies. Targets of this investigation are:

- Find out whether the establishment of subspecies would be reasonable or not;
- Looking for any ontogenetic relation to rib density
- Investigate any stratigraphic relation to rib density.

## II. Location, stratigraphy and material

The specimens were collected at several well known outcrops within the Vaucluse predominantly around Carniol, Oppedette, Rustrel, Banon, and in the Sault area.

Southern Europe / Mediterranean		Revision	old scheme	
Albian	<i>Leymeriella tardefurcata</i>			
A P T I A N	upper	<i>Hypacanthoplites jacobi</i> <i>Acanthoplites nolani</i> <i>Parahoplites melchioris</i> <i>Epicheloniceras nodosocostatum</i>	Gargasian	
	lower	<i>Dufrenoyia furcata</i>	<i>Dufrenoyia furcata</i>	
		<i>Deshayesites deshayesi</i>	Bedoulian	Bedoulian
		<i>Deshayesites weissii</i> <i>Deshayesites ruarkyriscus</i>		
Barremian	<i>Martelites sarasini</i>			

Fig. 2: Ammonite zones of the Aptian.

Wherever possible the specimens are related to their find level above the base of the marls and to the associated fauna. We found three distinct levels with three assemblages: a lower with frequent *Cheloniceras cornuelianum* and *martini* d'ORBIGNY, a middle with *Zuercherella zuercheri* JACOB and an upper one with *Acanthoplites* sp., the latter occurs underneath the belemnite rich dark grey marls. Following recent stratigraphic revisions we adjust Lower Aptian to Bedoulian respectively Upper Aptian to Gargasian in positioning the zone of *D. furcata* to the Lower Aptian as shown on fig. 2.

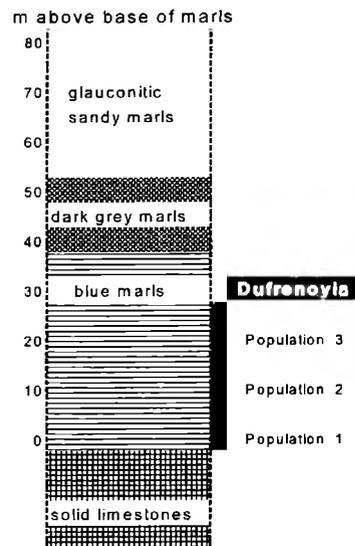


Fig. 3: Aptian generalized section.

However, the associated fauna indicates that *D. furcata* reaches from the uppermost Lower Aptian into the Upper Aptian and, in general, is typical for the lower part of the marl series above the solid limestone. At some localities marls are deposited from the zone of *Deshayesites deshayesi* d'ORBIGNY.

Therefore, the often applied simplification, Gargasian = marls on top of the solid Urgonian limestones, is misleading as a transition from Bedoulian into the Gargasian is located within the marls and also within

the presence of *D. furcata*. This stratigraphic boundary is expected to be located within the population 2 level.

### III. Statistic approach

The variation analysis is based on 277 well preserved specimens collected at defined stratigraphic levels and selected from a total of 1138 specimens. The parameters investigated are the maximum diameter, the height and width of the last whorl, the umbilical width and the number of all ribs on the last whorl which equals the number of elongated nodules (clavi) fencing the venter. In the next step the parameters are combined to XY-plots in order to find meaningful combinations. The following results were achieved:

1. the number of ribs differs from a minimum of 24 to a maximum of 50. The minimum trend at 24 ribs is clearly expressed over 1.5 to 7 cm diameter. The maximum trend is not precisely defined as only a few specimens are furnished with more than 42 ribs. Moreover, the maximum seems to be restricted on smaller forms between 1.5 and 2.5 cm as shown on fig.4.

2. as also indicated on fig. 4, the number of ribs is generally reduced with growing diameter. Representative types are located on or near the potential trend line. Therefore, the mean type at 1 cm diameter is furnished with 40 ribs, at 2 cm with 34 ribs, and with 30 ribs at 3.5 cm diameter. Then, the trend curve approximates the minimum at 24 ribs with increasing diameter.

3. continuous transition is visible between all rib-types as shown on the histogram (fig. 5). Specimens with 25 to 36 ribs are predominant with four maxima at 26, 31, 34 and 36 ribs and cover 73 % of all types. Types with less than 25 ribs are generally rare and such with more than 36 ribs become progressively rare towards the maximum of 50 ribs.

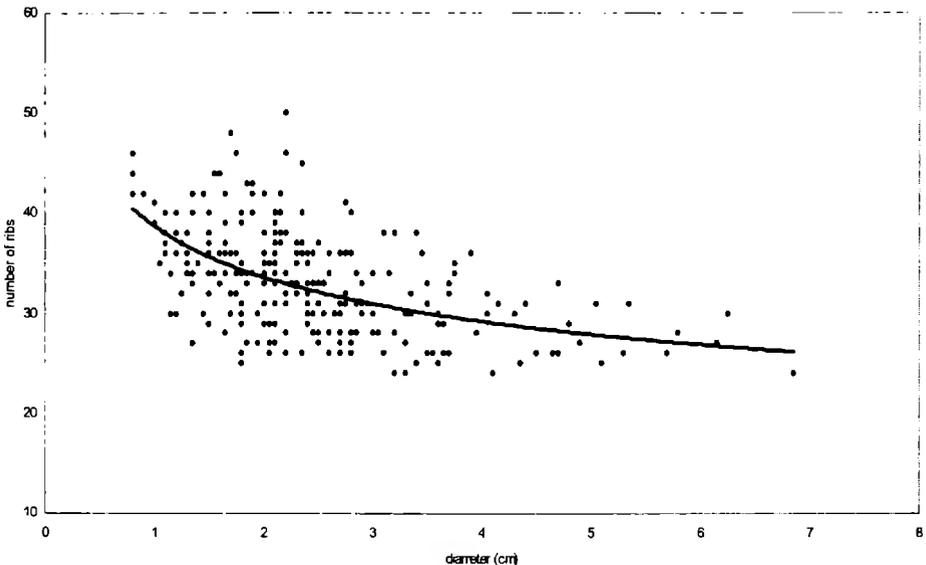


Fig. 4: Number of ribs vs. diameter and potential trend.

4. the whorl parameter, defined as ratio whorl height/whorl width, differ over a larger scale but are obviously indifferent to the diameter and the ontogeny of the specimen as shown on fig.6.

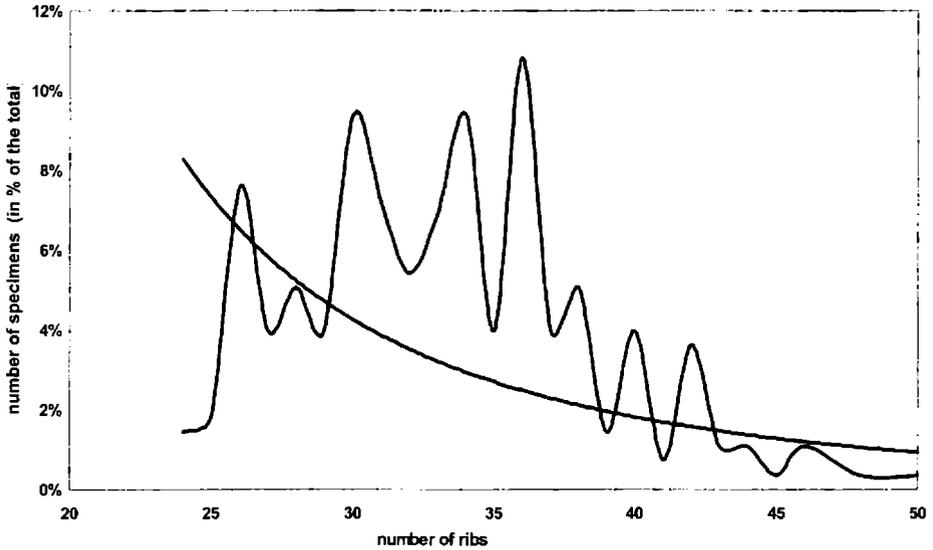


Fig. 5: Variation of rib number and potential trend.

The trend curve on fig. 4 may be used for checking whether published specimens of *Dufrenoyia furcata* SOWERBY are representative or reflect confusing extreme types. For this purpose the specimens need index parameters, their diameter (cm) and the number of ribs, e.g. combined as 2.2/30 type. So the specimen shown by MOOSLEITNER (2002, table 65, fig.6) is the 2.5/32 type and absolutely conform to the general trend. The other specimen shown on tab. 64, fig.2 represents the 1.2/38 type which also fits well. However, there is a limitation in counting ribs on juvenile forms.

Ribs are only weakly expressed in the early ontogenetic stadium and, therefore, difficult to be scored. Therefore, specimen with less than 0,8 cm diameter have been excluded from statistics. The typical *Dufrenoyia* - profile characterized by a flattened venter fenced by rather symmetric and exposed clavi is realized from diameters > 0,8 cm when specimen are able to stand on their venter. The inner whorls equal those of *Dehayesites* from which *Dufrenoyia* can be directly derived. Furthermore, the specimen documented by RICHTER (1994, fig. 176) represents the 3.5/32 type which is located a little above the trend line but still representative. The specimen shown in the internet (access: wanadoo.fr/herve.chatelier/fiches) is the 2.2/ 33 type and exactly on trend.

In general, all the above mentioned published specimens originated from the Vaucluse department turned out to be representative. It is assumed that the authors had been aware of the variability and selected only mean types. The overall average type from the Vaucluse can be specified as follows from the selected material.

- Diameter: 2,44 cm / 33 ribs
- Whorl height: 1,13 cm
- Umbilicus width: 0,75 cm
- Whorl height/width: 1,50

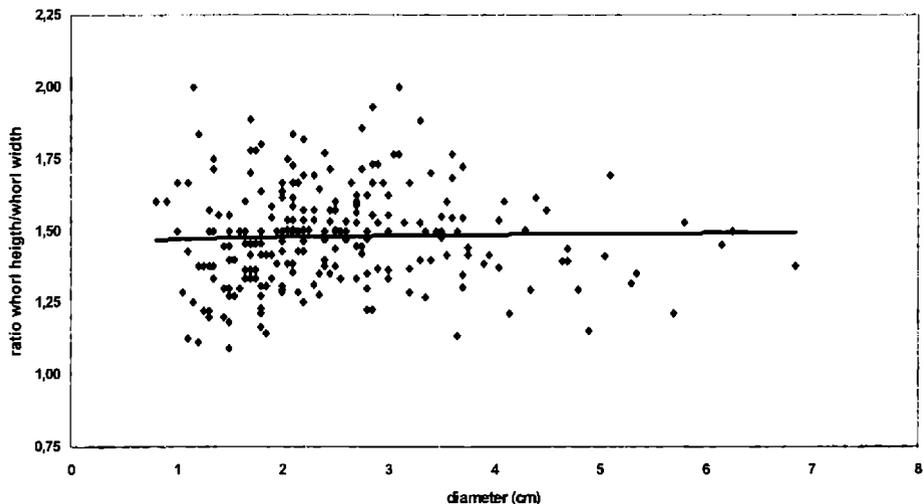


Fig. 6: Diameter vs. whorl ratio and potential trend.

A unique specimen of 22 cm diameter and 47 ribs is described by KEMPER (1968, table 24, fig.1) from the upper part of the Lower Aptian of the Bentheim area, Germany. This type is far outside of the fig. 4 trend line. The large diameter is easily to explain by the preservation of the entire shell (maximum diameter about 40 cm) in the Bentheim-marls. The surprising large number of ribs may be an indication for a distinct population with an extended variability.

A variation study about the very similar *Dufrenoyia texana* BURCKHARDT performed by BÜRL (1956) could not prove any relation between diameter and number of ribs. This may be caused by the small number of 36 evaluated specimens and the non-inclusion of forms < 2.5 cm. Consequently, trends between 2.5 and 0.8 cm diameter could not be detected.

The forms used in his statistics from one horizon at the base of Upper Aptian in the Cordillera Oriental/Columbia can be consolidated to an average 4.8/31 type which is still within the bandwidth of forms on fig. 4, but notably above the trend curve. As some specimens are considerably outside the bandwidth, showing extreme indices like 8.6/36, we anticipate a population with other variation ranges than *Dufrenoyia furcata*.

#### IV. Discussion

In the Vaucluse area *Dufrenoyia furcata* SOWERBY is only preserved as pyrite filled moulds representing the inner phragmocones of larger forms probably up to 40 cm diameter. Distribution of the size is controlled by diagenesis and varies in the outcrops and in the different stratigraphic levels.

The variability of the shell parameters and ornamentation is considerable high and affects the whorl parameters and the number and exposition of the ribs. The whorl parameters are probably influenced by compaction of the marls as some specimen seem to be slightly compressed which might have caused wider spread on fig. 6. In general, no relation could be found between the whorl parameter and the diameter as the trend curve turned out to be approx. straight and horizontal. A statistical relation could be demonstrated between the diameter and the number of ribs on fig. 4 which is not influenced by diagenetic deformation.

In view of the various transitions between all specimens which indicate only intra-specific variation, no benefit could be seen in splitting the species in two or more subspecies.

The population of *Dufrenoyia texana* BURCKHARDT collected by BÜRGL (1956, fig. 1) from one particular horizon show a peak on 30 ribs within a bulk from 30 to 32 ribs comprising more than 50 % of all specimens. This population is much more focussed on a common type than those found in the Vacluse. The explanation is rather simple. Sampling

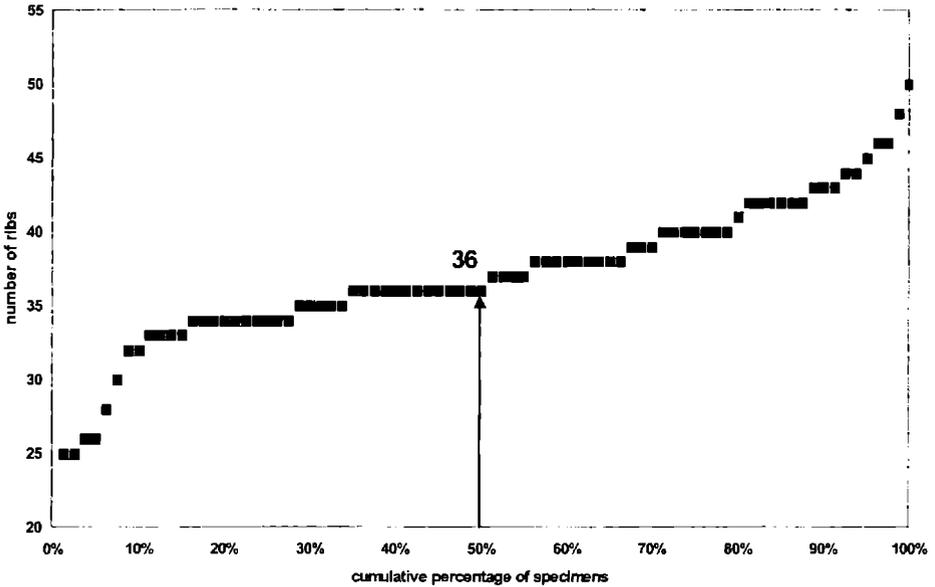


Fig. 7: Number of ribs/cumulative distribution population 1.

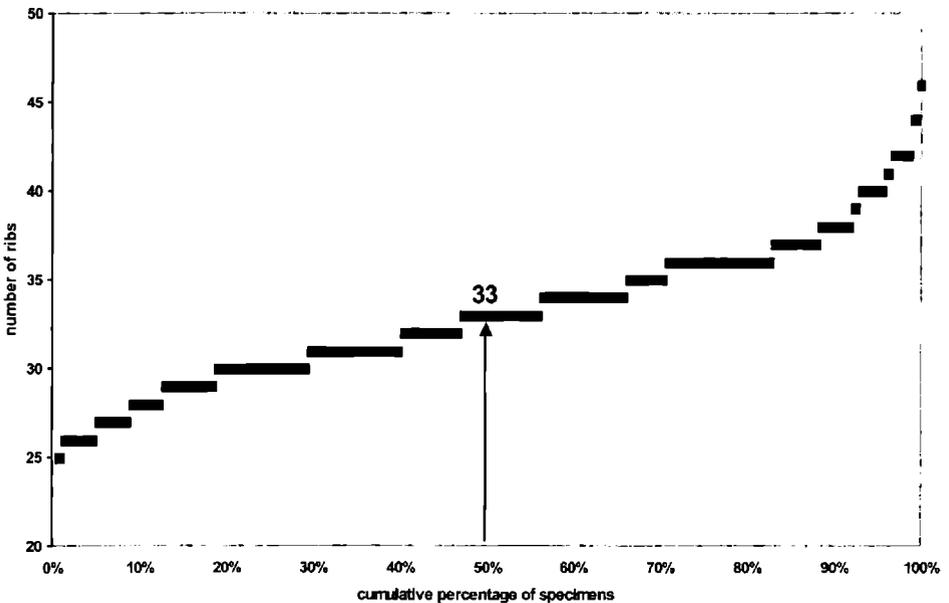


Fig. 8: Number of ribs/cumulative distribution population 2.

from only one level is like a snapshot of the population whereas collecting over the entire marl sequence is similar to a short movie demonstrating all timely changes.

Looking back on fig. 6 there are specimens in a mix of several horizons and populations and, therefore, no clear maximum is shown, but a broad band of common

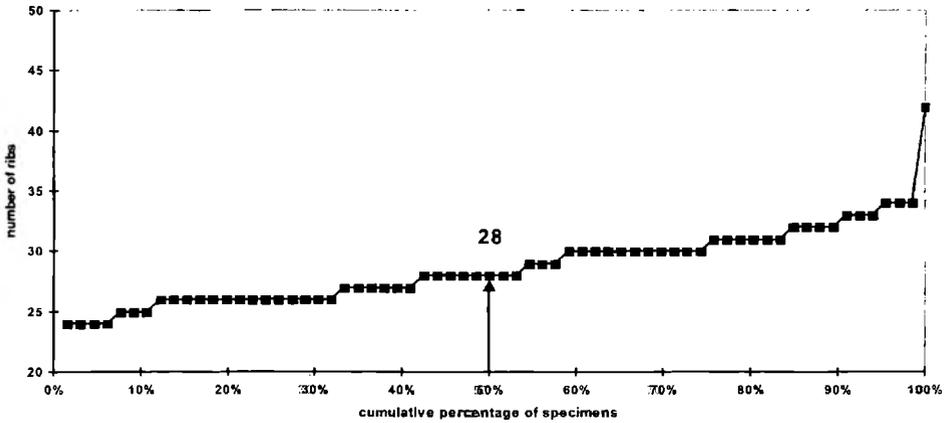


Fig. 9: Number of ribs/cumulative distribution Population 3.

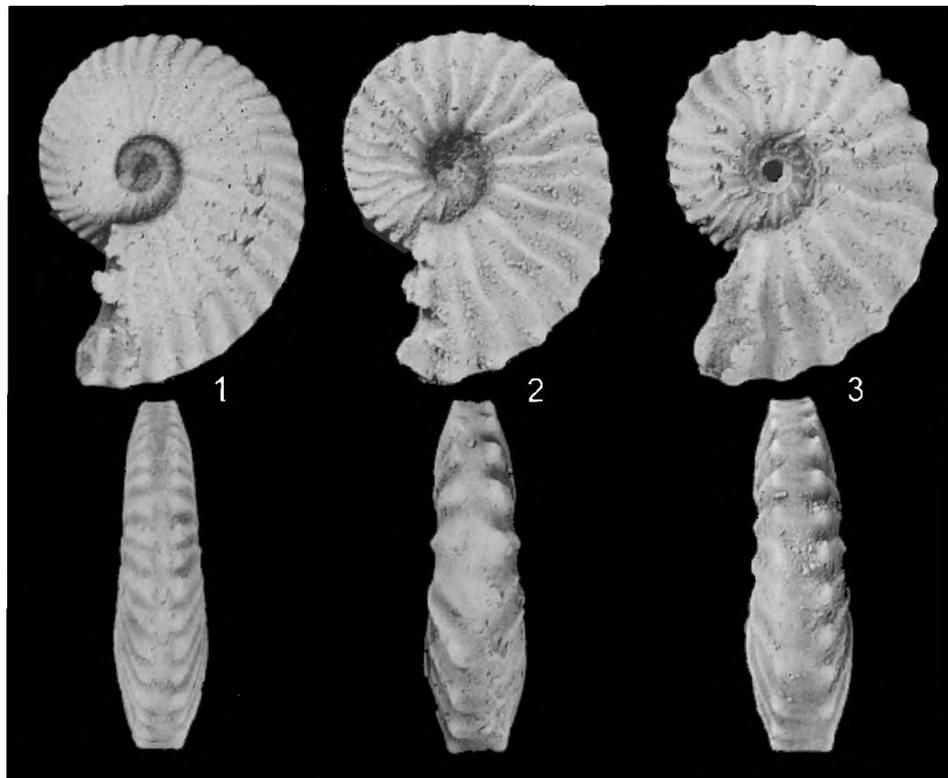
types with 26, 31, 34 and 36 ribs, each of them representing around 10 % of the population. In order to extract the bandwidth of ribs in single populations, the specimens were again investigated in relation to the three stratigraphic levels. These levels refer to terraces in the outcrops, where the fossils are condensed after erosion of the steep and slippery hill flanks. Digging for fossils in non weathered marls does not yield notable quantities of macrofossils as the fossil density is generally low. The additional statistical approach was targeted on mean (average) values, most likely values and median values related to a single level.

**Level 1** comprises the lowermost 5 m of the marls above the Bedoulian limestone. The average rib number of the 80 specimen comes up to 37, the most common form bears 36 ribs (peak) and the median value confirms 36 ribs at 50 % cumulative probability.

**Level 2** comprises more than 15 m of marls with a rather poor fossil content in the middle part of the section and contains probably more than one population. The 131 specimen show an average at 33 ribs, a most common form (peak) at 30/31 ribs and a median value of again 33 ribs.

**Level 3** fossils are collected approx. 30-40 m above the base of the marls just underneath the belemnite rich marls. Statistics based on 66 specimens indicate a significant shift towards a reduced number of ribs and their stronger exposition. The rib number is reduced to an average of 28, the most common form bears 30 ribs and the median value confirms 28 ribs at 50 % probability.

The statistical methods revealed a general trend in developing coarser sculpture elements towards the top of the sequence. This might be interpreted as an adaptive reaction to the prograding shallow water facies indicated by the deposition of sandy glauconitic marls on top of the Aptian.



**Fig. 10:** *Dufrenoyia furcata* SOWERBY, lateral and dorsal view of 3 common variants.  
 1: 3.1cm/38 ribs; 2: 3.1 cm/28 ribs, 3: 3.4cm/25 ribs.

Variant 1 is an indication for the level 1 population not far away from the origin of *Dufrenoyia*; variant 2 may be seen as an advanced transition from level 2 into level 3; variant 3 is typical for the level 3 population just before the extinction of the entire ammonoid family.

Additional investigation of the associated fauna together with a detailed track record of the specimens is needed to develop a stratigraphic model of *Dufrenoyia furcata*. In view of the notable intraspecific variation, this model cannot be based on a couple of finds but on a statistic mass of specimens which offers the possibility to detect slight changes of parameters affecting the population over a longer time. This approach may be one of the next year targets.

### Acknowledgements

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## References

- BÜRGL, H. (1956): La variabilidad de la amonita *Dufrenoyia texana* BURCKHARDT. - Boletín Geológico - Tomo **IV**, Nr. 2-3: 1-22, Bogota.
- DAGYS, A.S. & WEITSCHAT, W. (1993): Extensive intraspecific variation in a Triassic ammonoid from Siberia. - *Lethaia*, **26**: 113-121, Oslo.
- KEMPER, E. (1968): Geologischer Führer durch die Grafschaft Bentheim und angrenzende Gebiete.- Das Bentheimer Land, **64**, Verlag Heimatverein, Nordhorn.
- KEUPP, H. (2000): Ammoniten - Paläobiologische Erfolgsspiralen. - Jan THORBECKE Verlag, Stuttgart.
- LEHMANN, U. (1987): Ammoniten - Ihr Leben und ihre Umwelt. - ENKE-Verlag, Stuttgart.
- MOOSLEITNER, G. (2002): Fossilien sammeln in Südfrankreich. - GOLDSCHNECK-Verlag,
- RICHTER, A.E. (1979): Südfrankreich und seine Fossilien; Geologie und Paläontologie der Causses und Provence. - Franksche Verlagshandlung, Stuttgart.
- (1990): Gargas - Stratotypus des Gargasien. - Klassische Fundstellen der Paläontologie, Band II, GOLDSCHNECK-Verlag, Korb.
  - (1994): Ammoniten. - Gondrom-Sonderausgabe, Bindlach.