



Essay on the Variability in the Species *Douvilleiceras Mammillatum* Schlotheim (Ammonitina - Lower Albian) from Ambatolafia - Mahajanga Basin

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ABSTRACT

Douvilleiceras mammillatum (Schlotheim, 1813) belongs to the Albian Ammonite group of the southern Mahajanga Basin, northwest of Madagasikara. This work emphasizes the in-depth study of the variability of its dimensional characters and some quantifiable morphological characters. Statistical, univariate, bivariate and multivariate analysis are used. 57 good specimens in *Douvilleiceras mammillatum* collected from the Ambatolafia quarries constitute the materials of study. The results show the normal distributions of the characters studied and evidential correlations between the size of the shell, the whorl height and the whorl breadth, the width of the umbilicus, the number of ribs and the intercostal space during growth. There is a parallelism between changes in shell characteristics, growth of stages and environmental conditions. In Madagasikara, typical *Douvilleiceras mammillatum* and contemporaries are present and zonally useful for those sediments later than the *Lemuroceras aburensis* Zone and earlier than the occurrence of *Lyelliceras lyelli*.

Keywords: Douvilleiceras - growth - variability - Albian - Ambatolafia - Mahajanga basin

1. Introduction

Douvilleiceras (de Grossouvre, 1894), is a cosmopolitan genus that ranges through most of the Lower Albian and into the basal Middle Albian; the type species, *Douvilleiceras mammillatum* (Schlotheim, 1813) is a global marker fossil for this interval. Its geographic distribution extends from southern England to France, Switzerland, Germany, the Helvetic Zone of western Austria, Poland, Bulgaria, Romania, Georgia, eastwards to Kazakhstan, Turkmenia, northern India, Pakistan, Japan, British Columbia, California, Arizona, New Mexico, and Texas in the United States, Peru, Colombia, Brazil, Tunisia, Algeria, Gabon, Angola, KwaZulu-Natal in South Africa, Mozambique, Somalia, and Madagasikara. It is a characteristic ammonite for the Lower Albian biozone in Madagasikara, ammonite zonal scheme established by (Collignon, 1949, 1950a, 1950b, 1963, 1965a, 1965b), very abundant and well preserved in the fossil site of Ambatolafia *Cleonicer* zone (Rakotonimanana, 2006), southern part of the Mahajanga Basin (Besairie, 1971). *Douvilleiceras mammillatum* is an ammonite species designated by Schlotheim (1813). The morphological features characteristic of this ammonite are already described in the literature by the famous ammonitologists who could not ever do the complete statistics analysis. However, the biological conception of species in ammonites requires a thorough study of their dimensional characters. The knowledge of the growth of ammonite species needs a mathematic study. In this paper, 57 specimens of *Douvilleiceras mammillatum* from Ambatolafia locality were chosen as a studied subject. The aim is to show the possible modification during the growth by proving on statistic analysis of their size with morphological description of the different ontogenetic stages sequences. The objectives are to understand the variability and test the homogeneity and heterogeneity in the samples considered. It will be possible to highlight the use of *Douvilleiceras mammillatum* in Albian ammonite zonation.

2. Geological setting

The northern side of Mahajanga and Sitampiky cirques is flanked by an escarpment capped by the late Cretaceous flood basalts. Below are Cenomanian terrestrial grits overlying unconformably, Early Albian sediments of the Ambarimananga Formation resting in turn unconformably on glauconitic sandstones of Late Aptian age. The outcrop is obscured in places by land-slipping. The thickness and degree of representation of these Albian sediments varies according to the degree of down-cutting of the Cenomanian. (Besairie & Collignon, 1956a) To the west (Soalala) area of the outcrop, the succession is thick and contains later Albian deposits. The succession thins eastward into Bekipay (Sitampiky Cirque) and by the area of the river Mahavavy Sud is solely Early Albian in date (Rakotonimanana & Rajaonarivelo, 2023). The succession thins markedly at the junction between the Sitampiky and Mahajanga Cirques and is more incomplete in the area of Ambatolafia (Fig1).

The thickness increases rapidly eastward in the Mahajanga Cirque (Madirovalo subdistrict) in the Ambato-Boeni District. In the Berambo area east of the Betsiboka River, Middle and Late Albian sediments are preserved and this increase in thickness continues northward toward the Analalava district (Sofia region) (Besairie 1971).

The current view of a general depositional Mahajanga Basin area in north-west Madagasikara is not supported by the field evidence for the Albian. The Ambatolafia area with its reduced Early Albian succession, marks a tectonic structure between the Soalala – Mahavavy Sud basin in the west and the Mahajanga – Berambo - Sofia Basin to the east and north. The evidence suggests post Late Albian - pre-Cenomanian block faulting or, possibly, anticlinal folding followed by early Cenomanian erosion and the deposition of terrestrial deposits.

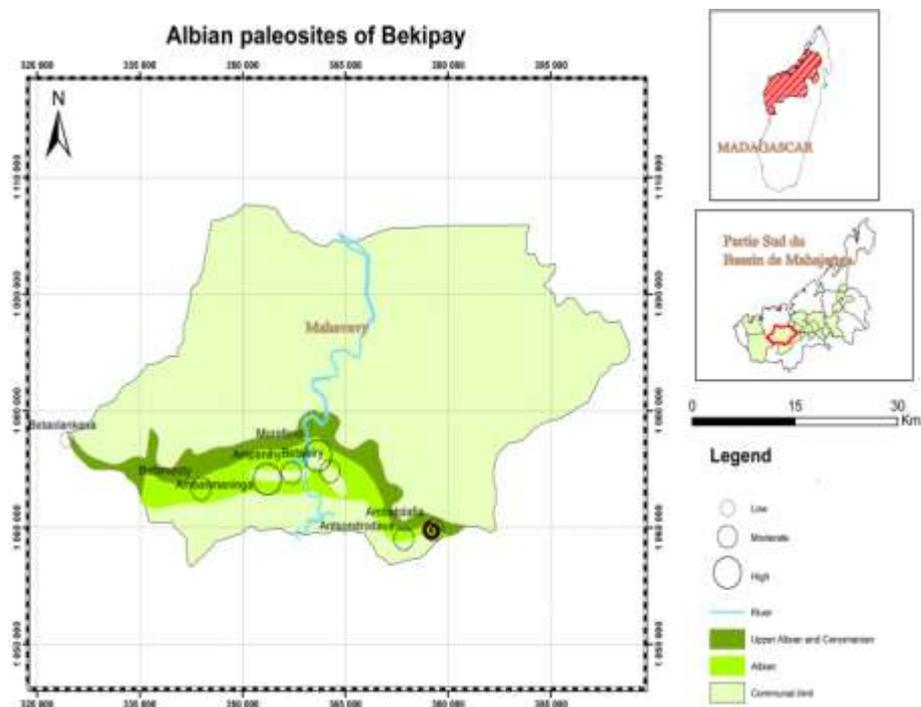


Figure 1: Location of the study site (source: BD 500 Foibentaontsarini Madagasikara)

3. Materials and methods

3.1. Materials

The studied materials come from the quarries of Ambatolafia, albian in the Commune of Bekipay, Mahajanga Basin. They are abundant in the glauconitic clay layer of greenish grey colour. 57 specimens that form the subject of the present paper are nearly so well preserved and pearly green. In all cases the structure of the wall is not destroyed, allow to show the element and to measure the thickness of the shell. Fortunately, the material available provides an opportunity for investigation of the growth stage in *Douvilleiceras mammillatum* from Ambatolafia locality That range from 18,42 to 55,59,mm in diameter. The specimen used are from a collection of ammonites kept for study by Rakotonimanana R M. The collection was made during an expedition in 2004. All specimens (Fig.2) coded AM-DM01 to AM-DM57 have been currently deposited in the laboratory of Paleontology and Biostratigraphy at the University of Antananarivo. The systematic paleontology of the samples is as follows:

Phylum: MOLLUSCA Linnaeus, 1758

Class: CEPHALOPODA Leach, 1817

Order: AMMONOIDEA Zittel, 1884

Suborder: ANCYLOCERATINA Wedmann, 1966

Superfamily: DOUVILLEICERATOIDES Parona & Bonarelli, 1897

Family: DOUVILLEICERATIDAE Parona & Bonarelli, 1897

Subfamily: DOUVILLEICERATINAE Parona & Bonarelli, 1897

Genus: *Douvilleiceras* de Grossouvre, 1894

Species: *Douvilleiceras mammillatum* Schlotheim, 1813



Figure.2: *Douvilleiceras mammillatum* chosen as the materials of study

3.2 Methods

The dimensional characters (Fig.3) are measured with a caliper. The specimens must be well preserved, not deformed or damaged. The maximum diameter (D) representative of the size of the animal is measured at the maximum shell dimension; the whorl height (Wh) and the whorl breadth (Wb) corresponding to each diameter are also measured, these variables give a real idea of the shape of the shell; the diameter of the umbilicus (U) shows ontogenic and/or intraspecific variability.

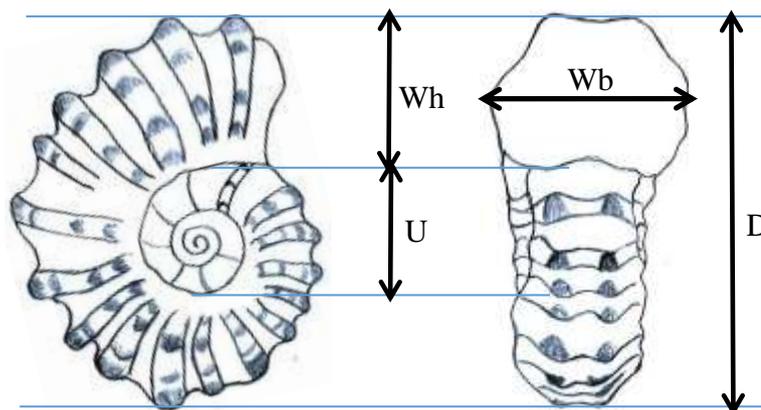


Figure.3: Dimensional characters measured in *Douvilleiceras mammillatum*

The indexes in relation to the diameter and the Wb/Wh ratio are calculated to check whether the variations are related to growth or other factors. The histogram of these ratio is used to detect possible polymorphism (uni, bi or polymodal curve).

The fluctuation of the number of ribs per half whorl as a function of diameter reflects changes in ornamentation during ontogeny, which appears to be largely dependent on variations in rib density. The intensity and/or sharpness of the ribs are clues to the interpretation of the living environment.

Univariate, bivariate and multivariate statistical analysis are carried out to test the homogeneity of these variables; to see the predominance of a growth stage; to know the links that may exist between two dimensional characters during the growth and the individual development

4. Results

4.1. Univariate analysis

In *Douvilleiceras mammillatum* species), the statistical parameters of the dimensional characters and ratio (Tab.I) constitute the results obtained in the univariate analysis

Table1: statistical parameter of the dimensional characters in *Douvilleiceras mammillatum*

	Min	Max	Mean	Std. error	Variance	Stand. dev	Coeff. var
D	18,42	55,59	32,374	1,012	58,410	7,643	23,608
Wh	7,4	24,56	13,281	0,478	12,999	3,605	27,147
Wb	10,82	30,75	17,544	0,478	13,034	3,610	20,579
U	5,82	18,29	10,780	0,317	5,716	2,391	22,178
Wh/D	0,302	0,571	0,409	0,005	0,001	0,038	9,200
Wb/D	0,267	0,648	0,550	0,008	0,003	0,058	10,629
U/D	0,276	0,389	0,335	0,003	0,001	0,023	6,889
Wb/Wh	0,562	1,905	1,356	0,027	0,040	0,200	14,756

Their frequency histogram of dimensionnal characters and ratio (Fig.4) are as a follow

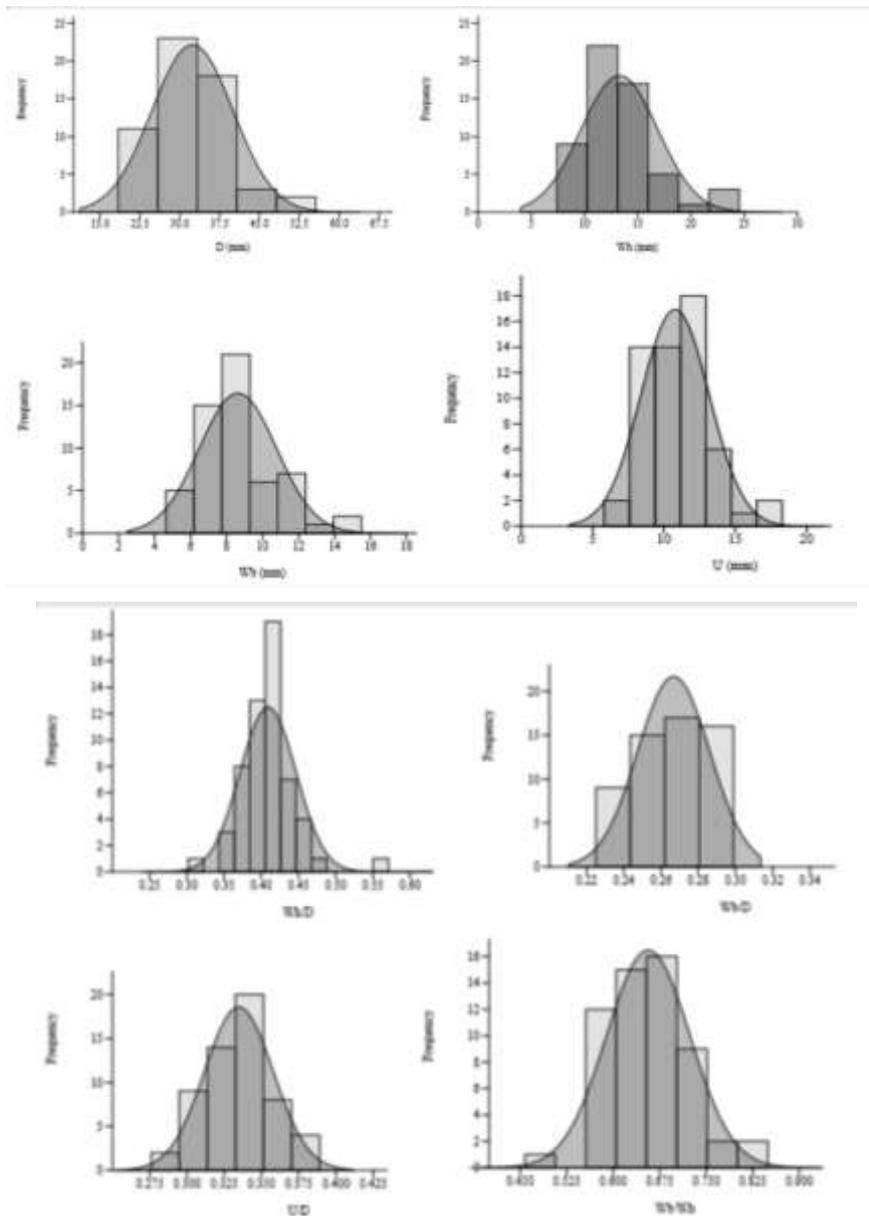


Figure 4: Frequency histogram of dimensional characters and their ratio in *Douvilleiceras mammillatum*

4.2. Bivariate analysis

The correlation matrix (Tab 2) highlights the importance of the relationships between dimensional characters.

Table 2: matrix of correlation between dimensional characters and ration

	D	Wh	Wb	U	Wh/D	Wb/D	U/D	Wb/Wh
D	1**							
Wh	0,93**	1**						
Wb	0,84**	0,74**	1**					
U	0,96**	0,90**	0,84**	1**				
Wh/D	0,13	0,46*	0,01	0,14	1**			
Wb/D	-0,57*	-0,58*	-0,05	-0,49	-0,19	1**		
U/D	-0,32	-0,27	-0,17	-0,03	0,06	0,35	1**	
Wb/Wh	-0,45*	-0,66*	-0,04	-0,40	-0,73**	0,79**	0,23	1**

** very significant correlation, * significant correlation

The results of the bivariate analysis confirm the results of the univariate analysis. *Douvilleicerias mammillatum* undergoes a multitude of variations in the dimensional characters of the shell during its development. This shows that during growth, the whorl height, whorl breadth and umbilicus increase with size (Fig.5).

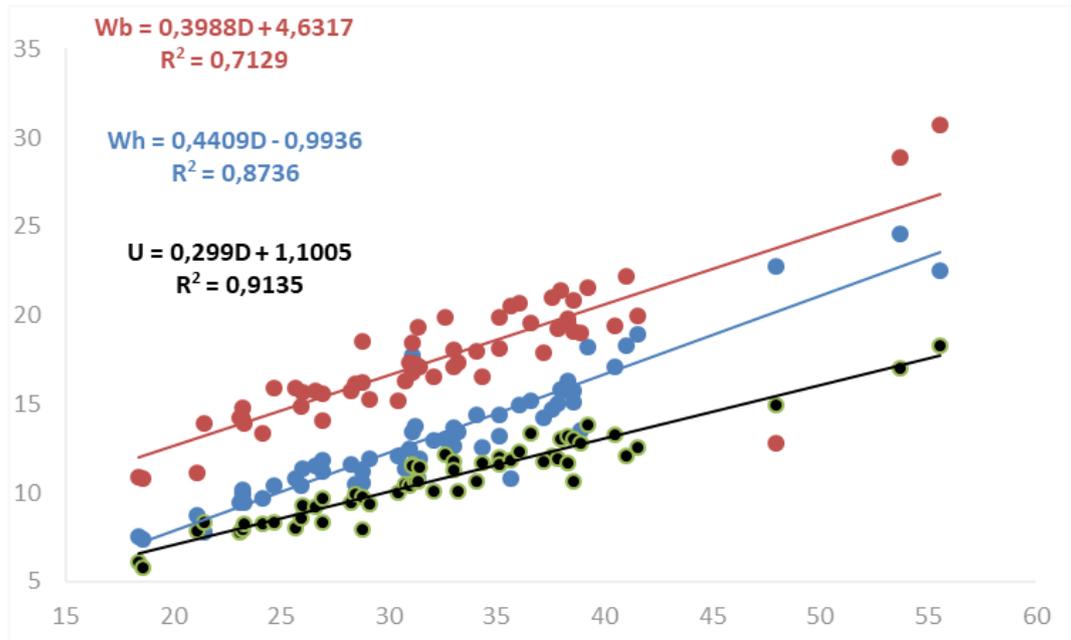


Figure 5: Scatter plot showing the growth of whorl height, whorl breadth and umbilicus as a fuction of diameter in *Douvilleicerias mammillatum*

4.3. Pricipal component analysis

The first two principal components (PC) account for 98.228 of the total variance., The umbilicus is somewhat involved with a barely significant contribution towards the negative values on the second principal component.

PC	% variance
1	94.103
2	4.125
3	0,12876

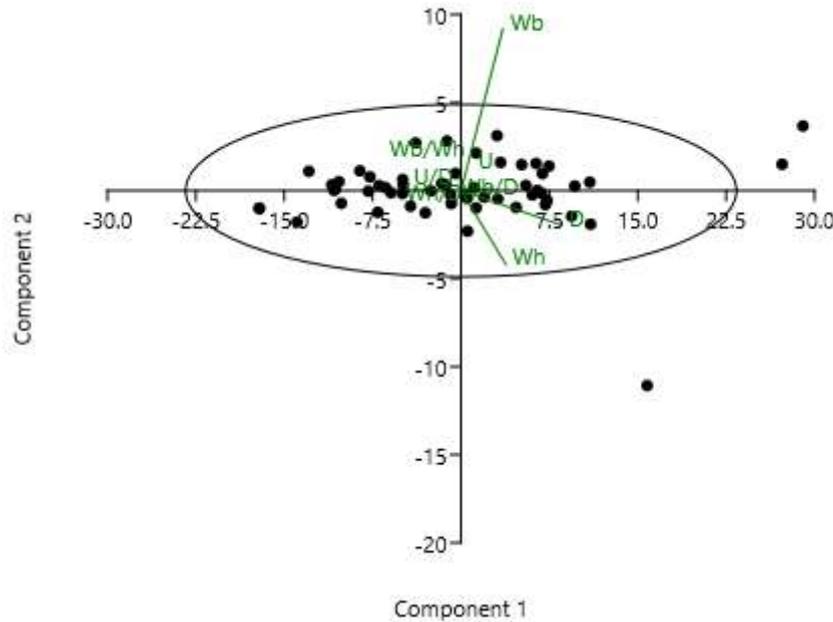


Figure 6: Principal component analysis in *Douvilleiceras mammillatum* from Ambatolafia

5. Discussion

5.1 Variability of dimensional characters in *Douvilleiceras mammillatum*

The wide diameter range from 18,42 mm to 55,59 mm is related to a juxtaposition of different growth stages. The high coefficients of variability, especially at the umbilicus, explain that within the sample studied, the age distribution is not balanced. Smaller individuals (phragmocones = young and adolescent stages) are dominant, some shells are adults with body chamber. The highly coefficient of asymmetry at the level of diameter, height and umbilicus indicates growth disharmonies between these various variables depending on the stages reached. The asymmetry implies the predominance of measurements made on phragmocones with a thicker, lower section ($Wb/D > 0.267$) compared to those with a body chamber.

The histograms of the dimensional characters (Fig.4) show discontinuities that are related to the presence of several ontogenic stages and the presence of intraspecific variability, there is the mixing of young and adult individuals. This means that individuals with low height have a wide umbilicus while individuals with high height have a narrow umbilicus. Despite this, these histograms are fitted to normal curves, the study population is a homogeneous group. All this explains that the variability of the characters highlighted within *Douvilleiceras mammillatum* ontogenetic.

The correlation matrix (Tab2) and scatter plots (Fig5) obtained in the bivariate analysis have implications for the stages of development. The correlation matrix emphasises the importance of correlation between dimensional characters. The growth of whorl height is disharmonic majoring closer of isometric ($Wh = 0.4409D - 0.9936$), $R=0,93$ indicates the same growth rate for whorl height and size, it seems that whorl height increases less rapidly than the diameter. Whorl breadth shows a marked minoring disharmony. $Wb = 0.3988D + 4.208$, the coefficient of correlation $R=0,84$. It increases less quickly than the diameter. So the correlation between these two characters is obviously less strong than for whorl height. The relative dispersion of its cloud is greater. This reflects the greater variability of the whorl breadth and this is consistent with qualitative observations that show that the rates of growth in whorl breadth were very diverse both for an individual during its development and for all specimens. The umbilicus shows a very slightly minoring disharmony, $U = 0.299D + 1.1005$, $R= 0.96$, the growth rate of the umbilicus is inversely proportional to that of the whorl height. The scattering of points reflects a high variability of this character during ontogeny. A slight break in slope was also noted around $D= 45$ mm corresponding to an opening of the umbilicus which coincides in most cases with the end of the phragmocone. The umbilicus, which is very narrow in the younger stages, seems to widen when the living quarters appear. The variation of whorl breadth with whorl height shows quite a large variability despite a high correlation $R= 0.74$. Whorl height increases faster than whorl breadth. The significant ($R= -0.57$) negative correlation of the ratio with the diameter indicates a certain dependence of the shape on the size.

The variance table and the components obtained in the multivariate analysis (Fig.6) led to explanations of the weight of each dimensional characters. The first component totalling 94.103% of the variance, reflects that the dimensional characters are very significant linked to growth: whorl height, whorl breadth diameter of the umbilicus vary with size. On the contrary, ornamentation would be independent of growth. Moreover, the factor provided by the variable number of ribs has the highest weight, and this character made it possible to distinguish the different growth stages of the individuals. Thus, ornamentation was used as a species diversification variable, especially in the second component, which accounted for 4.125% of the variance. In fact, during the sorting of the different morphotypes by morphological examination, only the size of the individuals and their ornamentation are the characters that the eye appreciates first.

5.2. Use of the genus *Douvilleiceras* in Albian ammonite zonation,

The assumption that the presence of *Douvilleiceras* indicates the *mammillatum* Zone in the sense of Spath's (1922) or Casey's (1957) concept, is demonstrably incorrect. The genus ranges at least from the Early Albian *Leymeriella acuticostata* Subzone (*L. tardefurcata* Zone) (Casey 1960, Kennedy and Kollmann 1979, Owen 1988, Kennedy et al. 2000) into the Middle Albian *Lyelliceras lyelli* Subzone. However, *Douvilleiceras* is useful in biozonation because, except for the early Middle Albian *Lyelliceras lyelli* Subzone occurrences, the genus is geographically widespread in deposits of Early Albian age in all faunal provinces (Kennedy and Klinger, 2014). Its species, however, are too long-ranging in occurrence and exhibit much the same morphological variation at more than one horizon to be useful in precise biostratigraphy. For this reason, Owen (1988) recognised a *Douvilleiceras mammillatum* Superzone to cover the range of the occurrence of *Douvilleiceras*. For the former *mammillatum* Zone in the European Province he recognised two Zones; an earlier *Sonneratia chalcensis* and a later *Otohoplites auritifformis*. These two Zones are applicable only to the European faunal Province and not outside of it. The recognition of a Superzone was to circumvent the widely held assumption that all occurrences of *Douvilleiceras* marked the equivalent of the European *chalcensis* and *auritifformis* Zones.

In Madagasikara, typical *Douvilleiceras mammillatum* and contemporaries are present and zonally useful for those sediments later than the *Lemuroceras aburense* Zone and earlier than the occurrence of *Lyelliceras lyelli*. Currently, there are no additional ammonite occurrences which permit precise correlation with the European province subzones of the *Otohoplites auritifformis* Zone.

6. Conclusion

During ontogenic development in *Douvilleiceras mammillatum*, the evolution of the characters seems evident in the qualitative and quantitative analysis, it is possible to distinguish four different successive stages of growth: embryonic stage, juvenile stage, adolescent stage and adult stage. Despite variability, the results of the uni-, bi- and multivariate analysis showed the homogeneity of the population studied by the scatterplots with normal distributions. The young individuals are dominant while the adults are few in number. There is a parallelism between changes in shell characteristics, growth of stages and environmental conditions. In Madagasikara, typical *Douvilleiceras mammillatum* and contemporaries are present and zonally useful for those sediments later than the *Lemuroceras aburense* Zone and earlier than the occurrence of *Lyelliceras lyelli*.

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