Morphometrical study of Choffat's vascoceratids from Portugal

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The vascoceratid specimens forming the basis of Choffat's monograph of 1898 have been restudied with the aid of standard methods of multivariate statistical analysis, applied to 15 measures of shell size and shape and 3 dichotomous variables. The visual appraisal of the morphological features led to a reduction in the number of species erected by Choffat. Two genera are recognized in the Portuguese material, namely, *Fallotites* and *Vascoceras*, the latter comprising *Vascoceras s. str.* and *Vascoceras* ("*Pachyvascoceras*"). The relationships between species have been placed on an evolutionary basis. The possibility of sexual dimorphism for *Vascoceras gamai* is briefly considered. The stratigraphical relationships between the species here considered valid are given. The statistical analysis largely supports the groupings made in the light of modern taxonomical principles. New information on the partition of variability in vascoceratid shells is yielded by the principal components analysis.

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Introduction

Choffat (1898) established the genus *Vascoceras* for ammonites that were "plus ou moins épaisses, parfois globuleuses, à région ventrale arrondie, ornées dans la jeunesse de côtes donnant lieu à des tubercules sur les flancs et à des tubercules ou des renflements allongés de chaque côté du siphon". Choffat then went on to say that apart from his *Vascoceras subconciliatum*, the tubercles weaken in the adult, with the peri-umbilical ones lasting longest. He grouped his many species into four categories, to whit:

Forms with one tubercle and a wide umbilicus, comprising, *Vascoceras gamai*, *V. mundae*, and a variety *subtriangularis* of *gamai.*

Sub-globose forms with rounded umbilical margin, comprising, *Vascoceras silvanense*, *V. douvillei*, *V. adonense.* Some doubtful material was also referred here.

Globose individuals with an angular umbilical margin, including, *Vascoceras amieirense*, *V. harttiforme*, *V. kossmati.*

Multituberculated forms, characterized by *Vascoceras subconciliatum.*

The material available to Choffat was inadequate for the determination of so many species within such a difficult group as the vascoceratids. In addition, all of the specimens are poorly preserved, being internal moulds in various states of weathering. The species were delineated on the grounds of habitus, tuberculation and ribbing and little emphasis was placed on the suture for, as Choffat observed, this varies from specimen to specimen; moreover, few specimens show adequately preserved sutures for study.

Choffat had difficulty in identifying his new species for, as noted for material from Nossa Senhora dos Olivais (Choffat 1898, p. 60), he was unable to assign these specimens to either *mundae* or *douvillei* with confidence.

Pervinquière (1907) revised the groupings proposed by Choffat and reduced the number of species by including *douvillei* in *durandi* and promoting the opinion that *amieirense* probably belonged to *douvillei* (thus *durandi*).

Later revisions have been made. The most extensive of these was that of Furon (1935), in which several subgenera were erected to accommodate the vascoceratids of the western Tethyan realm. *Pachyvascoceras*, for globular involute umbilicotuberculate vascoceratids, was thought to embrace the Choffatian species *silvanense*, *adonense*, *amieirense*, *douvillei*, *harttiforme* and *kossmati.* For non-globulose vascoceratids, he erected *Paramammites* for tuberculated forms (*subconciliatum* and Pervinquière's *Vascoceras polymorphum*), *Paracanthoceras*, for feebly ornamented vascoceratids with a complicated suture (*V.* (*P.*) *chevalieri* Furon), and, *Paravascoceras* for strongly ribbed, untuberculated ammonites with a simple suture (*Vascoceras cauvini* Chudeau, for example).

Furon's taxonomy was revised by Schneegans (1943), who noted the artificiality of the taxonomical units devised. This revision removed *Paracanthoceras* and *Pachyvascoceras* from the scene. In connexion herewith, he modified the definition of *Paravascoceras* of Furon, observing it now to comprise ammonites with a suture of the same pattern as *Vascoceras* and differing from that genus by lacking umbilical tubercles throughout growth and in having oval to globose whorls, ornamented with simple folds or ribs. Choffat's species *barcoicensis* was referred here.

Collignon's (1957) *Discovascoceras* was stated to encompass *Vascoceras amieirense* Choffat. Wiedmann (1959) created for *Vascoceras subconciliatum* the genus *Fallotites*. Freund and Raab (1969) inclined to follow the approach of Schneegans and, in their revision, rejected *Paracanthoceras*, *Pachyvascoceras*, as well as *Discovascoceras*, all of which were placed under *Paravascoceras*. This is, in essence, the point of view adopted by Barber (1957). Schöbel (1975), who wisely confined his argumentation to his material from Niger Republic, also rejected *Paracanthoceras* and *Pachyvascoceras*.

We have just seen how various authors have reacted when faced with the problem of determining vascoceratid collections. Often present in large numbers, as is the case in Africa, the great variability of the group brings confusion to the mind of even experienced palaeontologists.

At this juncture, we wish to point out one thing of importance, namely, that in none of these revisions has the author taken account of one of the prime reasons employed by Choffat in establishing his various species. This was the stratigraphical positions of the ammonites and the evolutionary sequence formed naturally by them. There is no doubt that Choffat was overly zealous in his taxonomy, but his judgment was a great deal better than subsequent workers have tended to give him credit for.

In order to arrive at a reasonably objective set of criteria for allocating the material of Choffat, we decided to restudy the original collection, housed in the Geological Survey of Portugal, using quantitative techniques as an adjunct to traditional methods of determining ammonites.

Qualitative determination of groups

As a working base, we determined what appear to us to be natural groups in the material, using what can be considered as key taxonomical characters for vascoceratids. We note that some of the specimens are fragmentary (e.g. *V. silvanense* and *V.? arnesense*).

Obviously, *Vascoceras subconciliatum* is readily distinguishable from all of the other *Vascoceras* considered here in that it possesses rows of tubercles on the flanks and ribs connected to these.

The other species of vascoceratids in our material seem to be marked by an evolutionary change in which the shells become more inflated with time in connexion with which the degree of involution increases. The body chamber also appears to undergo modification. As far as the umbilical tuberculation is concerned, the early representatives are provided with tubercules on all the whorls, but the persistence of tuberculation decreases gradually over time.

In accordance with the observations accounted for in the foregoing text, a qualitative grouping of the individuals of the Choffat collection may be made in the following manner.

A group comprising *Vascoceras gamai*, *V. mundae*, *V. adonense*, *V. grossouvrei*, *V. gamai* var. *subtriangularis*, and, with some reservation, *V.? barcoicense.*

A group comprising *V. douvillei* and, with some doubt, *V. amieirense.*

A group consisting of *V. harttiforme* and *V. kossmati.*

A group comprising solely *V. subconciliatum.*

List of specimens

The specimens studied derive from the Choffat taxonomical collection (numbered specimens) and from his stratigraphical collection (specimens denoted as PYB+number). Almost all of the specimens were determined specifically by Choffat. The following list includes references to the figures in Choffat (1898) where applicable; we use the original designations.

808 *V. gamai*, pl. VIII fig. 1; 808-1 *V. gamai*; 808-2 *V. gamai*, pl. VII fig. 2; 808-3 *V. gamai*, pl. VII fig. 4; 809-1 *V.* cf. *gamai*; 811 *V. gamai* var. *lissa*; 813 *V. gamai* var. *subtriangularis*, pl. VII fig. 5; PYB 5 *V. gamai*; PYB 6 *V. gamai*; PYB 11 *V. gamai*; 816 *V. mundae*, pl. X fig. 1; 816-1 *V. mundae*; 822 *V. adonensis*, pl. IX fig. 3; 835

Am. (*V.?*) *grossouvrei*, pl. IX fig. 1; 830 *Am.* (*V.?*) cf. *barcoicensis*, pl. XVI fig. 11; 831 *Am.* (*V.?*) *barcoicensis*; PYB 7 *V.?* cf. *barcoicensis*; 828 *V. subconciliatum*, pl. XVI fig. 1; 828-1 *V. subconciliatum*; 829 *V. subconciliatum* var. *inflata*, pl. XV fig. 3; 823 *V. douvillei*, pl. XI fig. 2; 823-1 *V. douvillei*, pl. XI fig. 3; 824 *V.* sp. aff. *douvillei*, pl. X fig. 3e.; 825 *V. amieirensis*, pl. XII fig. 1, 2; 826-1 *V. harttiformis*, pl. XII fig. 3; 827 *V. kossmati*; 827-1 *V. kossmati*, pl. XVI fig. 1; 827-2 *V. kossmati*, pl. XVI fig. 2; PYB 3, PYB 10, PYB 9, PYB 1, PYB 2, PYB 4 *Vascoceras* sp.

The specimens retain at least a part of the body chamber, with the exception of 808-3.

The measurements

The measurements (see Fig. 1) were made on the specimens directly and on a drafting of the section, constructed at the location of the maximum diameter. In some cases, where specimens are in an eroded state of preservation, or damaged, the variables for the whorl sections have been determined on the basis of symmetrical reconstructions. A simple graphical study of the measures, not repeated here, led to a preliminary grouping of the specimens which turns out not to greatly differ from the ideas expressed in Choffat's original publication. This study indicates, however, that

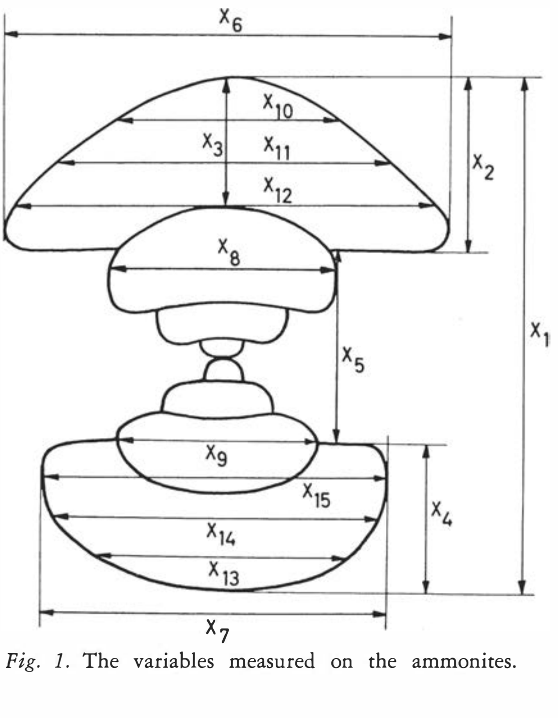

Fig. 1. The variables measured on the ammonites.

there is a fair degree of artificiality in the original specific categories, leading to the following revision of the taxonomic relationships between the species proposed by Choffat.

There is clearly a good deal of redundancy in the variables used in this study; in one case, that of the diameter $= x_1$; this measure is merely the sum of three other measures. This totally redundant variable was included, nevertheless, as it provides a useful basis for comparison in the graphical work.

The qualitatively based groupings of species

I The first main category is composed of the true *Vascoceras*. The species *gamai* and *mundae* grade imperceptibly into each other and there is no possibility of providing a clear delineation between them. Many of the other species described fall within the range of variation of *gamai-mundae*. We list below the forms separated out by Choffat, all of which fall, on qualitative appraisal, into the same specific category. — *V. gamai*, *V. gamai* var. *subtriangularis*, *V. gamai* var. *lissa*, *V. mundae*, *V. adonense*, *V.? grossouvrei*, *V.?* cf. *barcoicensis*, same identification for specimen from Lares (also specimens PYB1, PYB4, PYB9, not determined by Choffat).

These specimens constitute all of the evolute ammonites in the collection; they are rather compressed, in relation to the general condition in this genus. Umbilical tubercles occur right up to the last whorl, where they weaken. The internal whorls are feebly ribbed. The whorl section of the body chamber is mostly oval but it may be rounder or sub-trianguloid.

II The second species of true *Vascoceras* in the material is *V. barcoicense*. On the grounds of the visual study, the following forms as identified by Choffat appear to be referrable here. *V.? barcoicense* (Type), *V.? barcoicense* (specimen 831), from the mill at Almoxarife — this individual is close to the holotype. Finally, PYB 2, a specimen not determined by Choffat.

This group is close indeed to the foregoing and can really only be distinguished from it in that the shells appear to be more involute. However, considering the small number of specimens available, this may be an illusion. It was not possible to ascertain whether the inner whorls bear tubercles. The venter of the body chamber of the type bears feeble folds.

V. gamai and *V. barcoicense*, the two forms considered here, are the earliest vascoceratids to appear in the Portuguese Upper Cretaceous (dated by

Berthou & Lauverjat (1974 a, b) as being transitional from Cenomanian to Turonian).

The second main category comprises *Vascoceras* which are more involute and more inflated than those of the first category. All possess an umbilical tubercle on the inner whorls.

III The species of group III, *V. douvillei* and *V. amieriense*, although close in general habitus, may be kept apart on the grounds of differences in the whorl section. The species *douvillei* appears at the base of the Turonian, whereas *amieirense* evolved later. It has been claimed that this latter species has tubercules on the inner whorls, but, owing to the weathered state of all of Choffat's specimens, it is uncertain what the true situation is.

IV The group IV of the vascoceratids may be termed the group of *Vascoceras kossmati*. The species *harttiforme* and *kossmati* of Choffat, which cannot be held apart from each other, are placed here. The individuals of this species are involute, inflated, with a narrow umbilicus. The whorl section of the body chamber is depressed to trianguloid. Pervinquière (1907, p. 330) and Choffat (1898) both report umbilical tubercules within the group, although this could not be verified for the original material, owing to its poor state of preservation. Group IV, and *V. amieirense*, are the last vascoceratids to develop in the Portuguese Turonian (Lauverjat & Berthou 1975).

V The fifth group contains only one species, namely, *Fallotites subconciliatus*. The individuals of *subconciliatus* differ from *Vascoceras* s. str. in having ventral ornament. As Wiedmann (1959) indicated, the individuals of this species differ from the morphologically similar group of *Paramammites polymorphus* Pervinquière.

Stratigraphically, *Fallotites* appears at the same time as *Vascoceras douvillei*.

The morphometrical analysis

In the foregoing pages, we have presented a revision of Choffat's vascoceratids, using traditional methods of determining ammonites. We shall now test the reliability of these determinations by means of standard methods of multivariate statistical analysis (Blackith & Reyment 1971), in which account will be taken of all variables considered simultaneously. Our study is divided into several parts. Firstly, we shall examine the groups by Q-mode analysis. The groups will also be tested by multiple discriminant functions, an R-mode method. Finally, the variability of all the characters will be considered for the Portuguese vascoceratids, viewed as a whole, i.e., evolutionary unit.

Q-mode analysis

The Q-mode analysis was made using the method of principal coordinates (cf. Blackith & Reyment 1971). We analyzed 18 variables measured on 34 ammonites. Fifteen of the variables are continuous, being those indicated on Fig. 1. Three dichotomous variables were also included, to whit, the presence or absence of umbilical tubercles (x_{16}), visibility of ribs on the inner whorls (x_{17}) and the presence of ventrolateral ornamental features (x_{18}).

A matrix of similarity coefficients was formed between all individuals of the sample, using the method of Gower (1971). The required pairs of coordinates were then extracted from this matrix computing the suitably scaled principal components (Blackith & Reyment 1971, pp. 163—170). The computer program employed is an updated version of that given in Blackith & Reyment (1971, pp. 171—185).

In Fig. 2, the plot of the first and third principal coordinates is given. The first two axes account for 55 percent of the information in the similarity matrix. The first and third axes largely isolate three main clusters of specimens. There is a mixed cluster of ammonites of groups I and II and V in the middle portion of the plot. On the information presented in this plot, two of the three specimens of *Fallotites subconciliatus* are, as regards the growth pattern of the conch, similar. A specimen of group I plots on its own, near an ammonite of group V. The specimens of group IV cluster together, as do those of group III. The first coordinate axis attempts to range the specimens in order of increasing involution, thus, also in order of decreasing age. The ordering is somewhat confused, however, as the plot including the second axis appears to bring in the element of inflation of the conch which is only in part directly relatable to the degree of evolution of the umbilicus.

The third principal coordinate plotted against the second brings out the ornamental differences in the various categories.

The principal coordinates study seems to indicate that as far as the variables considered are concerned, our a priori groups are readily identifiable on axes 1 and 2 and 1 and 3. The second and third axes, utilizing the dichotomous information, single out group V. In both projections of the sample points, group II fails to be differentiated from group I. This failure might be a result of the small sample of our group II species, thence

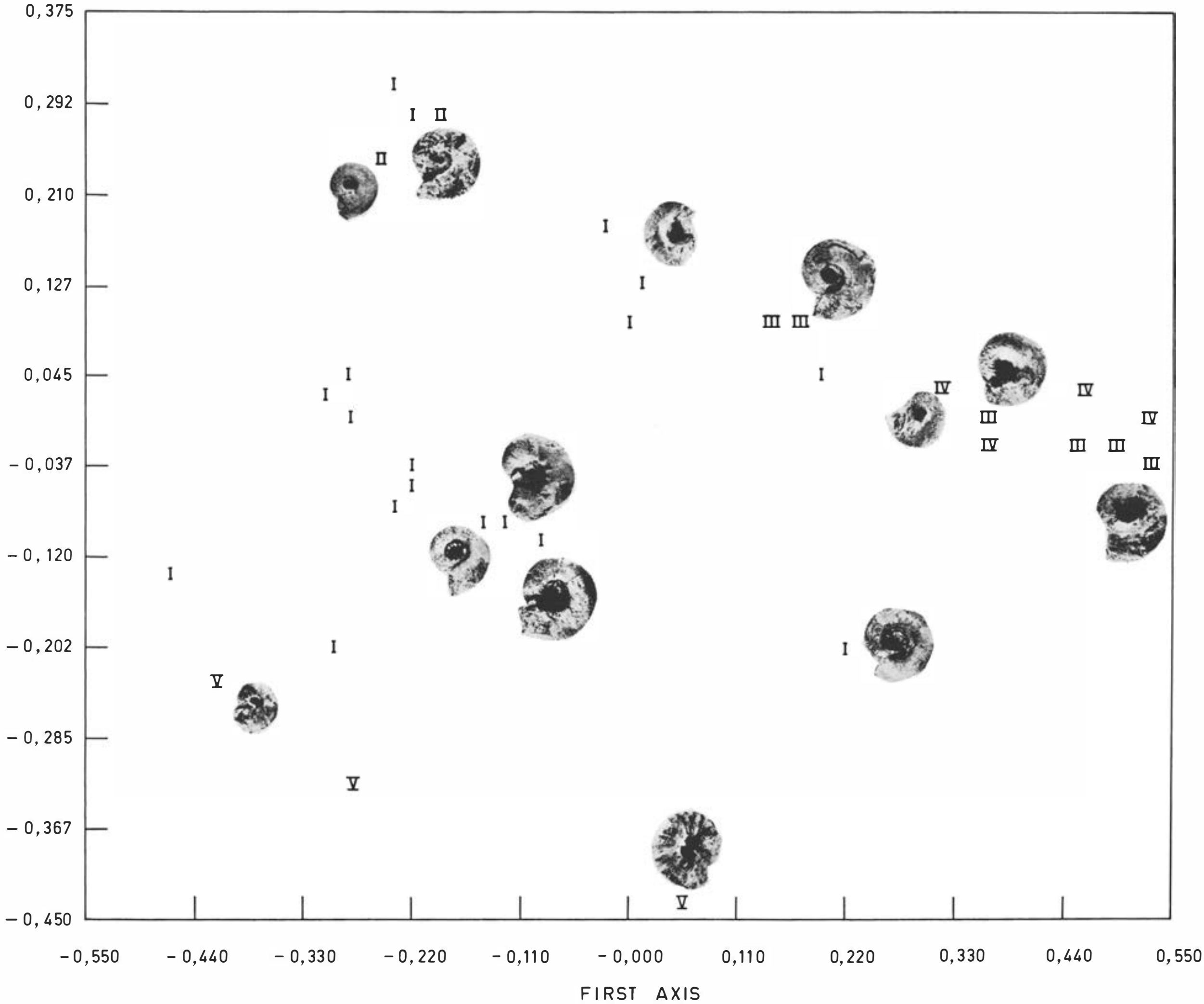

Fig. 2. Plot of the first and third axes of the principal coordinates analysis of the data. Photographs of some of the specimens supply an indication of the variation in form exposed by the graph.

insufficient information for a reliable analysis. We shall consider this question again further on.

A model to show the relationship between the 34 points in the three-dimensional space of the first three coordinate axes was made. A stereoscopic photograph of it is given in Fig. 3. It will be seen that homogeneous clusters are formed by groups IV and V, while group III separates out well, apart from the intrusion of a specimen of group I. Two specimens of group I are like those of group V, morphologically.

The 19 specimens of group I do not form a homogeneous cluster and they fall into four subdivisions. In one of these, groups I and II overlap, in the second, I and III overlap, in the third, there is no overlap with any other group, and in the fourth, group I individuals adjoin those of group V.

The specimens that resemble those of group II are "*V. gamai lissa*" and *Vascoceras* sp. indet. (we note here that we use Choffat's variety names as a means of identification, realizing full well that these lack biological significance). The specimens that mingle with group III are "*V. mundae*", "*V. gamai subtriangularis*", and "*V.* cf. *barcoicensis*". Both of the specimens adjoining the points of group V are *V. gamai.*

The homogeneous set of individuals of group

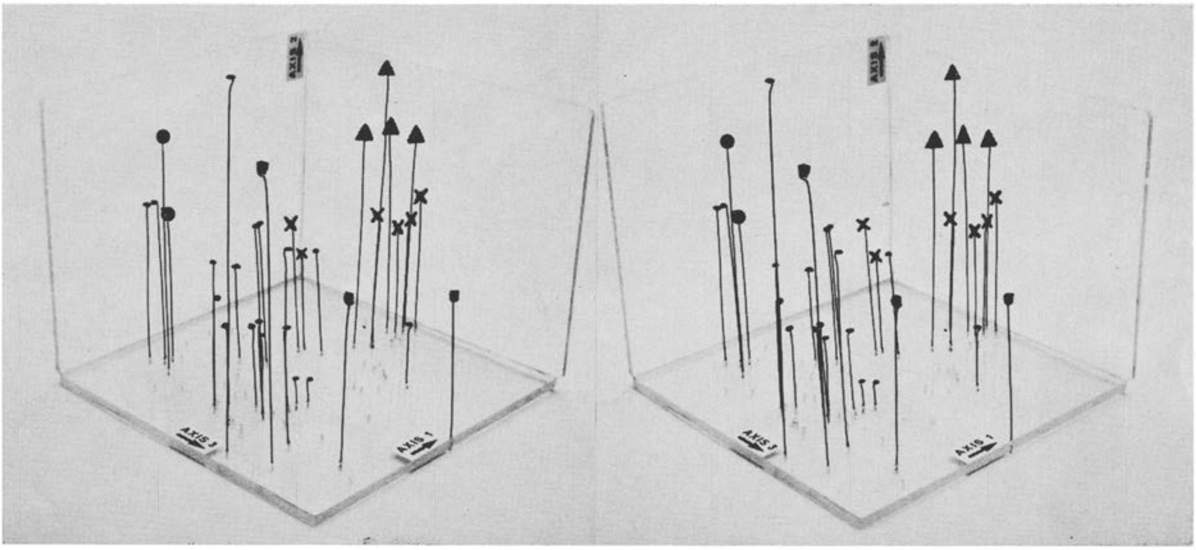

Fig. 3. Sterographic photograph of the plot of the 34 points for the first three coordinate axes. Small dots denote group I; black balls denote group II; crosses signify group III; triangles stand for group IV; black cubes denote group V.

I are identified under the names *gamai*, *mundae*, *grossouvrei* and *Vascoceras* sp. A single specimen, "*V. adonense*", lies on its own.

This figure brings out the fact that the original categories were artificial, and also that group I is heterogeneous, but this heterogeneity cannot be resolved unless the material available at present is augmented by larger collections. A possibility that should not be overlooked here is that these differences are of a sexual-dimorphic origin, of the kind described by Reyment (1971). This hypothesis might conceivably apply to the material of groups I and II which, although it does appear to show clusters into several small groups, can also be seen to lie in two major fields in the three-dimensional figure.

Testing the validity of the groups

The groups of ammonites produced by the preliminary visual study and graphical appraisal by simple methods were tested statistically by means of the multivariate analysis of variance and canonical variates analysis (see Cooley & Lohnes 1971, pp. 223—286) for an account of the calculations and Blackith & Reyment (1971) for examples of reifying the results). We used the computer program BMD07M (Dixon 1973, pp. 233—253), which is constructed so as to yield a step-wise consideration of the variables. All possible pairs of groups are compared against each other by the matrix of variance ratios and discriminant functions are computed for each of the groups against all other groups pooled. An individual is assigned to the group to which it is closest on the basis of the generalized distance criterion, from which an array of identifications is prepared for all groups and individuals, thus giving a means of determining the amount of overlap between the various groups. We note here that only the 15 continuous variables were used in this analysis.

The step-wise procedure retains all the variables and all 34 specimens identify correctly with their a priori groups, thus providing support for the preliminary revision and also for the validity of group II.

The linear discriminant function related to most of the information in the canonical variates may be approximately expressed as

$$-3{,}65x_1 + 3{,}66x_2 + 3{,}54x_4 + 3{,}82x_5 - 1{,}22x_7 + \\ + 0{,}95x_{15}.$$

This linear relationship shows which of the 15 variables are doing most of the work in discriminating the five groups. In fact, a future study of Portuguese vascoceratids from the point of view of discrimination and identification, would do well to concentrate on just four variables, notably, these for whorl heights and one for whorl thickness, leaving out the redundant variable x_1, and the largely redundant variable x_{15}. It will be recalled, that these redundant variables were introduced for charting the variation in shape, ana-

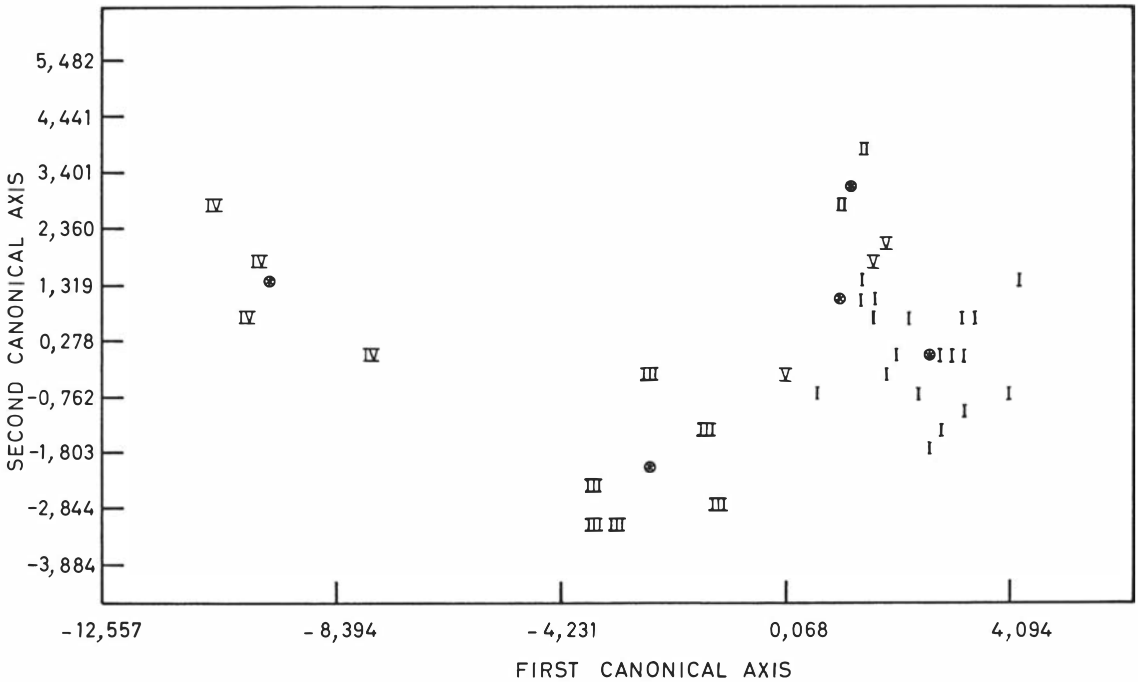

Fig. 4. Plot of the first two canonical axes for the discriminant function study.

lysed in the next section, and it is not to be expected that they would be useful for purposes of studying differences between groups.

In general, the present analysis gives an encouraging aura of support to the assignations of specimens to groups made on classical palaeontological grounds. The plot of the transformed canonical variate observational vectors for the first two axis is shown in Fig. 4. The horseshoe shape of the plot is probably due to there being a quadratic relationship between the eigenvectors. In general, there appears to be a satisfactory separation into discrete groups with, however, group V, the *Fallotites*, lying peripherally to group I, that of the *V. gamai* individuals. If, however, the information contained in the dichotomous variables had been includable, group V would have been well isolated.

We wish to note here briefly one, perhaps, rather suprising feature of the redundant variable x_1, namely, that when it was excluded from the step-wise analysis, one individual of group I classified incorrectly with group V. There is no doubt, from the present analysis, which is based on a very complete description of the shape of the shell, that the specimens of group V are extremely close to those of group I in habitus and, if it were not for the ornamental differences, it would be an uneasy matter to differentiate taxonomically between them. In this respect, a situation reminiscent of the *Subprionocyclus—Reesidites* transition (Reyment 1975) exists.

The analysis of shape variation

We shall now consider the question of shape variation in the entire sample of 34 individuals. In an evolutionary sense, we are here dealing with a homogeneous population, as all the species must be considered to be relatives. Statistically, this is hardly so, as indicated by the results of the coordinates analysis. As we have shown, it is apparent that there are differences in shape which set off two of the smaller groups quite clearly from the rest of the material (Figs. 2, 4). Notwithstanding this discontinuity in our collection, we propose to examine the overall variation in the vascoceratids by principal components analysis (cf. Jöreskog et al. 1975).

It is instructive to begin by examining the patterns contained within the matrix of correlations. This was the matrix selected for the principal components study, owing to the relative differences in variation in our variables. The principal components are based on several groups of specimens rather than a single homogeneous assemblage. The relationships that are observed are therefore a mixture of growth patterns in the several species, along with size and shape differences between the species. The aim of the analysis is to attempt to range the 34 ammonites in terms of size and shape.

Most of the correlations are rather high and a few of them very high. It is important to note, however, that the correlations tend to be lower than is what is usually observed in planispirally coiled cephalopod shells (cf. Reyment & Sandberg 1963). The ranges of the correlation coefficients are listed in Table 1.

Table 1. Ranges of correlation coefficients.

range	number of coefficients	range	number of coefficients
1,0 −0,901	12	0.50−0.401	11
0,90−0,801	23	0,40−0,301	14
0,80−0,701	10	0.30−0 201	6
0,70−0,601	6	0,20−0,101	4
0,60−0,501	10	0,10−0,000	9

There are striking patterns within the correlations. The highest values are found among the widths, whereas lower coefficients characterize the measurements parallel to the diameter. The widths tend to be best correlated with other widths and less well integrated with the variables located along the diameter. To a lesser extent, this is also true of x_1, x_2, x_4, and x_5, which are better correlated with each other than with the widths.

The eigenvectors of the correlation matrix and the percentages of the trace accounted for by each eigenvalue corresponding are listed in Table 2. The first eigenvector represents equal covariation in variables x_6 to x_{15}, thus indicating that

Table 2. Eigenvectors for the correlation matrix.

Variables	1	2	3	4	5	6	7	8
1	0,1052	−0,3838	−0,1313	0,0313	−0,0343	0.0711	0,0493	0,1280
2	0,1073	−0,3489	−0,1257	0,1358	−0,3142	−0.0122	0,1201	−0,2903
3	0,0274	−0,4525	−0,1008	0,1101	−0,4090	−0,2998	−0,0157	−0,3727
4	0,1283	−0,3001	−0,0030	0,2029	−0,3116	0.3260	−0 0547	0,7364
5	0,0735	−0,5389	−0,2612	−0,2677	0,6737	−0,0736	0,0456	0,0397
6	0.2775	0,1304	−0,0539	0,3248	0,0353	−0 0887	0,0703	−0.0390
7	0,3303	0,0167	0,0230	0,0511	0,0714	0,3605	−0,1896	−0.1895
8	0,3899	0,2086	−0,3243	−0,2675	−0,1037	0,1377	0,7301	0,0216
9	0,3360	0,1422	−0,2105	−0,5858	−0,2997	−0,3569	−0.4334	0.1642
10	0,2125	0,0196	−0,0339	0,2653	0,1938	−0,4552	−0,0711	0.2466
11	0,2519	0,0923	−0,0440	0,3250	0,1448	−0,2821	0,0011	0,1184
12	0,2811	0,1345	−0,0594	0,3284	0,0457	−0,1346	0,0332	−0,1039
13	0,3210	−0.1917	0,8528	−0,2207	0,0054	−0,1548	0,2340	0,0178
14	0,3215	−0,0294	0,0420	0,0029	0,0948	0,2355	−0,3155	−0,1828
15	0,3313	0,0098	0,0058	0,0187	0,0726	0,3531	−0,2357	−0,1800
Percentage of variance	69,43	14,92	5,45	3,23	2,47	2,02	0,95	0,83

Variables	9	10	11	12	13	14	15
1	0,1078	0,2164	0,0163	−0,1118	−0,0911	0,0135	0,8477
2	0,1498	0,6561	0,1203	−0,0378	−0,1472	−0,0047	−0,3802
3	−0,2588	−0,5116	−0,0972	0,0959	0,1656	−0,0012	0,0336
4	0,0361	−0,1772	−0,0043	0,0031	0,0522	−0,0139	−0,2607
5	0,1470	−0,1188	−0,0785	0,0400	0,0005	−0,0066	−0,2403
6	0,3279	−0,1956	−0,1215	0,4537	−0,5208	0,3794	0,0233
7	−0,1716	0,0050	−0,2165	0,2706	−0,1921	−0,7022	0,0315
8	−0,2009	−0,0903	0,1034	−0,0116	0,0718	0,0078	−0,0031
9	0,1814	0,0627	−0,0841	0,0234	−0,0474	−0,0254	−0,0091
10	−0,6138	0,1273	0,1152	−0,2297	−0,3329	−0,0267	−0,0419
11	0,0568	0,2534	−0,0373	0,4050	0,6835	−0,0482	0,0598
12	0,4693	−0,2287	−0,0519	−0,6400	0,0785	−0,2583	−0,0405
13	0,0607	0,0098	−0,0357	−0,0086	−0,0062	0,0059	−0,0009
14	−0,0178	−0,1441	0,8009	0,0228	0,0908	0,1583	0,0172
15	−0,2482	0,1076	−0,4798	−0,2616	0,1788	0,5167	−0,0325
Percentage of variance	0,42	0,15	0,09	0,07	0,02	0,00	0,00

most of the variation in the material lies with variability in the measures of breadth of the conch, hence the degree of inflation.

The second eigenvector, linked to 15 percent of the total variability, represents variation in the height dimensions, hence the "size" of the shells. This breakdown of the variation is interesting insofar as it partitions the spectrum of variation really into two uncorrelated parts, inflation and involution.

The remaining eigenvectors, linked to small amounts of the total variation, tend to be dominated by single breadth and height measures. The smallest eigenvector is worth a moment's consideration. It denotes that linear combination of variables that does not vary in the material and it is therefore not surprising to find that it is entirely made up of the variables x_1, x_2, x_4, and x_5, the latter three summing roughly to the first. This is a result of the fact that the variable x_1 is merely the sum of the other three variables. It will be remembered that it was included in full knowledge of the redundancy associated with it as it does give a base for gauging absolute size of specimens.

An interesting aspect of this analysis is provided by a consideration of shape variation in the vascoceratids under study in relation to the results of Raup (1966) on the geometry of the ammonoid shell. Raup defined the shape of planispirally coiled ammonoid shells by means of three parameters. Although our linear measurements are not the same as those of Raup, all the geometrical elements used by him can be detected in our fossils. His variable S denotes the shape of the generating curve. None of our variables exactly define this but it is roughly approximated by our fatness measures. This shows up in the first eigenvector of Table 2 as changes in inflation.

Raup's parameter D reflects the degree of involuteness of the conch. Variation in this property is described by the second eigenvector. Raup's W measures the rate of expansion of the whorl by two half diameters of the shell in the same plane. In our vascoceratids, this type of variation does not surface until the fifth eigenvector.

It is notable that about 70 percent of the variability in the vascoceratids is accounted for by measures of inflation.

Taxonomical conclusions

As a result of our study, we propose that Choffat's material be referred to two genera, *Fallotites* Wiedmann and *Vascoceras* Choffat, the latter being subdivided doubtfully into the categories *Vascoceras* s. str. and *Vascoceras* ("*Pachyvascoceras*") (following Schöbel 1975). The citation marks denote the taxonomically uncertain status of *Pachyvascoceras.*

Generally speaking, the taxonomy of *Vascoceras* s.l. has been centred around the degree of evolution of the shell and the nature of the ornament and it is well known that there is a rough trend in these characters through the Early

Table 3. Revision of the specimens of the Choffat collection.

Original name	Revised assignation	Reference in Choffat (1898)	Remarks
silvanensis (18)	not assigned	p. 57, pl. 8, fig. 5	
arnesensis (836)	not assigned	p. 68, pl. 14, fig. 3	
gamai (808, 809)	*Vascoceras* (*Vascoceras*) *gamai*	p. 54, pl. 7, figs. 1—4, pl. 8, fig. 1, p. 56, pl. 10, fig. 1, pl. 8, figs. 2, 4	Group I
var. *subtriangularis* (813),	,, ,,	p. 55, pl. 7, fig. 5	
var. *lissa* (811),	,, ,,	p. 55	
mundae (816), *adonensis* (822),	,, ,,	p. 59, pl. 9, fig. 3	
grossouvrei (835),	,, ,,	p. 68, pl. 9, figs. 1, 2	
cf. *barcoicensis* (830),	,, ,,	p. 67, pl. 16, fig. 11	
(PYB 7)	,, ,,	p. 67 (doubtful specimen)	
barcoicensis (831)	*V.* (*Vascoceras*) *barcoicense*	p. 67, pl. 17, fig. 1	Group II
douvillei (823)	*V.* ("*Pachyvascoceras*") *douvillei*	p .59, pl. 10, fig. 6, pl. 11, figs. 2—5	Group III
aff. *douvillei* (824)	,, ,,	p. 60, pl. 10, fig. 3	
amieirensis (825)	*V.* ("*Pachyvascoceras*") *amieirense*	p. 61, pl. 12, figs. 1, 2	
kossmati (827)	*V.* ("*Pachyvascoceras*") *kossmati*	p. 63, pl. 14, figs. 1, 2	Group IV
harttiformis (826)	,, ,,	p. 61, pl. 12, fig. 3	
subconciliatum (828, 829)	*Fallotites subconciliatus*	p. 64, pl. 15, figs. 1—3, pl. 16, fig. 4	Group V

Turonian. This is a fact that has often been ignored by revisors of the vascoceratids.

The specimens of the Choffat collection are here identified as indicated in Table 3.

Stratigraphy of the Portuguese vascoceratids

The vascoceratids from the mouth of the Rio Mondego of the "Beira littoral" appear in time in the following order.

Transition between Cenomanian and Turonian	*V.* (*Vascoceras*) *gamai*, *V.* (*Vascoceras*) *barcoicense* These species continue in the Turonian but become less numerous.
Early Turonian	
lower part	*V.* ("*Pachyvascoceras*") *douvillei*, *Fallotites subconciliatus*,
upper part	*V.* ("*Pachyvascoceras*") *amieirense*, *V.* ("*P.*") *kossmati.*

Statistical summary

The principal coordinates analysis indicates that there are genuine morphological groupings in the material but that group I is not homogeneous. This could be due to the small size of the sample but another possibility that ought not to be overlooked is that of dimorphism. Support for the validity of the five a priori groups was yielded by the multivariate analysis of variance and the step-wise discriminant function study in that all specimens assign correctly to their groups even with an equal probability of identification for each of the groups. The close evolutionary relationship between *Fallotites subconciliatus* and *Vascoceras gamai* is brought out by both of these analyses.

The principal components study shows the variation in our vascoceratids to consist mainly of two parts, to whit: a main portion (70 percent) deriving from variation in the degree of inflation of the shell and a portion (15 percent) connected with variation in the degree of involution of the shell. The invariant linear combination of the eigenvector connected to the smallest variance component could be shown to be an artifact of the measures of involution.

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A contribution to
Project MID-CRETACEOUS EVENTS

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