The main branch of Miocene *Gyraulus* (Gastropoda; Planorbidae) of Steinheim (southern Germany): a reconsideration of Mensink's data set

G.D.E. Povel

Povel, G.D.E. The main branch of Miocene *Gyraulus* (Gastropoda; Planorbidae) of Steinheim (southern Germany): a reconsideration of Mensink's data set. — Scripta Geol., Spec. Issue 2: 371-386, 4 figs., Leiden, December 1993.

G.D.E. Povel, Leiden University, Department of Population Biology, Systematic Zoology Section, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

Key words: Miocene, *Gyraulus*, main branch, multivariate analysis.

The data set of the so-called main branch of Miocene *Gyraulus*, collected and measured by Mensink, has been re-examined by means of multivariate methods. New information was obtained by presenting the percentage of specimens which have a keel on the second or third whorl in a bivariate way. In an earlier multivariate analysis Lindenberg & Mensink used only six characters, in the present paper an additional two characters have been used. However, as the number of characters is small, some of them have not been adequately measured, and because the identification of part of the specimens was questionable, the results may still be insufficient.

Contents

Introduction

Of the fossils found in the deposits of the Steinheim Basin (southern Germany), those of the planorbid genus *Gyraulus* show interesting developments. This ancient lake offers an excellent possibility to study gastropod evolution (Gorthner & Meier-Brook, 1985). Hilgendorf (1866) was among the first to recognise several sequences of gradual transitions in them, the so-called main branch, consisting of nine forms (Table 1), and the side branches (Nützel & Bandel, 1993). Specimens of its earliest form, viz. *G. kleini*, are also known from localities outside the lake, those of the other forms are not and are therefore endemic. Because of the variability of the taxa questions arose about their classification and how to explain the transitions between them.

Table 1. Taxa recognised by Hilgendorf (1866) in the main branch of the fossil members of *Gyraulus* from the Steinheim Basin, arranged in stratigraphical order. Mensink regarded *G. planorbiformis* as a transititional form in de development of *G. sulcatus* and *G. tenuis*. The three-character codes indicate the code for the species used in the analyses.

Gyraulus supremus (Hilgendorf, 1866)	sup
Gyraulus revertens (Hilgendorf, 1866)	**rev**
Gyraulus oxystoma (von Klein, 1847)	OXY
Gyraulus trochiformis (Stahl, 1824)	**TRO**
Gyraulus planorbiformis (von Klein, 1847)	pla
Gyraulus sulcatus (Hilgendorf, 1866)	SUL
Gyraulus tenuis (Hilgendorf, 1866)	TEN
Gyraulus steinheimensis (Hilgendorf, 1866)	ste
Gyraulus kleini (Gottschick & Wenz, 1922)	**kle**

To make it more explicit how many taxa there can be recognised in the sedimentary strata and how their development proceeds, Mensink (1964, 1984) accomplished very extensive and accurate excavations of the Steinheim lake deposits. He succeeded in sampling planorbid shells from 50 subsequent strata, which are labelled P_0-P_{49} from bottom to top. The occurrence of the various taxa in the subsequent samples is shown in Table 3. Of each specimen eight continuous characters of the initial three whorls were measured (Table 2), which were considered to contain sufficient characteristic information on the taxa.

To study the difference between the morphotypes, per sample and over the complete range of sampled beds, Mensink examined the variation of each character by means of graphical methods. First, of a sample the variation of the characters was summarised by means of histograms. The outline of the histograms was smoothened using sliding averages, after which all the histograms of a certain character were arranged in stratigraphical order in a single figure (Mensink, 1984, figs. 24-25). The figure was given a more tri-dimensional effect by filling up the gaps between the histograms by extrapolation, and by shading the slopes of the hill ridges by short strokes. In this way the graphs displayed the differentiation of the taxa more strongly than the gently sloping smoothened histograms could otherwise do. So, a more or less subjective interpretation of the variation of the samples was implemented in a landscape-like graph of hill ridges. In Mensink's figure, however, the bases of the graphs are not drawn, i.e. those parts of the frequency distributions which account for the variation of a certain taxon in the various samples. Moreover, as there is a large amount of overlap in the values of each character, it was not possible by this approach

Table 2. Continuous characters used in the present paper.

1. Height 1st whorl;
2. Width 1st whorl;
3. Height 2nd whorl;
4. Width 2nd whorl;
5. Height keel 2nd whorl;
6. Width keel 2nd whorl;
7. Height keel 3rd whorl;
8. Width keel 3rd whorl.

to display a clear objective difference between the taxa for a single character.

On the basis of these graphs, which were supposed to display the variation of a character in the course of time, Mensink concluded that each of them contains a compatible pattern of differentiation. One of the landscape-like graphs, i.e., that of character 4 (see Table 2: width 2nd whorl), was considered to display most clearly the development of the main branch of *Gyraulus*, and was chosen as a synopsis of the analyses (Mensink, 1984, fig. 25). It shows the uncarinated, small, planispiral *G. kleini* at the root. This differentiates into *G. steinheimensis* (combined with the similar *G. tenuis*), which has a very faint short or continuing subsutural carina, and *G. sulcatus*, which has both a subsutural and a more abapical carina, giving the whorl a bi-angular shape. *G. sulcatus* changes into *G. oxystoma*, which is planispiral and has an oval shaped aperture and a faint keel, or no keel at all, and through an intermediate form with a moderately raised whorl height (named *G. planorbiformis*) into the trochospiral *G. trochiformis*. Then the planispiral *G. oxystoma* develops further into *G. revertens*, from which finally *G. supremus* splits off.

The recognition in an objective way of the number of morphotypes in a sample, and the delimitation of the taxa in the subsequent samples, was performed by Lindenberg & Mensink (1979), using multivariate statistical methods. Next to the information on the individual characters also the relations between them are incorporated into an estimate of overall similarity. The analyses were based on the first six characters shown here in Table 2. The use of only two keel characters was done because a problem was discovered in the way these characters were measured. Many samples, however, contain specimens which do have a keel on the third whorl. Therefore it seems worthwhile to re-examine the data set of Mensink, in order to investigate whether the characters of the keels may display more information, and in which way this relates to the differentiation of the forms.

Lindenberg & Mensink (1979) found that in each sampled bed the specimens of a certain morphotype group together in a number of subclusters. The relations between these subclusters of the subsequent samples were also investigated and showed on some points, viz., the grouping of the subclusters of the same morphotype, a resemblance with Mensink's (1984) univariate landscape-like graphs. However, the large gaps between the forms as shown in a scatterplot of a Principal Component Analysis revealed, that the gradual changes from one form into another, as displayed by the univariate graphs, could not be confirmed. In the present study it is investigated whether it is possible to present this horizontal and vertical multivariate pattern of differentiation of the clusters in another way.

Material and methods

The, handwritten, data set of Mensink was available to this research. It consists of 50 subsets, labelled as samples P_{00} to P_{49}. The samples P_{00} (85), P_{03} (112), P_{04} (95), P_{05} (99), and P_{30} (95) excepted, each sample consists of 100 individually numbered and identified specimens. Of each specimen up to eight continuous characters (Table 2) have been measured in a mm scale. All statistical and multivariate analyses were performed by means of the computer program package for Bioinformatic Pattern Analysis, BIOPAT, on the Leiden University's IBM-mainframe (Hogeweg & Hesper, 1972).

Shells with and without a keel on a whorl

The histograms and landscape-like graphs of Mensink (1984), which illustrate the dimensions of a keel (characters 5-8), do not display the amount of specimens of a sample which have a keel. Rather, these figures give the impression as if all the specimens of a certain sample have a keel at both whorls. This is because the characters of the keels have been measured only when a keel was present. In this way the characters obtained a binary part (keel/no keel) and a continuous part (keel low/keel high) (Lindenberg & Mensink, 1979). The histograms and graphs gave only a univariate description, the bivariate relation between the presence/absence of a keel on either of the two whorls does not show. From analyses of the data set it appeared, that in those samples which contain specimens which have a keel, some have only a keel on the second or the third whorl, or on both. When of each sample the percentage of specimens which have a keel on a single whorl, or on both is counted, not an abrupt but a more gradual image of the occurrence of a keel on a whorl arises (Table 3).

Table 3 shows that in the data set of Mensink, P_{00} consists of only flat and unornamented specimens (*G. kleini*). From P_{01} to P_{11} the percentage of specimens without a keel varies, having a maximum in P_{04}, and then it gradually decreases. Just as in *G. kleini*, specimens of *G. steinheimensis* have no keel. However, in P_{05} to P_{09} a few (3-10) specimens occur which have a keel on the third whorl.

Specimens recognised as *G. tenuis*, occurring in P_{01} to P_{09}, have mainly a keel on the third whorl, some on the second. Gradually the number of specimens with a keel on both the second and third whorl, increases.

Table 3a-b shows that from P_{01} to P_{32}, the range over which *G. sulcatus* and *G. trochiformis* developed, quite a substantial amount of specimens occurred with only a short keel on the second whorl. In this same period the more heavily keeled specimens which have a keel on both the second and third whorl, are not always present in each sample (e.g. P_{15}-P_{17}, P_{23}-P_{25}, and P_{27}), and disappear in P_{29}. During the transition to *G. oxystoma* (P_{29}-P_{32}) the percentage of specimens with a short keel on the second whorl further decreases. Then, during the transition to *G. supremus* from P_{41} onwards specimens with a keel re-appear, mainly having a keel on the third, or the second and third whorl.

The clustering of specimens

The height of a keel on the second or third whorl was measured relative to the

Table 3. Species distribution in the sampled section and statistics of *Gyraulus* main branch samples from Steinheim.
1-7: The occurrence per sample of the seven taxa of the main branch of *Gyraulus*. Pj = sample number; 1 = *G. kleini*; 2 = *G. steinheimensis*; 3 = *G. sulcatus*; 4 = *G.trochiformis*; 5 = *G. oxystoma*; 6 = *G. revertens*; 7 = *G. supremus*. a-d: Percentage of specimens which have or have not a keel: a = no ribs; b = a rib on the second whorl only; c = a rib on the third whorl only; d = a rib on the second and third whorl.
CC = Cophenetic Correlation between the similarity and ultrametric matrix for each sample; PC1, PC2 = the percentage of explained variation by the first and second Principal Axes of a Principal Coordinate analysis of a similarity matrix of Euclidian distances between the specimens.

1	2	3	4	5	6	7	Pj	a	b	c	d	Pj	CC	PC1	PC2
						o	P49	1		53	46	P49	.70	.50	.21
						o	P48	5	4	54	37	P48	.55	.36	.20
						o	P47	-	1	63	36	P47	.75	.51	.17
						o	P46	2	1	47	50	P46	.75	.51	.18
					o	o	P45	1	5	66	28	P45	.66	.48	.20
					o	o	P44	1	10	65	24	P44	.73	.57	.17
					o	o	P43	4	1	87	8	P43	.57	.30	.24
					o		P42	100	-	-	-	P42	.37	.36	.33
					o	o	P41	70	-	26	4	P41	.66	.44	.24
					o		P40	100	-	-	-	P40	.51	.42	.33
					o		P39	100	-	-	-	P39	.43	.44	.30
					o		P38	100	-	-	-	P38	.38	.43	.41
					o		P37	100	-	-	-	P37	.41	.46	.34
				o	o		P36	100	-	-	-	P36	.73	.56	.29
				o	o		P35	100	-	-	-	P35	.57	.41	.30
				o	o		P34	100	-	-	-	P34	.66	.66	.21
			o	o			P33	100	-	-	-	P33	.59	.59	.25
				o			P32	89	11	-	-	P32	.88	.63	.19
			o	o			P31	88	12	-	-	P31	.87	.66	.17
			o	o			P30	80	20	-	-	P30	.85	.61	.20
			o	o			P29	50	50	-	-	P29	.72	.66	.12
			o	o			P28	20	45	-	35	P28	.54	.40	.27
			o				P27	5	95	-	-	P27	.48	.45	.24
			o				P26	-	76	-	24	P26	.41	.42	.24
			o				P25	-	100	-	-	P25	.45	.37	.33
		o	o				P24	-	100	-	-	P24	.40	.67	.15
		o	o				P23	1	99	-	-	P23	.69	.67	.13
		o	o				P22	-	36	1	63	P22	.57	.46	.16
		o	o				P21	-	45	1	54	P21	.46	.43	.17
		o		o			P20	-	39	-	61	P20	.59	.47	.19
		o		o			P19	-	63	-	37	P19	.63	.38	.25
		o	o	o			P18	-	42	-	58	P18	.56	.40	.21
		o	o	o			P17	2	98	-	-	P17	.63	.58	.16
		o	o	o			P16	1	99	-	-	P16	.60	.59	.17
		o	o	o			P15	-	100	-	-	P15	.55	.46	.22
		o	o	o			P14	-	53	-	47	P14	.61	.44	.24
		o	o				P13	-	5	-	95	P13	.42	.30	.26
			o				P12	-	16	-	84	P12	.58	.31	.25
			o				P11	-	66	-	34	P11	.60	.38	.24
	o	o	o				P10	4	30	8	58	P10	.41	.38	.32
	o	o	o				P09	42	6	14	38	P09	.53	.45	.22
	o	o					P08	47	1	19	33	P08	.64	.48	.24
	o	o					P07	57	3	9	31	P07	.77	.58	.16
	o	o	o				P06	22	3	18	57	P06	.63	.43	.22
	o	o					P05	65	3	9	23	P05	.74	.51	.21
	o						P04	96	-	3	1	P04	.33	.39	.25
	o	o	o				P03	67	9	13	11	P03	.70	.35	.30
	o	o	o				P02	88	-	12	-	P02	.73	.47	.24
	o	o	o				P01	82	-	14	4	P01	.82	.49	.21
	o						P00	100	-	-	-	P00	.47	.45	.36

preceding first or second whorl, respectively. As explained above, the dimensions of a keel were measured only when a keel was present, as a result the difference between specimens with and without a keel has been overemphasised. In their multivariate analyses Lindenberg & Mensink (1979) tried to reduce this influence by replacing the zero values, when a keel was not present, by a small, normally distributed, random value. This distorted the correlation with the other characters. In order to further reduce the influence of the mere presence/absence of a keel on the coefficient of overall similarity - four characters, i.e. 50% consist of features of the keels - Lindenberg & Mensink (1979) used only the first six characters (Table 2), leaving out the characters of the keel on the third whorl. Specimens with a short keel on the second whorl only, occur over a long range of samples, from P_{03} to P_{32} and then from P_{43} to P_{48}. Yet, a substantial number of specimens have a keel on the third whorl only. A consequence of the use of these six characters is that those specimens in the data set which have no keel on the second whorl, e.g. *G. tenuis*, *G. planorbiformis*, *G. sulcatus*, and *G. supremus* (Table 3b: column c), in this respect very much resemble the specimens of *G. kleini* and *G. revertens* which have no keel at all. Thus, by not including the keel on the third whorl, a taxonomic link may have been left out of the analyses.

The 'width' of a keel is the distance, measured perpendicular to the shell axis, between the most elevated part of the keel and the upper suture of the whorl. When a specimen has no keel, i.e. 'keel hight' = 0, its 'keel width' is considered missing and is left out of the calculation of the overall similarity.

For the present study, as in Lindenberg & Mensink (1979), the characters were standardised by ranging and the Euclidean Distance D, containing size and shape differences, was used as a measure of overall similarity. A UPGMA cluster analysis has a high cophenetic correlation with the similarity matrix and is more sensitive to the hierarchical differences between the clusters than to their densities (Fig. 1). The cluster analysis according to Ward's criterion (WARD) considers the within-cluster density also, by which it more directly identifies small spherical groups and may display a large ultrametric between-cluster distance (Fig. 2). For these reasons WARD was preferred as cluster analysis.

In addition to a dendrogram, the pattern in the Q-mode similarity matrix was also analysed by means of the scatterplot of the first two main axes (Fig. 3) obtained by a Principal Coordinate Analyses (PCOA). As it does not use a cluster criterion, a PCOA is not a cluster analysis. Moreover, it may not display the gaps between the clusters in the centre of the scatterplot as clear as at its periphery (Sneath & Sokal, 1973). However, the disadvantage of WARD is that it always shows 'distinct' clusters. By comparing the dendrogram with the scatterplot, it is possible to verify whether there is a gap in the distribution of the specimens (Fig. 3).

Sample P_{00}

A WARD dendrogram of the P_{00} sample, containing only specimens of *G. kleini*, showed various clusters. However, as the scatterplot of a PCOA of the Q-mode distance matrix showed a uniform distribution of specimens, the sample was considered homogeneous.

Samples P_{01}-P_{10}

The dendrogram and the PCOA scatterplot of P_{01} show a distinct grouping of the specimens into two main clusters with an ultrametric distance twice as large as that found in P_{00}. One cluster contains all but one specimen of *G. tenuis*, the other all the specimens of *G. steinheimensis* and a single *G. tenuis*. The main cause for this grouping is the presence or absence of a keel, viz. *G. steinheimensis* has no keel, whereas 14 specimens of *G. tenuis* have a keel at the third whorl, and four on the second and third whorl. Except for P_{04}, which contains only specimens of *G. steinheimensis*, both these types occur from P_{01} to P_{09}. In each sample two to ten specimens have been recognised by Mensink as transitions between the two. From P_{05} onwards, more and more specimens of *G. steinheimensis* exhibit a keel.

In P_{02}-P_{04}, and P_{06} some specimens of *G. sulcatus* occur, clustering with those of *G. tenuis*. From P_{09} onwards their number increases, P_{10} contains almost exclusively specimens of *G. sulcatus*, in addition to a few specimens which Mensink labelled *G. trochiformis* or *G. steinheimensis*. It is subdivided into five subclusters, consisting of a composite of the three last-mentioned taxa, depending on the presence or absence of a keel on the second and/or the third whorl. The PCOA scatterplot displays no clear gap in between the subclusters shown by WARD. From P_{10} onward almost all the specimens have a keel.

Samples P_{11}-P_{24}

From P_{11} to P_{13}, the samples are mainly composed of specimens of *G. planorbiformis*, some *G. sulcatus*, and transitional states to *G. trochiformis*. The dendrogram of P_{11} shows a similar subdivision of the subclusters as described for P_{10}. The PCOA scatterplots display two areas with a difference in density and without a gap in between, those of P_{12} and P_{13} are completely homogeneous. In P_{12} and P_{13}, the amount of specimens with a keel on both whorls increases, whereas in P_{14} it decreases again (Table 3). P_{15}-P_{17} contain only specimens with a keel on the second whorl. The subdivision into clusters is mainly due to the increase of the height of the shell (Table 2: characters 1 and 3) in one of the clusters. In P_{18}-P_{21} the subdivision is likewise mainly caused by specimens with a planispiral shape which have a keel on the second and third whorl, or on the second whorl only. In P_{22} the subdivision into trochospiral and planispiral shapes reappears. P_{23} and P_{24} have a few specimens labelled *G. sulcatus*, which are clustered together with other planispiral specimens of *G. planorbiformis*, or its transitions to *G. trochiformis*.

Samples P_{25}-P_{36}

Although P_{25}-P_{29} contain a mix of specimens with a keel on the second, the third, or on both whorls, they show dendrograms with homogeneous clusters. Next to clusters with *G. trochiformis*, P_{27} has four specimens labelled *G. oxystoma* in a single cluster. In P_{28} the distinctness of the clusters of these forms is obvious. The number of specimens of *G. oxystoma* increases, whereas that of *G. trochiformis* decreases. In P_{33} only specimens of *G. oxystoma* occur, while in P_{34} specimens of *G. revertens* and transitions of *G. oxystoma* to *G. revertens* occur. The clustering of the specimens of both forms is almost homogeneous. The difference between the forms lies in the fact that *G. revertens* is smaller and flatter than *G. oxystoma*.

Samples P_{37}-P_{49}

In P_{37}-P_{40} and P_{42} only *G. revertens* occurs. In P_{41} the specimens of *G. supremus*, having a keel on the third or the second and third whorl, are clustered together apart from the specimens of *G. revertens*. In P_{43}-P_{45} a few transitions of *G. revertens* to *G. supremus* occur; all of these have a keel, but they are not homogeneously grouped. The main clusters that can be recognised are caused by specimens having a keel on the third whorl, or on the second and third whorl. The dendrograms of P_{46}-P_{49}, having only specimens of *G. supremus*, display the same division. Specimens which have no keel are grouped with those which have a keel on the third whorl only, whereas specimens which have a keel on the second whorl are grouped with those having a keel on both the second and third whorl.

Information reduction and the arrangement of the samples

In order to reduce the variability and the number of items in the analyses, each

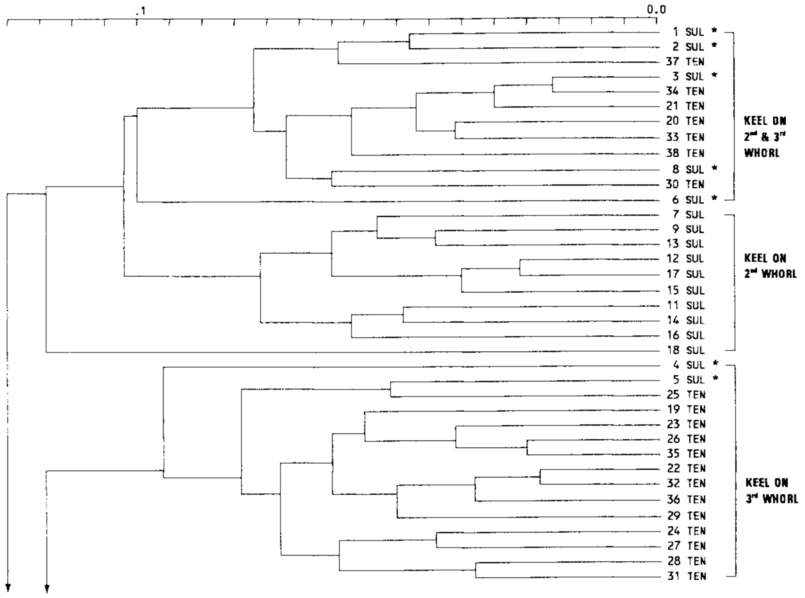
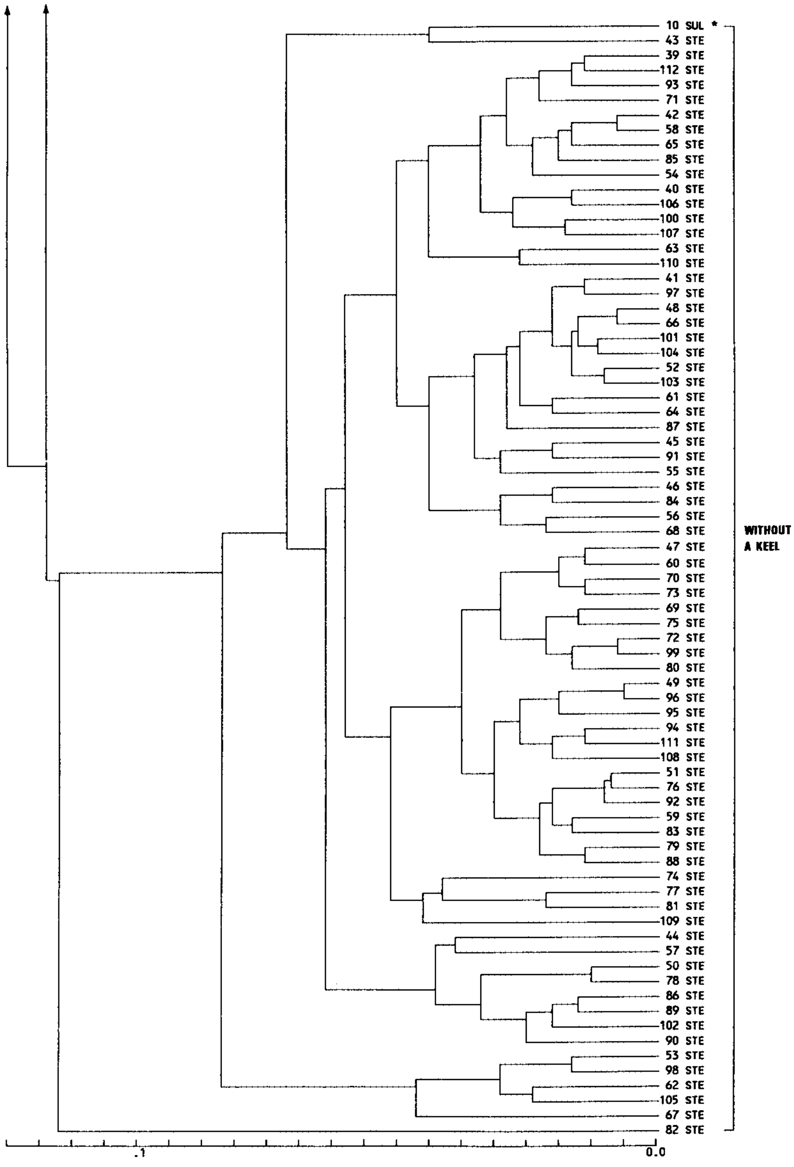


Fig. 1. UPGMA dendrogram of Euclidean distances D between specimens of sample P_{03}. The first main branch has two subclusters, one containing specimens with a keel on the second and third whorl, the other with specimens with a keel on the second whorl only. Furthermore, an isolated specimen is present with a similar position of the keel. The other main branch has a subcluster with specimens with a keel on the third whorl, and a subcluster with specimens with no keel at all. Abbreviations of the specific names as given in Table 1. Cophenetic correlation = 0.82.

cluster of specimens was described by its centroid, i.e. the average value of each character. In the samples 135 clusters were recognised, a smaller number than in Mensink (1984). In a subsequent step an effort is made to represent the relationships between the multidimensional centroids in a single figure. The histograms shown by Mensink (1984) are oriented 'horizontally' relative to the origin of their scale. In order to obtain a more or less similar condition, but now using the overall similarities between the centroids instead of a single character, the similarity of each centroid was calculated relative to a single example. The centroid of sample P_{00}, containing specimens of the uncarinated, small, and planispiral *G. kleini* was chosen as a reference. The similarities, represented by the abscissa, were ranged between 0, i.e. equal



to *G. kleini*, and 1. Next, the similarities of the 50 samples were arranged in a vertical manner by representing them according to their relative position in the sedimentary sequence (Fig. 4). In this way a graph was constructed which to some extent resembles the one made by Mensink for the frequency distributions of each character.

The correlations between the characters (Table 4) show a grouping into two independent clusters, one for the characters of the whorls, and one for the keels (Table 2). Also, because the X-axis displays the overall similarity relative to P_{00}, it may represent various factors, depending on the loadings of the characters. From P_{01}-P_{10} this factor will be the presence/absence of a keel. From P_{14}-P_{32}, the component is the height of the whorls, from P_{32}-P_{40} the width of the whorls and whether the planispiral shell is smooth or not; from P_{41}-P_{49} the presence of a keel again plays an important role.

The way the keel was measured influenced the WARD cluster analyses and the overall similarity of the centroids relative to P_{00}. These characters have a large weight. In those instances where the centroids contain specimens of either with or without a keel, the scatterplot displays an abrupt gap between the taxa (e.g. P_{00} to P_{11} in the scatterplot of Fig. 4). However, the clusters of *G. tenuis* and *G. sulcatus* in P_{05} to P_{10} which very much resemble that of P_{00}, contain mainly small specimens (P_{05}, P_{06}, P_{08}, and P_{09}). Moreover, some of the clusters are a mix of specimens of *G. steinheimensis* which have no keel (P_{07}, and P_{10}). Those clusters of which the specimens have a

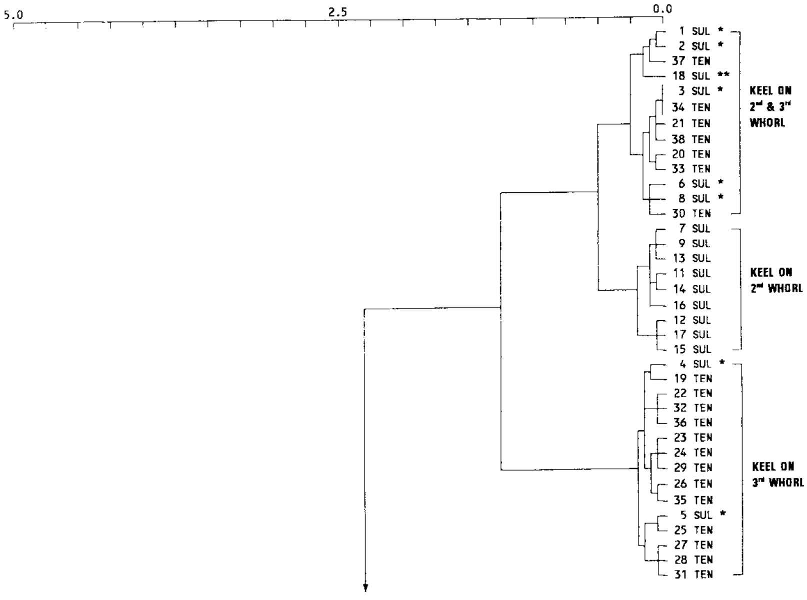


Fig. 2. WARD dendrogram of Euclidean distances D between specimens of sample P_{03}. The specimens of the first main branch have a keel on the second or third whorl, those of the second branch are uncarinated (*G. steinheimensis*). Type 1 = specimens with a keel on the second and third whorl: 6 of *G. sulcatus* (*), one having a keel on the second whorl (**), and 7 specimens of *G. tenuis*; type 2 = *G. sulcatus*, having a keel on the second whorl; type 3 = *G. tenuis*, having a keel on the third whorl. Abbreviations of the specific names as given in Table 1. Cophenetic correlation = 0.70.

keel on the second and third whorl are mainly located at the outer margin of each sample and have been marked by a dot in Fig. 4. From P_{11} to P_{26} almost all clusters have keeled specimens (Table 3). In this period a further increase of the height of the shells occurs, starting in character 3 (P_{15}) and later also in character 1 (P_{22}), which gives a further increase of the spread along the X-axis of the trochospiral *G. trochiformis*. Except for P_{23}, which has a main cluster of specimens of *G. sulcatus* mixed with three specimens of *G. planorbiformis*, specimens of *G. sulcatus* which occur in P_{13} to P_{15}, P_{17}, and P_{24} are heterogeneously grouped with the other clusters of *G. planorbiformis*. The differentiation of the uncarinated, planispiral *G. oxystoma*, starting in P_{27},

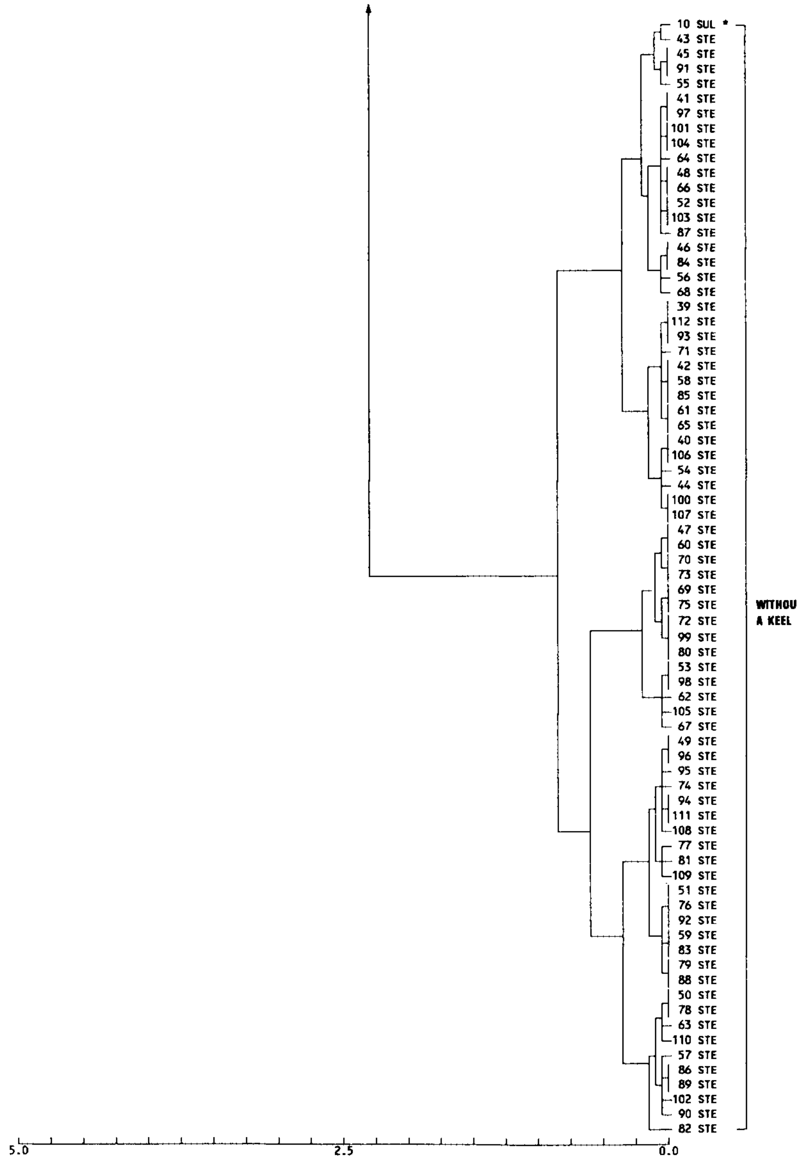


Table 4. Correlation coefficients between the characters of the data set of the centroids.

	Character	Correlation Coefficient							
1.	Height 1st whorl	1.							
2.	Width 1st whorl	0.100	1.						
3.	Height 2nd whorl	0.442	0.270	1.					
4.	Width 2nd whorl	0.033	0.631	0.295	1.				
5.	Height keel 2nd whorl	0.010	-0.084	0.123	0.210	1.			
6.	Width keel 2nd whorl	-0.145	-0.303	-0.249	-0.307	0.036	1.		
7.	Height keel 3rd whorl	0.109	-0.296	-0.016	-0.374	0.275	-0.027	1.	
8.	Width keel 3rd whorl	-0.108	-0.090	-0.332	-0.214	-0.135	0.087	0.458	1.

again shows a gap between the clusters with transitions of *G. planorbiformis* to *G. trochiformis*, which both have a keel.

From P_{34} to P_{42} *G. oxystoma* splits up into the smaller and flatter *G. revertens*. From P_{41} onwards *G. supremus*, which has a keel, splits up from *G. revertens*. As explained above, because *G. revertens* has no keel the distribution of the clusters of *G. revertens* and *G. supremus* shows a large gap.

Lindenberg & Mensink (1979) stated that from P_{00}-P_{10} specimens of *G. kleini* occur. However, in the data set the sample of P_{00} is the only one which comprises specimens of this form. It may be concluded from the large similarity between the clusters of *G. steinheimensis* and *G. kleini*, that some of the uncarinated *G. steinheimensis* specimens have been later recognised as *G. kleini*, without changing their labels in the data set. I suspect that this may also have happened with other specimens, e.g. *G. sulcatus*.

The specimens which have been recognised as *G. sulcatus* by Mensink are only labelled as such, i.e. they have not been characterised in the data set by their second keel and angular shape. Because of this lack of information and because the results of the multivariate analyses are based solely on the few available characters in the data set, the dendrograms and scatterplots of the PCOA and Fig. 4 do not show a clear differentiation of this taxon. From P_{02} to P_{10} specimens of *G. sulcatus* are mixed mainly with those of *G. tenuis*. From P_{12} to P_{24} they are mixed with those of *G. planorbiformis*. On the basis of an analysis of the centroids using only characters 1-4 (Table 2), thus excluding the factor of the keel characters, it was clear that centroids labelled pla and *SUL* (Table 1; Fig. 4) are very similar to the centroid of P_{00} and grouped together, showing a gap between the centroids labelled p-T and **TRO** both of which have a - more or less - trochospiral shape. Hence, it seems reasonable to join the transitions of p-T and **TRO** into *G. trochiformis*. As it is not clear from the characters how a transition from the typical *G. sulcatus* characters to those of *G. planorbiformis* takes place, it remains questionable from these results whether these two taxa should be joined, as Mensink proposes.

During the development of these forms, there are certain moments at which their variability increases, after which a differentiation occurs (Mensink, 1984: 37-45). It has been checked whether this variation is also shown by the percentage of explained variation by the first two principal axes of a PCOA (Table 3). In P_{10}-P_{13} the PCOA shows a decrease in overall variability, whereas from P_{14} onwards, i.e. the transition from planispiral to trochispiral specimens, it increases. However, in the other cases mentioned by Mensink (1984) this change in overall variability is less clear.

Concluding remarks

The analysis of the way a keel occurs on the second or third whorl and the bivariate presentation of these characters, displayed new information which otherwise could not be made clear from the histograms or landscape-like graphs of Mensink (1984). The characters displayed in a bivariate way show a gradual incline and decline of the number of specimens with a keel in the subsequent samples (Table 3). Since the presence of a keel on the second or third whorl is of some significance for explaining the differentiation of the taxa in the course of time, it was valuable to use all these characters in a multivariate analysis. However, the fact that no measurements of the height relative to the preceding whorl are available of specimens in which a keel is absent remains a drawback of the informational contents of the data set.

The WARD cluster analyses in combination with the PCOA scatterplots were

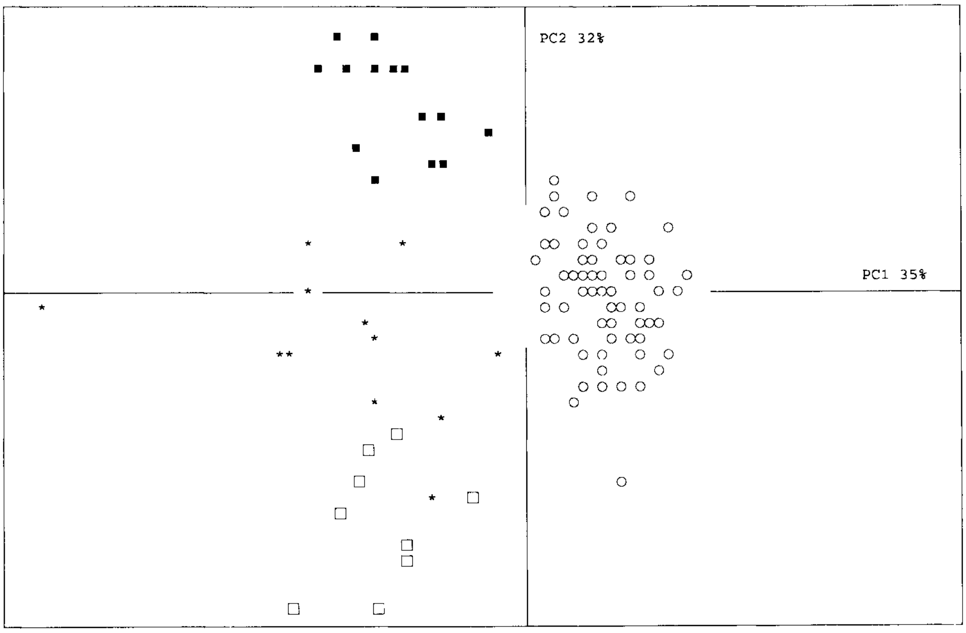


Fig. 3. PCOA Scatterplot of the first two main axes of a Principal Coordinate Analysis. The analysis is based on the Euclidean distances D between specimens of sample P_{03}. The specimens are labelled according to the WARD cluster analysis (Fig. 2). Specimens which have been given * (type 1), □ (type 2), and □ (type 3) are subclusters of the first main cluster, specimens of the second main cluster are indicated by O (type 4). The difference between the first and second main cluster is because the specimens of the first have a keel, and those of the second have not, viz. the dispersion of the specimens by PC_1. The dispersion by PC_2 is mainly caused by the presence/absence of a keel on the second or third whorl. Half the amount of specimens of subcluster 1 comprises both *G. tenuis* and *G. sulcatus*, having a keel on the second and third whorl. Subcluster 2 contains only *G. sulcatus* with a keel on the second whorl. Subcluster 3 contains specimens of *G. tenuis* and a single *G. sulcatus* with a keel on the third whorl. The second main cluster contains exclusively unkeeled specimens of *G. steinheimensis*. Types 1-3 as in Fig. 2.

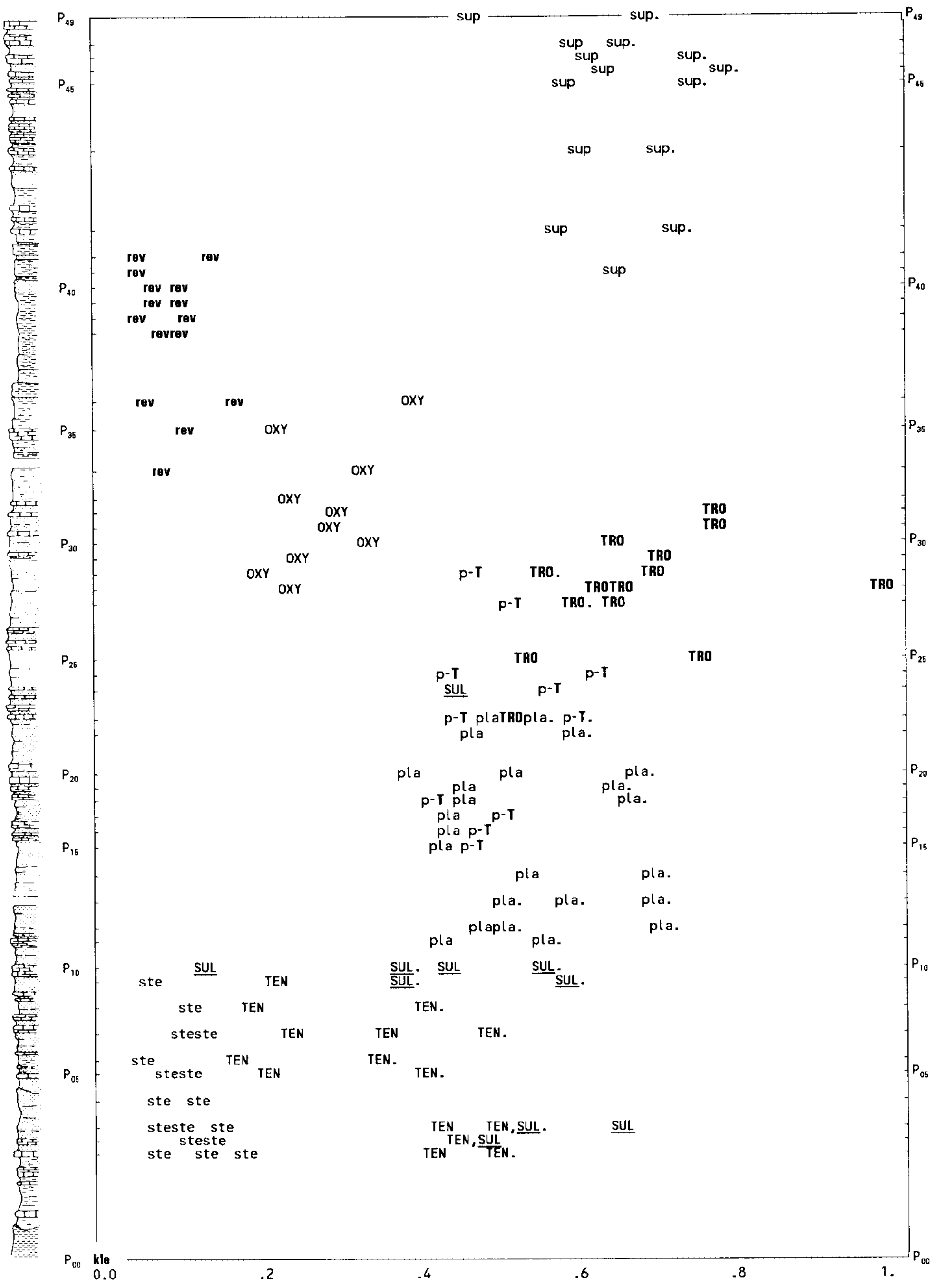
helpful tools to detect clusters in the samples. However, the state of Mensink's data set permits only a limited conclusion by means of a multivariate approach. The number of continuous characters is small. Much information which lies in the delicate, smooth and gradually changing outline of the surface of a whorl is lost, when but a simple 'height' or 'width' of such a complex structure is measured. Moreover, a lot of specimens show transitions from one stage into another by which the scarce informational contents of the few characters do not permit a sharp delimitation of the taxa. Another problem is that for some specimens (P_{01-10}) the a-priori identification showed to be questionable, which makes the results not always reliable in a taxonomic sense.

Generally speaking the results of the upper half of Fig. 3 of the present study agree with Mensink's results. In the samples which contain specimens of *G. planorbiformis*, *G. trochiformis*, and the transitions between the two, those with a trochispiral shape are rather well distinguished by the analyses. This may correspond with Mensink's statement that *G. oxystoma* developed from *G. sulcatus*, and that from *G. sulcatus* the line continues via *G. planorbiformis* to *G. trochiformis*. However, since in each sample of P_{11-28} distinct clusters of planispiral and trochispiral shells occur, contrary to Mensink's suggestion these two taxa have not been fused.

It has been observed that the presence or absence of a keel on the third whorl yields more information on the differentiation of *G. tenuis* relative to *G. steinheimensis*. It may be concluded from the consistent way these two taxa have been described in the data set and the separate way they behave in the analyses, that they are distinct. As mentioned above, it may also be that some of these specimens are incorrectly labelled. However, judging from the present results only, they are not similar and therefore they are not fused into a single taxon, e.g. *G. steinheimensis*.

Contrary to Mensink (1984) no specimens labelled as *G. kleini* were found in P_{01-10}. It may be that some specimens are not correctly labelled or that characters 1-4 contain insufficient information to distinguish between *G. kleini* and *G. steinheimensis*. Moreover, the delimitation of the *G. sulcatus* taxon remains uncertain on the basis of the dataset alone. To obtain a better understanding of the distinction and differentiation of all these taxa, the information of their descriptions should be extended. To describe the outline of the gradually curving surface of a whorl of a planorbid shell by a few continuous characters showed to be unreliable. In order to obtain a more stable estimate of overall similarity between the specimens it would be a better approach to base this on many measurements from several landmarks (Povel, 1992; Verduin, 1982).

Fig. 4. Scatterplot of the centroids. The X-axis represents the Euclidean distance D, ranged between 0 and 1, of the centroids relative to the centroid of P_{00}. The Y-axis shows the subsequent positions of the samples P_{0-49} according to their position in the stratigraphic succession, with the same distance between the samples as in Mensink (1984; Figs. 24 & 25). The differentiation from *G. planorbiformis* into *G. trochiformis* is by an increase of character 3 followed by an increase of character 1 (see Table 2). Therefore, those pla/**TRO** clusters which are planispiral are labelled pla, those which show an increase of character 3 are labelled p-T, and those which show an increase of character 1 and 3 **TRO**. A dot behind a label of a centroid indicates that the specimens have a keel on the second and third whorl (Table 3). Abbreviations of the specific names as given in Table 1.


P49
sup sup.
sup sup.
sup sup.
sup sup.
sup sup.
P45
sup sup.
sup sup.
rev rev
rev
rev rev
rev rev
rev rev
revrev
sup
P40
rev rev OXY
rev OXY
P35
rev OXY
OXY
OXY
OXY
OXY
OXY
OXY
OXY
TRO
TRO
TRO
TRO
TRO
p-T TRO.
TROTRO
TRO
p-T TRO. TRO
P30
TRO TRO
p-T p-T
SUL p-T
P25
p-T plaTROpla. p-T.
pla pla.
pla pla pla.
pla pla.
p-T pla pla.
pla p-T
pla p-T
pla p-T
P20
P15
pla pla.
pla. pla. pla.
plapla. pla.
pla pla.
SUL SUL. SUL SUL.
ste TEN SUL. SUL.
ste TEN TEN.
steste TEN TEN TEN.
P10
ste TEN TEN.
steste TEN TEN.
ste ste
steste ste TEN TEN,SUL. SUL
steste TEN,SUL
ste ste ste TEN TEN.
P05
P00
kle
0.0
.2
.4
.6
.8
1.

Acknowledgements

I am much indebted to the members of the Department of Palaeontology at Bochum University (Germany), for their kind support by making Mensink's collection and data set available to me. Special thanks are given to Professor R. Belov for his interest and efforts to provide as much information as possible on this subject. Also H. van Bostelen is acknowledged for his efforts to check the data sets, arrange these in computer files, and perform some initial analyses.

References

Gorthner, A., & C. Meier-Brook, 1985. The Steinheim Basin as a paleo-ancient lake. In: U. Bayer, & A. Seilacher, (eds). Sedimentary and evolutionary cycles. — Springer, Berlin etc.: 322-334.

Hilgendorf, F., 1866. *Planorbis multiformis* im Steinheimer Süszwasserkalk. Ein Beispiel von Gestaltveränderung im Laufe der Zeit. — W. Weber, Berlin: 1-36.

Hogeweg, P., & B. Hespers, 1972. Program system for bioinformatic pattern analysis (BIOPAT). — Bioinformatica Dept., Utrecht Univ. (unpublished internal communication).

Lindenberg, H.G., & H. Mensink, 1979. Multivariate Gruppierungsmethoden in phylogenetisch orientierter Paläontologie. (Am Beispiel von Gastropoden aus dem Steinheimer Becken). — Berliner geowiss. Abh., A, 15: 30-51.

Mensink, H., 1984. Die Entwicklung der Gastropoden im Miozänen See des Steinheimer Beckens (Süddeutschland). — Palaeontographica, A, 183: 1-63.

Nützel, A., & K. Bandel, 1993. Studies on the side-branch planorbids of the Miocene crater lake of Steinheim am Albuch (southern Gemany). — Scripta Geol., Spec. Issue, 2: 00-00.

Povel, G.D.E., 1992. Preliminary report on the multidimensional patterns occurring in continuous characters of *Albinaria* shells. In: C. Meier-Brook (ed.). Proceedings of the Tenth International Malacological Congress, Tübingen, 1989. — Unitas Malacologica, Tübingen: 141-146.

Sneath, P.H.A. & R.R. Sokal, 1973. Principles and practice of numerical taxonomy. — Freeman, San Francisco: i-xiii, 1-573.

Verduin, A., 1982. How complete are diagnoses of coiled shells of regular build? A mathematical approach. — Basteria, 45: 127-142.

Manuscript received 19 February 1993, revised version accepted 24 April 1993