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SHAPE VARIATION IN *SPIROPLECTAMMINA SPECTABILIS* (GRZYBOWSKI)

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The morphology and intraspecific variation of *Spiroplectammina spectabilis* (Grzybowski) is investigated based upon topotype material. Linear measurements and eigenshape analyses of species of *Spiroplectammina* described from California show them to be conspecific with *S. spectabilis*. Two ecophenotypic forms are distinguished: *S. spectabilis* forma *trinitatensis* — a robust Eocene variety, and *S. spectabilis* forma *perplexa*, a minute, compressed form.

Key words: *Spiroplectammina spectabilis* (Grzybowski), morphology, variation, eigenshape analysis, Paleogene, Carpathians.

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INTRODUCTION

Spiroplectammina spectabilis (Grzybowski) originally described from Paleogene flysch deposits from the Carpathian Geosyncline, is a useful Maastrichtian — upper Eocene stratigraphic and paleobathymetric marker for deep sea sediments. However, this species has been a source of taxonomic confusion for a number of years due to the wealth of junior synonyms described in the literature, owing to its variable morphology.

Grzybowski (1898, 1901) described a number of forms that are now considered synonymous to *S. spectabilis*, and later American workers, i.e. Cushman (1928, 1934), Cushman and Campbell (1934), Lalicker (1935), Cushman and Siegfus (1939), Cushman and Renz (1948), Frizzel (1943), Israelsky (1951) and Todd and Kniker (1952) added more names to the list. Hiltermann (1972) gives a detailed review of the morphology, stratigraphic distribution and paleoecology of *S. spectabilis* based upon topotypes from the Carpathian flysch.

The aims of this study are to provide explanations to certain taxonomic problems by assessing the intraspecific variation within an assemblage of Carpathian topotypes, employing data from Hiltermann (1972), and comparing their morphology with topotypes from American localities and from the deep sea.

METHODS

Linear measurements of specimens housed at the U.S. Natural History Museum in Washington, D.C. were made by means of an optical micrometer, and statistical tests were performed on obtained data. Computational formulae for Analysis of Variance, Tukey-Kramer and Student's t-tests were taken from Sokal and Rohlf (1981).

The shapes of outlines of specimens (observed shapes) were investigated by the use of eigenshape analysis, a morphometric procedure developed by G.P. Lohmann at the Woods Hole Oceanographic Institution. The merits of this method lie in its ability to organize sets of microfossil outlines according to similarities and differences in their shape. Methodology is described in greater detail by Lohmann (1983) and Lohmann and Malmgren (1983).

Essentially, to register shapes of *S. spectabilis*, laterally oriented specimens are viewed through a video camera mounted on a petrographic microscope, and their outlines are digitized by a microprocessor-controlled video image digitizer, a system developed by Fico (1980). Shape of the specimens is represented by the normalized shape function $\phi^*[1]$ of Zahn and Roskies (1972) which is the net angular change in direction ϕ at each step around the perimeter [1] of a closed form. Comparison of outlines is achieved by rotating shapes of individuals, represented by their shape functions, to positions of maximum similarity. Shape differences between compared outlines were analyzed using eigenshape analysis, which is mathematically almost identical to an R-mode principal components analysis.

The first eigenshape is an average of all the real shapes in the sample. The principal dimension of shape variation about the average is revealed by the 2nd eigenshape. This can be used to register intraspecific variation, either attributable to ontogenetic growth, or to different ecophenotypes. Variation between individuals within a sample can be assessed by calculating the percentage of variance represented by each eigenshape and by the amount of correlation of observed shapes with the eigenshapes. To investigate variability between samples, another eigenshape analysis is performed on the first eigenshapes of each sample. The second eigenshape of the subsequent analysis then quantifies the variability between samples.

Electron micrographs were made on a JOEL-U3 Scanning Electron Microscope.

Spiroplectammina spectabilis (Grzybowski) 1898
(pls. 12 and 13; figs. 1—4)

1898. *Spiroplecta spectabilis* Grzybowski: 293, pl. 12: 12.
1898. *Spiroplecta brevis* Grzybowski: 293, pl. 12: 13.
1898. *Spiroplecta foliacea* Grzybowski: 294, pl. 12: 14, 15.
1898. *Spiroplecta costidorsata* Grzybowski: 294, pl. 12: 11.
1901. *Spiroplecta clotho* Grzybowski: 224, pl. 8: 18.
1928. *Spiroplectoides clotho* (Grzybowski) Cushman et Jarvis; 101, pl. 14: 13, 14.
1928. *Spiroplectoides clotho* (Grzybowski) Cushman; 159, pl. 28: 6.
1934. *Spiroplectoides clotho* (Grzybowski) Cushman; 42, pl. 6: 19—23.
1934. *Spiroplectoides californica* Cushman et Campbell: 70—71, pl. 9: 15, 17.
1934. *Spiroplectoides spectabilis* (Grzybowski); Cushman: 43, pl. 6: 25—26.
1935. *Bolivinopsis clotho* (Grzybowski) Nuttall; 125—126, pl. 14: 23, 23.
1935. *Spiroplectammina mexiaensis* Lalicker: 43, pl. 6: 5, 6.
1937. *Bolivinopsis spectabilis* (Grzybowski); Glaessner: 364, pl. 2: 13, 14.
1939. *Spiroplectoides directa* Cushman et Siegfus: 26, pl. 6: 7, 8.
1943. *Spiroplectammina grzybowski* Frizzel: 339, pl. 55: 12a, b, 13. (with synonymy).
1946. *Spiroplectammina grzybowski* Frizzel; Cushman et Renz: 20, 5: 34—38.
1947. *Spiroplectammina grzybowski* Frizzel; Cushman: 5—6, pl. 4: 12, 13.
1948. *Bolivinopsis directa* (Cushman et Siegfus); Cushman et Renz: pl. 5: 6.
1948. *Spiroplectammina trinitatensis* Cushman et Renz: 11, pl. 2: 13, 14.
1949. *Spiroplectammina trinitatensis* Cushman et Renz; Cushman et Stone: 76, pl. 13: 17.
1951. *Spiroplectammina perplexa* Israelsky: 12—13, pl. 3: 9—14.
1952. *Spiroplectammina brunswickensis* Todd et Kniker: 6—7, pl. 1: 16.
1953. *Bolivinopsis trinitatensis* (Cushman et Renz); Beckmann: 339, pl. 17: 1, 2.
1959. *Spiroplectoides directa* Cushman et Siegfus; Mallory: 116, 117, pl. 3: 5.
1959. *Spiroplectammina grzybowski* Frizzel; Mallory: 117, pl. 3: 3.
1960. *Spiroplectammina spectabilis* (Grzybowski); Geroch: 56, pl. 6: 10, 11, pl. 10: 12.
1962. *Spiroplectammina spectabilis* (Grzybowski); Hillebrandt: 32, pl. 2: 26, 27.
1964. *Spiroplectammina perplexa* Israelsky; Martin: 51, pl. 2: 14a, b.
1964. *Bolivinopsis spectabilis* (Grzybowski); Kisselman: *in*: Subbotina: 191—193. pl. 26: 20—23. (with synonymy)
1966. *Spiroplectammina spectabilis* (Grzybowski); Huss: 39, pl. 6: 13, 14.
1969. *Bolivinopsis spectabilis* (Grzybowski); Hanzliková: 22, pl. 2: 12.
1970. *Spiroplectammina clotho* (Grzybowski); Mjatliuk: 100—101, pl. 30: 3a, b, 4.
1970. *Spiroplectammina spectabilis* (Grzybowski); Mjatliuk: 101—103, pl. 10: 15, pl. 30: 5a, b, 6, 7.
1972. *Spiroplectammina spectabilis* (Grzybowski); Hiltermann: 43—61, pl. 1, 2. (with synonymy).
1972. *Bolivinopsis spectabilis* (Grzybowski); Hanzliková: 48, pl. 10: 8.
1973. *Bolivinopsis trinitatensis* (Cushman et Renz); Douglas: pl. 3: 4.
1974. *Spiroplectammina spectabilis* (Grzybowski); Szczechura et Pożaryska: 30—31, pl. 1: 1—4.
1978. *Bolivinopsis spectabilis* (Grzybowski); Decima et Bolli: 790, pl. 1: 3.
1981. *Spiroplectammina spectabilis* (Grzybowski); Gradstein et Berggren: 260, pl. 4: 1—5.

1981. *Spiroplectammina spectabilis* (Grzybowski); Morgiel et Olszewska: 16, pl. 4: 1, 2.
1982. *Spiroplectammina spectabilis* (Grzybowski); Beckmann *et al.*: pl. 6: 19, 20.
1982. *Spiroplectammina spectabilis* (Grzybowski); Miller *et al.*: 22, pl. 2: 2, 3.
1983. *Spiroplectammina directa* (Cushman et Siegfus); Berggren et Aubert: pl. 1: 7, 8.
1983. *Bolivinopsis spectabilis* (Grzybowski); Tjalsma et Lohmann: pl. 1: 11, pl. 9: 8—10.
non 1976. *Bolivinopsis spectabilis* (Grzybowski); Rögl: pl. 3: 23—25.

Description

The test is free, generally large for the genus, with an initial planispiral coil, followed by a longer biserial arrangement of chambers. The planispiral part is large in macrospheric generation, with 4—7 chambers, may have depressed umbo and may be wider than the subsequent biserial part. Microspheric forms possess a minute initial spire which is normally somewhat broader than the initial portion of the biserial part. The biserial part in the microspheric generation initially increases gradually in size, later with nearly parallel sides, and generally possesses lower and more numerous chambers than the macrospheric form. The biserial part in both generations is rhomboid in cross-section, consists of up to 36 chambers in the adult, possesses nearly parallel sides, and may decrease in breadth toward the apertural end. Sutures are normally flush or slightly depressed, may become slightly limbate, and in the biserial part are inclined to the longitudinal axis approx. 60°. Sutures are curved in the spiral portion of the macrospheric generation, and may be slightly raised and may end in a small spinal process. The peripheral margin is acute, generally straight in the biserial portion, but may be weakly keeled or dentate in extreme forms. The wall is finely finished, predominantly silicious-arenaceous, and imperforate. The apertural end is sub-angular. The aperture is in the form of a narrow slit at the base of the last chamber.

DISCUSSION

Grzybowski (1898, 1901) described five species of *Spiroplecta* from the Eocene of the Carpathian flysch which later workers considered representing a plexus of forms. These are shown in fig. 1, along with species concepts according to various authors.

Figure 1 illustrates that different combinations of the above forms have been collectively called *S. spectabilis* by different authors. Confusing matters more is the fact that early investigators used the specific designation *clotho* for forms synonymous with *S. spectabilis*. Cushman (1927, 1934), Cushman and Jarvis (1928, 1932) and White (1929) described forms from the Paleocene of Trinidad and the Velasco Shale as *Spiroplectoides*(?) *clotho* (Grzybowski), and Nuttall (1935) placed specimens from the upper Eocene Pauji Shale of Venezuela as well as Cushman's forms in *Bolivinopsis clotho*. These were considered to contain microspheric forms similar to *Spiroplecta foliacea* and *S. clotho* (fig. 1) and macrospheric forms resembling *S. spectabilis*. However, the specific designation *S. clotho* was erected three years later than *S. spectabilis*, and the above authors were wrong in applying this name to forms with large initial spires. Moreover, Cushman (1934) separates *S. clotho* from *S. spectabilis*, even though he considered the former to possess a macrospheric form with an overall morphology identical to *S. spectabilis*, albeit of smaller dimensions. Mjatliuk (1970) recognizes Cushman's designation and illustrates specimens of *S. clotho* (Grzybowski) from the (?)Paleocene of the Eastern Carpathians. These specimens most closely resemble *S. foliacea* Grzybowski, and here are included in *S. spectabilis* (microspheric forms). In this study, no microspheric individuals of *S. spectabilis* were found that are as broad as the specimen of *S. clotho* illustrated by Grzybowski (1901), nor were such forms encountered in the literature. Similarly, the holotype of *S. foliacea* represents an end member in Hilterman's (1972: fig. 1) plot of the ratio of width/length vs. number of chambers. It appears that most microspheric forms possess a biserial part that is intermediate in width between that of *S. clotho* Grzybowski and *S. foliacea* Grzybowski.

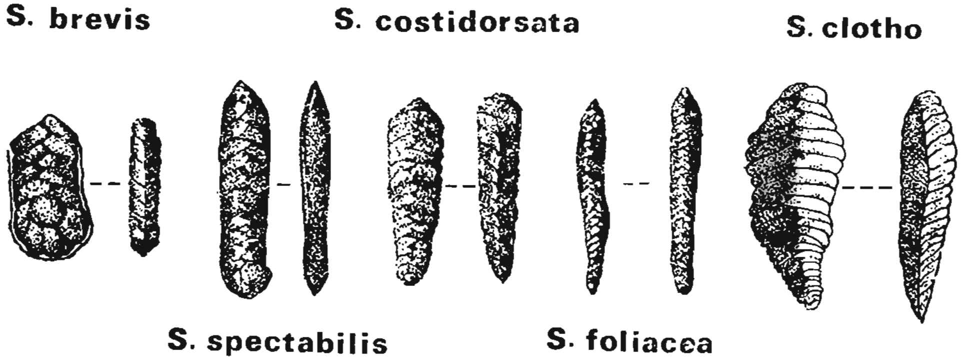

Fig. 1. Five species of *Spiroplecta* described by Grzybowski [redrawn after Grzybowski 1898, 1901], all considered synonymous to *Spiroplectammina spectabilis* in this study. Also listed are taxa placed in *S. spectabilis* by previous authors.

Author:	Species Concept:
Cushman (1934)	*brevis, spectabilis*
Glaessner (1937)	*brevis, spectabilis, foliacea*
Maslakova (1955)	*brevis, spectabilis, clotho*
Kisselman (1964)	*brevis, spectabilis, foliacea, clotho*
Mjatliuk (1970)	*brevis, spectabilis, foliacea, ?clotho*
Hiltermann (1972)	*brevis, spectabilis, foliacea, clotho*

Two species of *Spiroplectoides* (*recte Spiroplectammina*) and one species of *Spiroplectammina* have been described from deep-water sediments of California which fit within the morphologic variation of *S. spectabilis*, and therefore must be considered synonymous. These are: *S. californica* Cushman et Campbell, *S. directa* Cushman et Siegfus, and *S. perplexa* Israelski. Measurements of the type series of species housed at the U.S. Natural Museum are presented in table 1. The stratigraphy of the type formations is shown in fig. 2.

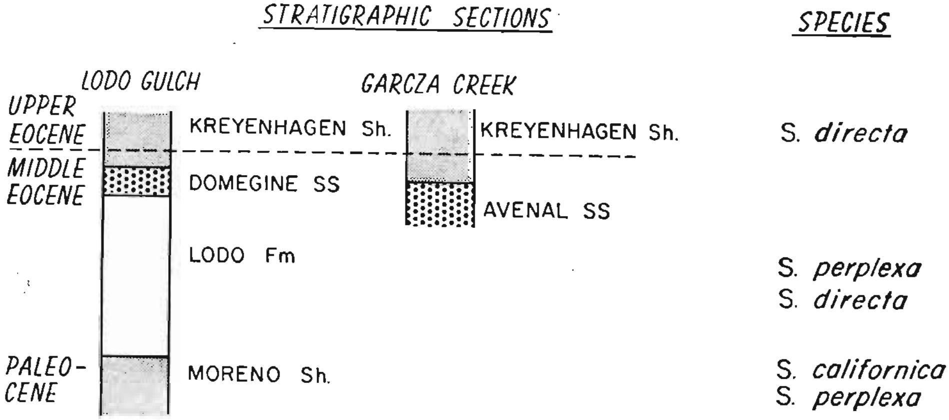

Fig. 2. Stratigraphy of the Californian type formations for *S. californica*, *S. directa* and *S. perplexa*, after Poore (1976).

Spiroplectoides california Cushman and Campbell (1934), from the Chico Fm. at Devils Den and Moreno Shale of California, reportedly possesses a siliceous-arenaceous wall, and "is allied to species from Trinidad and Mexico". Comparing *S. californica* with *S. clotho* (Grzybowski) *sensu* Cushman, Cushman and Campbell maintained that the chambers of this form are not as low and broad as in the latter species, and that the microspheric form is not so definitely lance-shaped. *S. californica* was described as "varying in thickness at the apertural end, which becomes as thick as broad", but close examination of type specimens reveals that in each case maximum thickness is less than max. width of the biserial portion of the test. The holotype (Cushman Collection No 21294) is .28 mm in breadth and .21 mm in thickness, and the four paratypes are even thinner with regard to width. A Tukey-Kramer test of the means in table 1 indicates that the type series from California does not differ significantly from specimens of *S. spectabilis* from Znicz, Witryłów and Biecz.

Spiroplectoides directa was described by Cushman and Siegfus (1939) from the middle-upper Eocene Kreyenhagen Shale near upper Garza Creek, California. This species was reported to possess a relatively thin, perforate, "calcareous" wall, but the holotype (Cushman Coll. 25445) is translucent, and apparently siliceous-arenaceous. A Student's t-test of measured parameters does not reveal any significant differences ($P < .1$) between the holotype and specimens from the Moreno Shale measured in this study. Cushman and Siegfus (1939) report the aperture as terminal, but the holotypes depicted in pl. 6, figs. 7, 8 are apparently broken at the apertural end, thus giving the aperture the appearence of being in a terminal position. This designation was also used by Cushman and Renz (1948) to describe Eocene forms from Trinidad. The single archived specimen from the Navet Fm. is nearly indistinguishable from the holotype, possessing equal number of chambers, and being only .04 mm longer, .03 mm wider and .01 mm thicker.

Spiroplectammina perplexa Israelsky (1951) was described from the Lodo Fm. of California, which occupies a stratigraphically intermediate position between the Moreno and Kreyenhagen Shales (fig. 2). Israelsky reported the occurrence of this form throughout the lower half of the Lodo Fm. On the other hand, Berggren and Aubert (1983) place specimens from Zone P 10 of the lower Lodo Fm. in *S. directa*. Both Israelsky (1951) and Martin (1964) describe the test as "smooth, minutely granular, with largely silicious cement". Israelsky's species concept for micro- and macrospheric forms of *S. perplexa* is in aggreement with that of Cushman (1934) for *S. spectabilis* [i.e. forms with slightly larger spires (=*S. brevis* Grzybowski) corresponding to macrospheric forms, and those resembling *S. spectabilis* Grzybowski — microspheric forms.]. Included in Israelsky's synonymy are macrospheric forms described by Cushman (1934), Cushman and Jarvis (1928) and Cushman and Renz (1946) as *S. clotho*.

Morphologically, *S. perplexa* closely resembles both *S. californica* and *S. directa*, but the holotype is strongly compressed and decreases in width distally. However, Martin (1964) reports the sides as being parallel in specimens from the lower Moreno Fm. A Student's t-test of thickness measurements indicates that the holotype and paratype do not differ significantly ($P < .05$) from specimens from the lower Moreno Shale measured in this study (sample M-1). The type specimens also do not differ from specimens from Luneburg ($.2 < P < .1$) described by Hilterman (1972) as *S. spectabilis*, 90% of which decrease in width distally.

Spiroplectammina mexiaensis was described by Lalicker (1935) from the Eocene Mexia Clay Member of the Wills Point Formation in Texas. In linear dimensions, this form most closely resembles *S. directa*, but the two specimens in the Cushman Collection are unusual in that occasional mafic grains are used in the construction of the test. Lalicker describes the species as possessing 4 or 5 chambers in the spiral portion of the test, but the paratype possesses three chambers in the initial portion. Hiltermann (1972) and Szczechura and Pożaryska (1974) consider this form conspecific with *S. spectabilis*.

S. grzybowskii Frizzel (1943) was originally described from the "?upper Cretaceous" from a well near Negritos, Peru, but the lectotypes designated by Frizzel are the specimens from the Lizard Springs Fm. illustrated by Cushman and Jarvis (1928) as *S. clotho*. Cushman (1947) accepted the designation *S. grzybowskii*, reporting it to occur in the Santa Anita Fm (Venezuela), Mel Paso Shale (Peru), Lizard Springs Fm, and in the Velasco Shale. Cushman remarks, however, that the relation of this species to *Bolivinopsis clotho* is unclear. Israelsky (1951) and Martin (1964) later included Cushman's specimens from Lizard Springs into the synonymy of *S. perplexa*. In samples from Lizard Springs examined in this study, *S. spectabilis* occurs infrequently, and specimens are minute and delicate, with translucent, entirely siliceous-arenaceous and very finely finished tests (pl. 12: fig. 7, 8). The measured parameters of the paratype (Cushman Coll. 39551) fit within the confidence intervals of Carpathian specimens. Most authors list *S. grzybowskii* as a junior synonym of *S. spectabilis*.

Two species of *Spiroplectammina* were described by Todd and Kniker (1952) from the upper Eocene Agua Fresca Shale of Southern Chile, which contains a fauna that bears a striking resemblance to that described from the Kreyenhagen Shale. One of these, *S. brunswickensis*, is herein considered to represent the macrospheric form of *S. spectabilis*. Todd and Kniker maintain that *S. brunswickensis* differs from *S. directa* in its more elongate and compressed test and lack of keel, but add that the two species "seem to be closely related and may prove indistinguishable".

Cushman and Renz (1948) describe a species of *Spiroplectammina* from the middle-upper Eocene from the Navet and Hospital Hill Formations of Trinidad. *S. trinitatensis* Cushman et Renz (1948) is described as differing from typical specimens of *S. spectabilis* in its slightly larger and more inflated test. Specimens housed at the U.S.N.M. are relatively coarse-grained, yellow-white in color, and differ significantly in thickness from Carpathian specimens ($P < .01$). Beckmann (1953) illustrates upper Eocene specimens from the Mount Hillaby Fm of Barbados that are nearly 2 mm in length. However, Cushman and Stone (1949) dipict a much less robust form from the Eocene of the Verdum Fm. (Peru). In this study, one sample from the upper Eocene (NP21/22; M-P. Berggren, pers. comm.) of the Oceanic Fm. of Barbados contained well-preserved specimens with robust, inflated tests occasionally possessing dentate peripheries. These forms, described by Beckmann (1953) as *Bolivinopsis trinitatensis*, occur in an abyssal assemblage containing diverse planktic and calcareous benthic foraminifera. Microspheric individuals are more numerous than macrospheric forms, possessing biserial parts that are initially rather slender (pl. 12: fig. 13). One particularly robust microspheric specimen possesses 36 chambers in the biserial part alone, and is of the dimensions reported by Beckmann (1953).

Table 1

Means and Standard Deviations of measured specimens (length, width and thickness measured in mm)

Locality	length	width		thickness	number of chambers	n
		spire	biserial			
Biecz	.92±.17	.36±.05	.33±.05	.18±.03	16.7±2.9	29
Witryłów*	.88±.07	.33±.04	.31±.04	.16±.03	**	5
Znicz*	.83±.07	.29±.05	.28±.04	.15±.01	20.0±1.4	6
Luneburg*	.49±.16	.19±.03	.20±.03	.11±.03	17.9±4.3	53
NorthSea	.63±.09	.21±.03	.21±.04	.12±.02	19.5±2.9	9
Moreno — 1	.52±.05	.15±.02	.18±.02	.09±.01	21.8±2.4	6
Moreno — 3,4	.65±.15	.28±.04	.28±.06	.17±.03	**	6
DSDP 112/14-3	.35±.04	.12±.01	.12±.01	.08±.01	16.7±1.8	11
S. perplexa (type series)	.36±.01	.18±.03	.15±.0	.07±.01	16.5±0.5	2
S. directa (holotype)	.46	.20	.18	.11	16	1
S. californica (type series)	.81±.16	.29±.02	.30±.02	.19±.02	20.0±3.5	5
S. mexiaensis (type series)	.53±.06	.19±.01	.19±0	.11±.01	16.0±4	2
S. trinitat. (type series)	1.25±.23	.42±.03	.40±.03	.24±.02	23.5±3.3	4
S. grzybowskii (paratype)	1.22	.27	.30	.14	30	1

* — calculated from Hiltermann (1972)   ** — data not available

Single-classification ANOVA of thickness measurements in mm

Source of Variation	d.f.	SS	MS	F	% Variance
Among samples	9	.2030	.022556	42.96***	79.1
Within samples	120	.06294	.000525		20.9

***(P < .001)

Tukey — Kramer test of multiple comparisons between pairs of means of thickess

	DSDP	M-1	Lun	N.S.	Zni	Wit	M-3	Bie	cal	trin
DSDP	—									
M-1	.01	—								
Lun	.03	.02	—							
N.S.	.04*	.03	.01	—						
Zni	.07**	.06**	.04	.03	—					
Wit	.08**	.07**	.05**	.04	.01	—				
M-3	.09**	.08**	.06**	.05	.02	.01	—			
Bie	.10**	.09**	.07**	.06	.03	.02	.01	—		
cal	.11**	.10**	.08**	.07	.04	.03	.02	.01	—	
trin	.16**	.15**	.13**	.12**	.09**	.08**	.07**	.06**	.05**	—

*(.05 < P < .01)   **(P < .01)

SHAPE ANALYSIS

In addition to varying in linear parameters, macrospheric specimens of *S. spectabilis* vary considerably in the relative proportions of their initial spires. In an effort to determine the relative magnitude of this variation, eigenshape analysis was applied to all macrospheric individuals (including juveniles) from five samples; Biecz, Moreno P-1, Moreno P-2, North Sea, and DSDP 112/14. In each sample, *S. spectabilis* was the only species of *Spiroplectammina* present, therefore no bias was introduced through preselection of specimens. The within-sample variance for each sample is given in table 2.

Biecz

This sample is derived from the Silesian Unit of the Polish Flysch Carpathians near the town of Biecz, and may be considered topotype material for *S. spectabilis*. Figure 3 shows the range of observed morphotypes plotted according to their eigenshape correlations. The axes are R-mode principal components and represent a continuous range of shapes, which differ from one another in the amplitude of correlation with the associated eigenshape functions. 81% of the shape variation in this sample is represented by the first eigenshape (the black figure at the top of figure 4). The second eigenshape describes the next 3% of the variation, and is attributable to forms with larger or smaller initial spires, the former possessing positive correlation with the second eigenshape and the latter negative correlation values. In this population, 26 specimens cluster together with greater than 85% correlation with the first eigenshape and ±.15 correlation with the second. The five specimens below 85% are aberrant juveniles. Specimens from this sample are robust, with inflated tests (thickness = .18±.03 mm), generally possessing depressed sutures

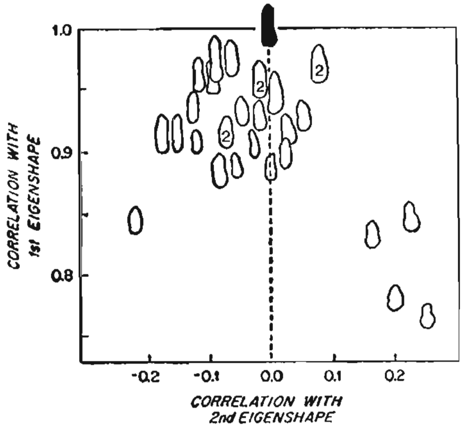

Fig. 3. Range of observed shapes from a single sample from Biecz arranged according to shape, with hypothetical first eigenshape (figure in black). The number (2) inside a shape indicates overlapping specimens

and indented peripheral margins. As shown in table 2, the intraspecific variability is high in comparison with other samples (This is evident from the relatively low variance accounted for by the first two eigenshapes). In this sample, *S. spectabilis* is the numerically dominant taxon.

Moreno Shale

Two samples from this formation were analyzed. Specimens from the upper parts of this formation correlate closely with the topotypes from Biecz (fig. 4), thereby confirming the synonym status of "*S. californica*".

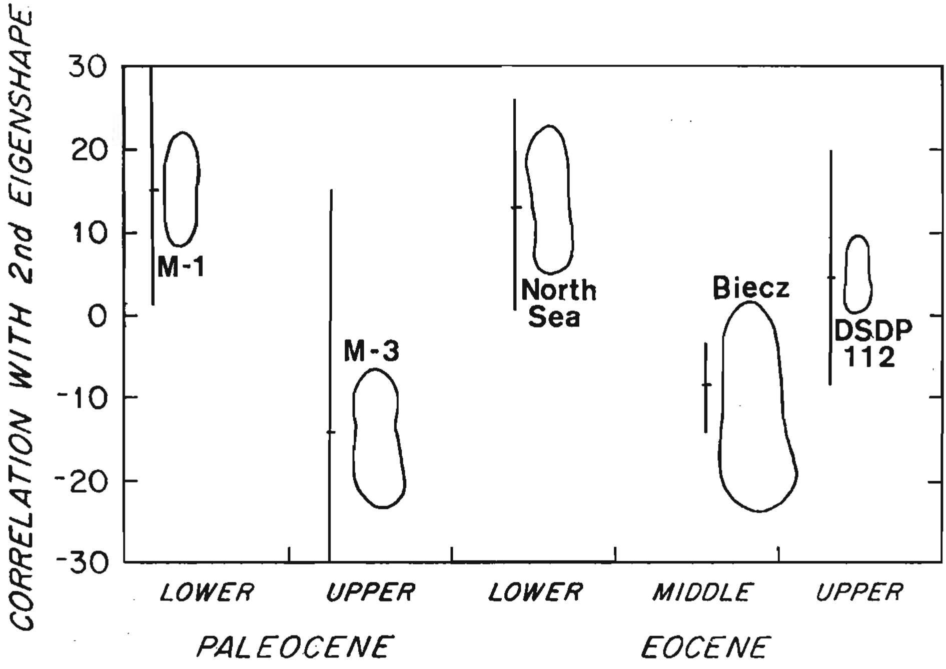

Fig. 4. Correlation of the first eigenshapes of the within-sample eigenshape analysis (average shape of each sample) with the second eigenshape of the between-sample eigenshape analysis. Lines represent 95% confidence intervals of the correlation of observed shapes with the second eigenshape of each sample.

Individuals from the lower part of the formation are somewhat smaller in size and possess relatively smaller spires.

North Sea

Specimens for analysis are derived from the Mobil well 9/13-5, drilled between Norway and the Shetland Islands, from a depth of 7450 feet. In this region, *S. spectabilis* occurrs only in the Paleocene and lower Eocene and does not extend into the *Cyclammina amplectens* Zone (middle Eocene). This is due to a faunal change in the Eocene. Specimens from this well are robust, with many chambers in the biserial part, and show best correlation with specimens from the lower Moreno Shale.

DSDP Site 112/14-3

This sample is derived from the late middle Eocene of the Labrador Sea, and *S. sepctabilis* is the dominant agglutinated taxon. Specimens are minute, narrow, white in color, and relatively coarse grained. In high magnification, it is apparent that the organism employed much coccolith debris in the construction of the test wall (pl. 12: fig. 9). These specimens show rather low correlation to the previous four samples, although their average shape most closely corresponds to the statistically average shape of all samples. Gradstein (in press), basing on material from the Labrador Sea, maintains that Eocene forms of *S. spectabilis* are flatter than Paleocene forms.

The eigenshapes of the first eigenshape analyses were compared with each other by the use of a second shape analysis to give a hypothetical average shape for all samples. 96.9% of the variance of this shape is represented by the 1st eigenshape, with the 2nd eigenshape accounting for 1.6%. These values are much higher than those obtained for observed shapes in the first eigenshape analysis (table 2) suggesting that less between-sample variability exists than within-sample. Figure 4 illustrates the between-sample variability of the species by showing the first eigenshapes of each sample plotted against their correlations with the second eigenshape of the between-sample eigenshape analysis and geologic age. Average shapes from each sample differ mostly in the relative proportion of the initial spire.

Table 2

Listing of samples included in eigenshape analysis with the number of specimens per sample (n), and the variance represented by the 1st and 2nd eigenshapes (VE1), (VE2)

Sample	n	VE1	VE2
Biecz	31	81.5%	3.1%
112/14-3	11	82.3%	5.2%
Mor. P-1	9	86.7%	3.3%
Mor. P-3	7	70.9%	16.0%
North Sea	9	87.7%	3.6%

Ecophenotypic forms

Hilterman (1972) showed the synonymy of Grzybowski's forms by plotting the ratio of width/length against the number of chambers. The main distinction between assemblages of specimens measured in this study can be found by calculating the mean ratio of thickness/width for each sample. However the utility of such a derived variable should not be overemphasized because of the resulting wide confidence interval.

S. perplexa displays the lowest mean ratio (.47) of measured specimens, while highest values ($>$.6) are shown by *S. californica*, *S. trinitatensis* and in sample DSDP 112/14-3, but confidence intervals overlap. Although the types of *S. perplexa* and *S. trinitatensis* significantly differ in size from typical forms of *S. spectabilis*, the value of separating them is debatable, since the morphology of all the forms is generally similar. In Carpathian literature, *S. trinitatensis* and *S. perplexa* are not distinguished as separate species, and such forms are considered to fit within the variation of *S. spectabilis*. *S. trinitatensis* most commonly occurs in Upper Eocene "Velasco-type" faunas containing abundant calcareous benthic and planktic foraminifera. Specimens corresponding to *S. perplexa* are mostly reported from Paleocene and lower Eocene rocks, but are also found in the Upper Eocene. Therefore they do not represent subspecies in the paleontological sense, and size and shape differences must be attributed to environmental factors. However, it must be considered of some importance to maintain a taxonomic distinction between these two variations within *S. spectabilis*.

Following the practice of Feyling-Hanssen (1972) of using trinomial nomenclature for ecophenotypes, it is suggested here that *S. trinitatensis* and *S. perplexa* be regarded as such, with robust forms refered to *S. spectabilis* forma *trinitatensis*, while minute compressed forms placed in *S. spectabilis* forma *perplexa*.

RELATION BETWEEN *SPIROPLECTAMMINA SPECTABILIS* AND OTHER SPECIES

Brouwer (1965) includes the species *Spiroplectammina cubensis* (Cushman and Renz, 1937) in his synonymy of *S. spectabilis*, however, this form is specifically distinct. The stratigraphically younger *S. cubensis* differs from *S. spectabilis* is possessing a large, evolute initial coil and a long and flaring biserial part. The specimen illustrated by Douglas (1973) possessed two full whorls in the initial spire. A possible intermediate form is *S. elgansoensis* Todd and Kniker, described as possessing a very slender and compressed test, with calcareous cement. The biserial part of this species possesses very low and numerous chambers (44 in the holotype) and the spiral portion contains 12 chambers in 1 1/2 whorls. Kisselman (*in*: Subbotina, 1964) illustrates two robust species of *Spiroplectammina* from Maastrichtian platform deposits of Western Siberia which appear to be homeomorphs of *S. cubensis*, except for the coarser nature of the agglutinated grains comprising the test. These are *S. ancestralis* Kisselman and

S. variablis (Neckaya). Co-occurring with these are *S. brevis* Kisselman (*non* Grzybowski) and *S. brevis modesta* Kisselman, which resemble stunted or juvenile forms of the above two genera, although *S. brevis* is reportedly thicker.

Spiroplectammina rosula (Eherenberg) with its two synonyms — *Bolivinopsis capitata* Yakovlev, and *Spiroplectammina flexuosa* (Reuss) — is an upper Cretaceous species described from epicontinental deposits in Europe and the Gulf Coast. It differs from *S. spectabilis* in its predominantly calcareous test, much higher chambers, and narrower biserial part, which often displays constrictions. *Spiroplecta rosula* Ehrenberg was designated the type species for Cushman's genus *Spiroplectoides*, whereas *B. capitata* was the type species for *Bolivinopsis*. Both genera are herein considered synonymous with *Spiroplectammina*.

PALEOECOLOGY AND PALEOBATHYMETRY

Hiltermann (1972), on the basis of analogy with recent and cold water forms, maintained that *S. spectabilis* is indicative of deep waters. This species is a common constituent of the so-called "*Rhabdammina*" or "flysch-type" and "Velasco-type" foraminiferal faunas in the upper Maastrichtian to upper Eocene. The paleoecology of these faunas has been discussed by numerous authors [Brouwer 1965; Jurkiewicz 1967; Szczechura and Pożaryska 1974; Berggren and Aubert 1975; Książkiewicz 1975; Gradstein and Berggren 1981; Beckmann *et al.* 1982; Miller *et al.* 1982; Kaminski 1982; Gradstein *et al.* 1983; Scott *et al.* (in press)]. A synthesis of the above studies provides an ecological model suggesting flysch-faunas are associated with cool, turbid, deep-water environments with old (i.e. sluggish) bottom water and pelagic substrates with high organic matter content, though the relative importance of any particular parameter is not yet clear.

The cosmopolitan nature of *S. spectabilis* is shown by its distribution in sediments from the DSDP, which can be assigned reasonably accurate paleodepths using the backtracting method of Berger and Winterer (1974). Table 3 lists the reported occurrence of *S. spectabilis* from the world oceans.

Although the distribution of flysch-faunas is controlled to a greater degree by the geochemical conditions at the sediment-water interface rather than simply by water depth, most of the above depths are in the lower bathyal — abyssal range. Although of anomalously shallow paleodepth, Site 403 contains a Velasco-type fauna with a high percentage of planktonic species, similar to the Lizard Springs Fm.

In terrestrial outcrops, *S. spectabilis* is commonly found in Alpine flysch deposits throughout Europe (Glaessner 1937; Hillebrandt 1962; Geroch 1960; Huss 1966; Jurkiewicz 1967; Mjatliuk 1970; Hanzliková 1972; Hiltermann 1972; Szczechura and Pożaryska 1974; Butt 1981; Beckmann *et al.* 1982;). Depth estimates for sediments containing this taxon range from upper bathyal to abyssal. The Lower Paleogene bathymetry of the Silesian flysch basin, was determined by Książkiewicz (1975) [by analogy of fossil foraminifera with recent forms] as middle to upper bathyal. Beckmann *et al.* (1982) give a lower bathyal depth (1500—2500 m.) for the Lower Paleogene Scaglia at Monte Giglio, which reportedly contains a Velasco-type fauna.

Table 3

Recorded occurrence of *S. spectabilis* in selected DSDP sites. Paleodepths were calculated by means of the backtracking procedure of Berger and Winterer (1974).

DSDP Site	Age	Paleodepth	Reference
20c	L. Paleocene	2825 m	Tjalsma and Lohmann (1983)
94	E. Eocene	2060 m	Tjalsma and Lohmann (1983) Worzel *et al.* 1973
112	M. Eocene	3000 m	Miller *et al.* (in press)
167	Eocene	3000 m	Douglas (1973)
208	Maastrichtian	1000 m	Burns and Webb (1973)
357	E.—M. Eocene	1725 m	Tjalsma and Lohmann (1983)
360	M. Eocene	2000 m	Melguen (1978)
361	L.—U. Eocene	3500 m	Melguen (1978)
364	M. Paleocene	1500 m	Melguen (1978)
385	U. Maastrichtian	4700 m	McNulty (1979) Tucholke and Vogt (1979)
403	M.—U. Eocene	250-900 m	Murray (1979)
549	E.—U. Eocene	2400 m	Miller *et al.* (in press)

In California, the lower Lodo Fm. and the Moreno Shale contain Velasco-type faunas and are interpreted as middle — lower bathyal (Berggren and Aubert (1983), Martin 1964), whereas the Oceanic Fm. of Barbados is considered to have been deposited at abyssal depths.

A noteworthy feature of the occurrence of *S. spectabilis* is that in some samples, predominantly Eocene, it dominates the assemblage. Todd and Kniker (1952) report *S. brunswickensis* to be very abundant in the upper Eocene middle Agua Fresca Shale, and erect a *S. brunswickensis* Zone. High abundances were also reported by Miller *et al.* (1982), who erect a *S. spectabilis* Zone for the Lower Middle Eocene of the Labrador Shelf.

In the Polish Flysch Carpathians, Geroch (1960) reports more numerous *S. spectabilis* in the Hieroglyphic Beds [middle — upper Eocene] than in the underlying Ciężkowice Beds of the Silesian Unit, and Bieda (1969; pl. 48) illustrates a middle Eocene assemblage from the Hieroglyphic Beds of the Skole Unit with this form numerically dominant. In DSDP Site 112, agglutinated diversity is lower in samples with abundant *S. spectabilis*, and the fauna is stunted. This may suggest that *S. spectabilis* was tolerant of marginal paleoenvironmental conditions.

Conclusions

1) Marked heterogeniety exists between assemblages of *S. spectabilis* from different localities. Significant differences occur mainly in the relative thickness of the test, which tends to be greater in Eocene samples. Variation in parameters such as length and number of chambers are not as meaningfull, since these are dependent upon ontogenic development. Eigenshape analysis shows that specimens vary most in the relative proportions of the initial spire, with within-sample shape variation greater than between-sample variation.
2) Morphologic comparison of specimens from different localities described under various taxonomic headings show the following specific designations to be synonymous with *S. spectabilis*: *S. californica*, *S. directa*, *S. mexiaensis*, *S. grzybowskii*, *S. brunswickensis*, and *S. clotho* of early authors.
3) Multiple comparisons of linear measurements suggests that *S. spectabilis* represents a plexus of intergradational forms, though end members can readily be distinguished. It is suggested here that the designation "*trinitatensis*" be applied to thick, robust, predominantly middle and upper Eocene forms of the *S. spectabilis plexus*. Likewise, the name "*perplexa*" may be retained to describe small, laterally compressed forms. The former locally occurs in "Velasco-type" faunas, while "*perplexa*" has been observed from both "flysch-type" and "Velasco-type" faunas. Both formae may be regarded as ecophenotypes.
4) *S. spectabilis* is a cosmopolitan species, commonly present in Upper Maastrichtian — upper Eocene "flysch-type" and "Velasco-type" faunas from Tethyan and Boreal realms, sometimes occurring in large numbers. Bathymetric interpretations of the faunas in which this species normally occurs range from middle bathyal to abyssal.

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ZMIENNOŚĆ OTWORNICY *SPIROPLECTAMMINA SPECTABILIS* (GRZYBOWSKI)

Streszczenie

Na podstawie materiału topotypowego badano morfologię i zmienność wewnątrzgatunkową *Spiroplectammina spectabilis* (Grzybowski), (Foraminiferida, Textulariina). Analiza „eigenshape" pozwala stwierdzić, że największa zmienność istnieje w proporcjach spirali początkowej i że zmienność wewnątrz zespołów jest większa niż pomiędzy zespołami. Porównanie pomiarów *S. spectabilis* sugeruje, że gatunek ten stanowi zbiór form pośrednich, aczkolwiek można wyróżniać formy końcowe. Testy statystyczne przeprowadzonych pomiarów wykazują znaczną nierównomierność parametrów pomiędzy próbkami pobranymi z różnych rejonów. Znaczące różnice w grubości skorupki pozwalają na wyróżnienie dwóch form w obrębie badanego gatunku: *S. spectabilis* forma *perplexa* i *S. spectabilis* forma *trinitatensis*. Nazwa *S. spectabilis* forma *perplexa* może być stosowana do oznaczania drobnych i spłaszczonych form, zaś *S. spectabilis* forma *trinitatensis* dla form większych i bardziej wypukłych od typowych okazów *S. spectabilis*.

EXPLANATION OF THE PLATES 12 AND 13

Plate 12

1. Specimen of *S. spectabilis* from Biecz (Polish Flysch Carpathians) macrospheric form. ×80.
2. Biecz — macrospheric form. ×80.

3. Biecz — bizzare macrospheric form. ×80.
4. Microspheric form from Biecz. ×80.
5. *S. spectabilis* from the Moreno Shale of California macrospheric form. ×100.
6. Moreno Shale — microsphaeric form. ×100.
7. Specimen from DSDP Site 112 (upper Eocene). microspheric form. ×100.
8. DSDP Site 112 — macrospheric form. ×100.
9. Enlargement of specimen in fig. 8 showing details of test wall. ×900.

Plate 13

1. *S. spectabilis* forma *trinitatensis* from the Oceanic Fm of Barbados microspheric form. ×40.
2. Barbados — juvenile microspheric form. ×40.
3. Barbados — macrospheric form. ×40.
4. Specimen from the Lizard Springs Fm. of Trinidad microspheric form, ×150.
5. Lizard Springs — macrospheric form, ×150.
6. *S. spectabilis* from the North Sea microspheric form, ×80.
7. North Sea — macrospheric form, ×80.
8. North Sea — macrospheric form, ×80.


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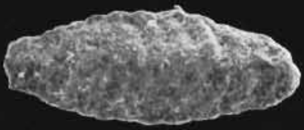
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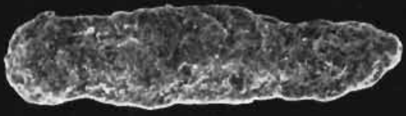
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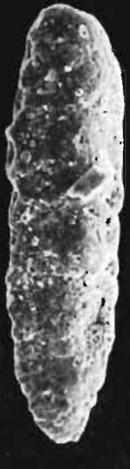
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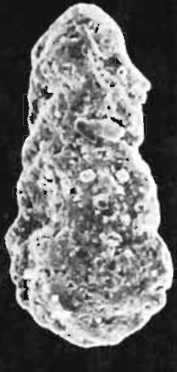
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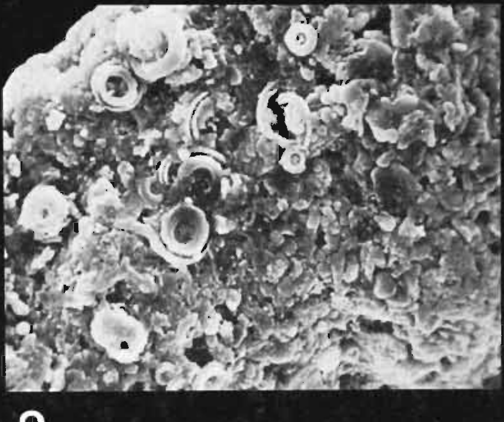
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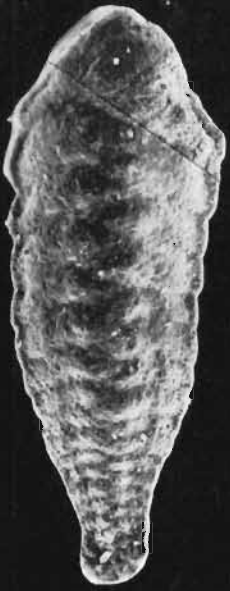

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