# The reciprocity between coiling direction and dimorphic reproduction in benthic foraminifera

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#### ABSTRACT

There are various opinions as to what parameter influences the coiling directions in foraminifera. "Do microspheric and megalospheric generations have different coiling ratios?" is an unanswered question in foraminiferal studies. Per view of this, an attempt is made to study the relationship between mode of reproduction (sexual/asexual) and coiling direction (dextral/sinistral) in the benthic foraminiferal species *Rotalidium annectens* (Parker & Jones). Proloculus (initial chamber) size is taken as an indicator of changes in reproductive behaviour.

The present study is based on the observations made on 17722 specimens of this species from 186 samples, obtained from 3 sediment cores (representing a time span of about 9,500 years) from the shallow water region off Karwar, west coast of India. The results indicate an inverse relationship between mean proloculus size and dextrality (% of dextral forms) which is statistically confirmed. The correlation value (r = -0.57) between the two parameters is above the level of significance at 99% level. Therefore, it is inferred that microspheric generation (smaller proloculus) prefers dextral coiling and coiling in benthic foraminifera appears to be influenced by mode of reproduction. *J. Micropalaeontol.*, **11** (2), 221-228, December 1992.

#### INTRODUCTION

In nature many organisms such as gastropods, bacterial colonies (*Bacillus mycoides*), the spiral vascular conductors of some plants and the spiral distribution of leaves, show differences in coiling direction. Many trochospiral foraminiferal species possess asymmetric tests in which chambers are arranged in a cone-like spiral. This spiral may coil either in an anti-clockwise, sinistral (left handed) or in a clockwise, dextral (right handed) direction.

These changes in coiling direction are the most commonly studied morphological variable exhibited by foraminifera (reviews by Scott, 1974 and Kennett, 1976; Hallock & Larson, 1979; Lena, 1981; Vincent & Berger, 1981; Hornibrook, 1981, 1982; Kalia & Chowdhury, 1983; Weaver, 1983; Duprat, 1983; Healy-Williams et al., 1983; Hallock, 1986; Caralp, 1987; Corliss & Chen, 1988; Renzi, 1988; Boyle, 1989; El-Nakhal, 1990; Collins, 1990 and many others) with emphasis on their value as a tool for local stratigraphic correlation and/or paleoclimatic studies. For some species arguments have been made in favour of their use as paleotemperature indicators, although a number of contradictions have been observed and they fail to consistently correlate with cold and warm periods (Thiede, 1971; Parker, 1971; Olsson, 1974). For example, higher dextral/sinistral ratios in the planktonic foraminiferal species G. truncatulinoides has been considered to be an indicator of higher temperature in the North Atlantic (Bandy, 1960; Takayanagi et al., 1968; Bé, 1969) and in the Pacific Ocean (Parker & Berger, 1971) although off Portugal and Morocco mostly dextral G. truncatulinoides were found in glacial sediments (Thiede, 1971). Wollin et al. (1971) had the same opinion. This could be due to the disagreement concerning the temperature conditions of species, as some

species appear to be more tolerant of low temperature in the southern hemisphere than in the northern hemisphere (Bé, 1969; Boltovskoy, 1969, 1970; Bé & Tolderlund, 1971). Kennett & Huddlestun (1972) indicated that the same species may show more one response to a particular environment.

Similarly, different species may show different responses in the same region. To quote a few, in Red Sea cores, Herman (1965) found sinistral *G. bulloides* as an indicator of cold water, whereas, sinistral *G. sacculifer* indicated warmer conditions. In the North Atlantic, *G. quinqueloba* showed no preference between dextral and sinistral, *G. pachyderma* displayed a seasonal alternation in preferred coiling direction, whereas *G. truncatulinoides* had a distinctly preferred coiling direction regardless of season or temperature. (Tolderlund & Bé, 1971).

Discrepancies have also been reported in benthic species such as *R. beccarii* where sinistral forms were found to be in abundance in cooler water by Longinelli & Tongiorgi (1960). However, observations in other areas have not confirmed this relationship (Boltovskoy & Wright, 1976). Similarly, Brooks (1967) and Malmgren (1984) did not find any clear relationship of coiling direction to the environment.

These contradictions lead to various alternative explanations. Lipps (1979) summarised them as (i) salinity, (ii) watermass, (iii) seasonal effect, (iv) test size, (v) water depth, (vi) asexual-sexual generation, (vii) water temperature, (viii) sorting processes, (ix) differential predation, (x) geographically isolated gene pools, (xi) different species, (xii) ice habitat, (xiii) water density, (xiv) paleomagnetism, (xv) evolutionary phenomena, (xvi) reproductive strategy. He further stated that insufficient evidence was available to confirm or disprove these suggestions. However, he selected



**Fig. 1** (a) Showing Dimorphism (microspheric/megalospheric forms) (b) Showing coiling direction (dextral/sinistral forms) in *Rotalidium annectens* (Parker & Jones).

only two hypotheses for detailed discussion: one was temperature control, as it was used very commonly and the other was the difference in reproductive strategy related to productivity of water. Even the recent attempt by Collins (1990) to study the relationship between temperature and coiling direction by eliminating factors of life cycle stages and possible ontogenetic changes, has yielded only partial success, as dextrally coiled *Bulimina marginata* and *B. aculeata* were found strongly associated with warm temperatures but failed to show any consistent relationship of sinistral dominance in cold temperatures. Nevertheless, no significant attempt has been made to study the relationship of coiling direction with reproductive behaviour (asexual-sexual generation) in foraminifera.

In view of the above, we decided to investigate the relationship between coiling direction and reproduction. For this purpose an attempt is made to study the relationship between coiling direction, expressed in terms of dextrality:percentage of dextrally coiled specimens in a population and dimorphism, expressed in terms of mean proloculus (initial chamber) size, a phenomenon related to sexual and asexual reproduction.

This study is based on a large number of specimens of the benthic foraminiferal species *Rotalidium annectens* (Parker & Jones) (Fig.1), obtained from three sediment cores collected off Karwar, central west coast of India. This species has been selected due to the fact that, (i) it exhibits dimorphism (Figs 1a, 2a, 2b) (Nigam, 1988) and dextral/sinistral coilings (Fig. 1b); (ii) its large size and (iii) its abundance in shallow marine sediment.



Fig. 2 Specimens of *R. annectens* showing bimodality and thus existence of dimorphism.

The large size (0.30—1.30mm) and abundance ensure statistically reliable measurements of proloculus size as well as calculation of mean proloculus size (MPS) and percentage of coiling ratios.

## MATERIALS AND METHODS

The three cores were collected during three different cruises in the Arabian Sea off Karwar near the mouth of the Kali river (a) the first core, GV 3713 (at 14° 53.1'N; 73° 57.9'E), 1.16m long and 20m deep was collected during the 150th cruise of R.V. *Gaveshani*. The core was sampled at 2cm intervals (Fig. 3): (b) the second core SK 27B/8 was 4.80m long and collected on board O.R.V. *Sagar Kanya* during her cruise No. SK 27B at latitude 14° 49.43'N and longitude 73° 59.37'E at a water depth of 22m. This core was sampled at 5cm intervals (Fig. 3): (c) the third 6.7m long core SK 44/13 (at 14° 43.80'N; 74° 0.2.649'E) was taken on board O.R.V. *Sàgar Kanya* during her 44th cruise, at a water depth of 22m. Only the portion below 4.50m in this core was utilized and sampled at 5cm intervals (Fig. 3).

These cores represent recent Holocene time as one sample (300-305cm) from core SK 27B/8 and two samples (455-460 and 600-605cm) from core SK 44/13 (dated by <sup>14</sup>C method using Accelerator Mass Spectrometer) show an age of  $3,510\pm60$ ;  $6,200\pm90$  and  $8910\pm160$  years BP respectively.

198 samples from the three different cores were washed through a  $60\mu$ m sieve and oven dried. The resulting specimens were kept in dorsal view and the direction of progression of new chambers noted. In a dextrally coiled specimen, new chambers are added in a clockwise manner, while anticlockwise addition gives a sinistrally coiled specimen. The



Fig. 3. Map showing locations of the 3 cores.

ratio of these two forms can be counted in any assemblage.

Features associated with reproduction need more attention. it is well known that the shape, size and proloculus size of tests of foraminifera belonging to the species are different. This dimorphism is related to reproduction and the two forms are known as megalospheric and microspheric. Size is the simplest to measure and some workers (Thiede, 1971; Steuerwald & Clark, 1972; Vella, 1974) noted a tendency in several planktonic species for the coiling direction to be related to the size of the specimens. However, dimorphism in planktonic foraminifera has yet to be demonstrated.

In benthic foraminifera, at least in the case of *Rotalidium annectens* (Parker & Jones), proloculus size can be easily measured. Moreover, the size of the proloculus and the direction of coiling (which is decided by addition of a few chambers soon after formation of the first chamber) will remain unchanged with the growth of specimens, and hence will be independent of size. Therefore, for the present study the proloculus size is taken as a factor representing the modes of reproduction.

Computations for correlation coefficients and regression equations between dextrality and mean proloculus size were carried out on a ND 520 Computer at the Computer Centre of the National Institute of Oceanography. The levels of significance were determined from Table 7 of Fisher & Yates (1963).

The total number of specimens measured for mean proloculus size at different levels of cores are given in Tables 1 - 3. However, a few samples showing extremely poor (less than 20 specimens) occurrence of *Rotalidium annectens* were excluded from the present analysis due to paucity of the material. The final summary of data is given in Table 4.

#### RESULTS

This study is based on a total of 17722 specimens from 186 sediment samples from three cores representing a time span of about 9,500 years.



**Fig. 4.** Downcore variations in mean Proloculus size and percentage of dextral forms in core SK 27B/8. Line joining the squares is profile of raw data, whereas line joining the black circles is 5 point moving average.

Out of 17722 specimens, 11.26% of all specimens possessed dextral coiling. The general range of proloculus size is 0.025 to 0.125mm. The mean proloculus size of various samples shows a range of 0.040 to 0.068mm. It is important to notice that in each core the average mean proloculus size of specimens showing dextral coiling is invariably smaller than those coiled sinistrally (Table 5). This shows that dextrally coiled specimens are associated with smaller proloculus, which is a characteristic of sexually formed microspheric forms.

Similar results are obtained by plotting the down core variations of MPS and percentage of dextral specimens (Figs 4, 5, and 6). These curves show the absolute as well as five point moving averages at every data point. In each core the majority of the prominent peaks in the curves of percentage of dextral forms can be correlated with troughs in mps curves. This further indicated that dextrality in benthic foraminifera



**Fig. 5.** Down core variations in mean proloculus size and percentage of dextral forms in core SK 44/15. Line joining the squares is profile of raw data, whereas line joining the black circles is 5 point moving average.

is inversely correlated with mean size of proloculus.

We have computed the correlation coefficient (r) values between the percentage of dextral forms and mean proloculus size for every core (Table 4). The results show a consistent inverse relationship and all the (r) values are above the level of significance at 99% level (calculated as per Table 7 of Fisher & Yates, 1963). The collective plotting of MPS and percentage of dextral forms from all the three cores (Fig. 7) also exhibits a significant inverse relationship (r = -0.57) at 99% level of significance (r = <0.25).

# DISCUSSION

Boltovskoy & Wright (1976), while listing the significant unanswered or poorly stated questions, have raised the question "Do microspheric and megalospheric generations have different coiling ratios?". This suggests a genetic control for coiling direction.

It was already noticed by earlier workers (Thiede, 1971; Tolderlund & Bé, 1971; Steuerwald & Clark, 1972; Vella, 1974) that coiling direction may have its origin in reproductive



Fig. 6. Down core variations in mean proloculus size and percentage of dextral forms in core BV 3713. Line joining the squares is profile of raw data, whereas line joining the black circles is 5 point moving average.

strategies. Unfortunately, the ratio of megalospheric and microspheric forms is rarely determined in planktonic foraminifera (Thiede, 1971) as it is not very easy to differentiate these forms even if dimorphism exists. On the other hand, this is less problematic in benthic foraminifera as many benthic species show definite proof of dimorphism which can be quantified by measuring proloculus size.

However, the examination of the relationship between reproductive mode and coiling direction in benthic foraminiferal species has been more limited, perhaps due to the small proportion of benthic foraminifera in deep sea sediments.

The results of the present work indicate very clearly that mean proloculus size is inversely proportional to percentage of dextral forms (Figs 4, 5 and 6). This relationship has also



Fig. 7. Showing graphic relationship between MPS and dextrality (% of dextral forms).

been confirmed through statistical analysis of the data for regression equation and correlation coefficient (r) (Table 4; Fig. 7). It further suggests that microspheric generations have a tendency for dextral coiling, whereas sinistral coiling is favoured by megalospheric generations. Our conclusions are in agreement with the results of culture experiments on Rosalina floridana by Lee et al. (1963). They found that dextrally and sinistrally coiled forms occurred in both generations (microspheric/megalospheric) but sinistral coiling was found in 63 out of the 66 measured megalotypic (megalospheric) individuals, whereas the reverse situation occurs in the microtypic (microspheric) generations in which 28 out of the 34 measured specimens coiled dextrally. These observations were on specimens from a common environment. A similar relationship was also noticed by Myers (1940), who found that microspheric tests coiled dextrally, but megalospheric tests coiled sinistrally in Discorbis patelliformis.

In view of the foregoing account, it may be summarized that coiling direction in benthic foraminiferal species, including *R. annectens* (Parker & Jones) shows relationship with reproduction.

It is likely that reproductive mode (or even proloculus size independent of reproductive phase) is affected by environmental fluctuations. Over the Indian region, the increase in precipitation around 9,000 years BP (Prell *et al.*, 1990), 6,000 years BP (Singh *et al.*, 1972), 4,000 and 3,500 years BP (Nigam & Khare, 1992) must have contributed to the lowering of the salinity in coastal areas. In our results, these periods of low salinity are marked by relatively higher MPS values at approximately 3.00m (*ca.* 3,500 years BP) and 4.00m (*ca.* 4,000 years BP) depth in core SK 27B/8 (Fig. 4) and around 4.6m (*ca.* 6,000 years BP) and 6.00m (*ca.* 9,000 years BP) in core SK 44/ 13 (Fig. 5).

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Similarly, another period of climatic aridity around 2,000 years BP has been noticed elsewhere (Bryson & Swain, 1981) which is reflected in this study where a marked low value of MPS can be seen around 1.30m down the core which corresponds more or less to the dry phase.

This is in agreement with Nigam & Rao (1987) who noticed an inverse relationship between salinity and MPS of *R. annectens* in the coastal Arabian Sea. The observation that coiling ratio also varies in an inverse fashion, through the study section may imply an independent response to the same environmental signal.

The present study may be taken as a strong signal of the existence of a possible relationship between reproductive mode (or proloculus size) and coiling directions in benthic foraminifera. Since this study is based on a single species, for more general results the relationship should be tested in many other benthic species from different areas and also in culture experiments. H.**643**, 1-99.

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Sr. No.	Depth in core (cm)	No. of measurements	Sr. No.	Depth in core (cm)	No. of measurements	
1	0-5	113	<b>49</b>	240-245	58	
23	5-10 10-15	136	50 51	245-250 250-255	44 47	
4	15-20	202	52	255-260	115	
5	20-25	176	53	260-265	33	
6 7	25-30 30-35	195	54 55	265-270	48	
8	35-40	123	55 56	275-280	43 49	
9	40-45	173	57	280-285	26	
10	45-50	185	58	285-290	10	
11	50-55 55-60	108	59 60	290-295 295-300	61 28	
13	60-65	108	61	300-305	43	
14	65-70	111	62	305-310	37	
15	70-75	118	63	310-315	14	
10	80-85	123	65	320-325	10	
18	85-90	107	66	325-350	50	
19	90-95	109	67	330-335	41	
20	95-100	75	68 69	335-340 340-345	32 43	
22	105-110	38	70	345-350	64	
23	110-115	95	71	350-355	108	
24 25	115-120	43	72 73	355-360	51 74	
25	125-130	20 11	73	365-370	54	
27	130-135	24	75	370-375	9	
28	135-140	18	76	375-380	31	
29 30	140-145	29	78	385-390	62 44	
31	150-155	120	79	390-395	61	
32	155-160	104	80	395-400	84	
33 34	160-165	39	81 82	400-405 405-410	72	
35	170-175	99	83	410-415	92	
36	175-180	105	84	415-420	46	
37	180-185	70	85	420-425	67 44	
30 39	190-195	43 49	87	430-435	44 93	
40	195-200	59	88	435-440	75	
41	200-205	37	89	440-445	24	
42	205-210	69	90 91	450-455	47	
44	215-220	80	92	455-460	44	Table 1. Showing number of measurements at
45	220-225	68	93	460-465	52	different levels in core SK27B/8.
46 47	225-230	56	94	465-470	89 141	
48	235-240	85	96	475-480	107	
Sr. No.	Depth in core (cm)	No. of measurements	Sr. No.	Depth in core (cm)	No. of measurements	
1	450-455	98	23	560-565	91	
2	455-460	101	24	565-570	23	
3	460-465	77	25	570-575	51	
4 5	465-470	80	26	580-585	4 41	
6	475-480	95	28	585-590	96	
7	480-485	98	29	590-595	82	
8 9	485-490 490-495	92 91	31	595-600 600-605	60 44	
10	495-500	75	32	605-610	50	
11	500-505	56	33	610-615	68	
12	505-510 510-515	78	34	615-620 620-625	68 60	
14	515-520	34	36	625-630	48	
15	520-525		37	630-635	71	
16 17	525-530 530-535	74 81	38 39	635-640 640-645	33	
18	535-540	74	40	645-650	42	Table 2. Showing number of measurements at
19	540-545	73	41	650-655	20	different levels in core SK44/13.
20 21	545-550 550-555	78 75	42	655-660 660-665	4	
22	555-560	77	44	665-670		

Sr. No.	Depth in core (cm)	No. of measurements	Sr. No.	Depth in core (cm)	No of measurements	
1	0-2	157	30	58-60	29	
2	2-4	146	31	60-62	37	
3	4-6	158	32	62-64	29	
4	6-8	49	33	64-66	27	
5	8-10	35	34	66-68	45	
6	10-12	270	35	68-70	42	
7	12-14	200	36	70-72	27	
8	14-16	171	37	72-74	23	
9	16-18	143	38	74-76	31	
10	18-20	128	39	76-78	62	
11	20-22	123	40	78-80	33	
12	22-24	108	41	80-82	55	
13	24-26	90	42	82-84	77	
14	26-28	75	43	84-86	62	
15	28-30	96	44	86-88	66	
16	30-32	82	45	88-90	49	
17	32-34	99	46	90-92	80	
18	34-36	60	47	92-94	115	
19	36-38	55	48	94-96	99	
20	38-40	50	49	96-98	82	
21	40-42	75	50	98-100	59	
22	42-44	93	51	100-102	61	
23	44-46	33	52	102-104	90	
24	46-48	64	53	104-106	85	
25	48-50	44	54	106-108	76	
26	50-52	42	55	108-110	77	
27	52-54	44	56	110-112	79	
28	54-56	35	57	112-114	33	Table 3 Showing number of measurements at
29	56-58	27	58	114-116	64	different levels in core GV3713.
Sr. No.	Core	Total no.	Samples	Value of	Degree of	
	No.	of sample obtained	used for regression equation	r	confidence	
1	GV3713	58	58	-0.49	0.33	
2	SK278/9	96	80	-0.49	0.33	
2	SK44 /12	20 44	30	-0.36	0.40	
5	01111/10	11	57	-0.70	0.10	

**Table 4.** Showing total number of samples; samples used for the calculation of correlation coefficient (r) between dextrality and MPS and levels of significance for all three cores.

Core No.	Total forms	Range of MPS (mm)	Total dextral	Average MPS of dextral (mm)	Total sinistral	Average MPS of sinistral (mm)	
		min	max				
GV3713 SK27B/8 SK44/13	4463 10497 2762	.049 .043 .040	.068 .062 .062	450 957 589	0.036 0.043 0.037	4013 9540 2173	0.059 0.052 0.052

**Table 5.** Showing total number of forms; range of MPS; total number of destral forms; MPS of dextral forms; total number of sinistral forms and MPS of sinistral forms for all three cores.