THE SIZE OF DIATOMS

II. FURTHER OBSERVATIONS ON *RHIZOSOLENIA STYLIFORMIS* (BRIGHTWELL)

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(Plate V and Text-figs. 1, 2)

Since the appearance of Part I of this paper (Wimpenny, 1936), the measurement of diatom cell diameters has been continued and extended, rather special attention having been paid to *Rhizosolenia styliformis*, with which species this account is concerned. The unit of measurement (*ca* 4μ) and the technique used is the same as that outlined in Part I.

Through the kindness of the late Dr Stanley Kemp, F.R.S., Dr N. A. Mackintosh and the late Mr J. O. Borley, I have been able to examine material from the *Discovery* Expedition. Similarly, I am indebted to Mr Vedel Tåning for sending me samples collected by the *Dana* in the Atlantic, and to Miss Molly Mare (Mrs G. M. Spooner) for the loan of collections she had examined in connexion with the mackerel investigations made at the western entrance of the English Channel under the auspices of the Marine Biological Association. From the North Sea and Atlantic I have also received samples and information from Dr R. S. Clark, Dr J. B. Tait, Dr S. Gibbons and Miss H. Ogilvie of the Scottish Fishery Board. Finally, valuable material from the Antarctic was collected for me by Lt.-Commander S. Brooks from the whaling ship *Svend Foyn* during the season 1937–8. To all these sources I make my grateful acknowledgements.

The data have been condensed in Table I, where the mean diameter for each sample is shown. The recorded frequency distributions from which the various means have been obtained, together with the individual measurements, are being deposited at the Laboratory of the Marine Biological Association, where they will be available for examination by those interested.

The necessity of sorting the material into different varieties has not made it possible to obtain from it as much information as was first hoped, and all that can be said of the present collections is that there may be characteristic life cycles for the species type of this diatom in different places. The establishment of these life cycles, their meaning in terms of cell division and the effects of external agents, such as temperature and salinity, on cell diameter must remain the goal of future investigations. A similar extension of the work will be necessary in respect of the varieties and for the final elucidation of the taxonomic position.

Table I. List of Stations, Positions, Dates, Temperatures and Salinities at or near 20 m., Mean Diameters (in units of *ca* 4μ), Number of Diatoms Measured and Form

(The following abbreviations are used to indicate the ships concerned with the various collections: *George Bligh, GB*; *Onaway, O*; *Explorer, E*; *Discovery, D*; *William Scoresby, WS*; *Dana, Da*; and *Svend Foyn, SF*.)

St.	Lat.	Long.	Date	T° C. at 20 m.	S ‰ at 20 m.	Mean diam.	No. measured	Form
				Shetland and Faeroe areas				
*E*1	59° 23′ N.	0° 23′ W.	18/4/31	5·93	35·29	9·3	100	Not separated
*E*2	59° 30′ N.	1° 33′ W.	10/5/31	7·03	35·19	8·5	100	,,
*E*3	60° 06′ N.	0° 48′ W.	15/4/32	7·08	35·36	10·2	100	,,
*E*4	60° 45′ N.	0° 42′ W.	31/8/32	11·72	35·25	7·8	100	,,
*E*5	58° 21′ N.	0° 04′ W.	21/5/33	8·51	35·09	7·3	100	Var. *oceanica*
*E*6	60° 07′ N.	0° 45′ W.	7/6/33	9·18	35·37	9·5	100	Not separated
*E*7	61° 01′ N.	1° 29′ E.	30/5/34	8·52	35·37	8·4	100	,,
*E*8	60° 44′ N.	2° 28′ E.	19/4/35	7·75	35·35	9·8	100	,,
*E*9	61° 05′ N.	2° 10′ W.	14/6/36	9·52	35·39	6·9	100	Var. *oceanica*
*E*10	59° 21′ N.	3° 45′ W.	26/8/37	—	—	8·4	100	Not separated
*E*11	61° 02′ N.	7° 50′ W.	3/7/38	—	—	9·6	100	*Type
,,	61° 02′ N.	7° 50′ W.	3/7/38	—	—	8·45	100	*Var. *semispina*
,,	61° 02′ N.	7° 50′ W.	3/7/38	—	—	7·28	100	*Var. *oceanica*
*E*12	60° 01′ N.	1° 12′ E.	27/3/39	—	—	8·98	100	†Type

* The type, var. *semispina* and var. *oceanica*, occurred at this station in the following proportions: 61, 20 and 19.

† The type only was measured at this station, but both the varieties occurred there. Var. *oceanica* however did not occur in the random sample of 30 mentioned on p. 280.

St.	Lat.	Long.	Date	T° C. at 20 m.	S ‰ at 20 m.	Mean diam.	No. measured	Form
				South-west of British Isles				
GB–Mc10	48° 20′ N.	6° 40′ W.	18/4/39	10·95*	35·44*	7·82	100	Type
GB–Mc17	49° 06′ N.	9° 05′ W.	19/4/39	10·90*	35·44*	7·37	100	,,
GB–Mc23	50° 01′ N.	10° 18′ W.	20/4/39	10·88*	35·53*	7·70	40	,,
GB–Mc25	49° 36′ N.	9° 30′ W.	21/4/39	10·80*	35·50*	7·57	35	,,
GB–Mc6	48° 05′ N.	7° 53′ W.	3/6/39	12·48*	35·57*	8·17	100	,,
GB–Mc8	48° 58′ N.	8° 45′ W.	3/6/39	11·45*	35·40*	8·34	50	,,
				Firth of Forth Swirl area				
GB–B2	56° 21′ N.	1° 10′ W.	21/5/32	7·23	34·70	8·8	50	,,
GB–D12	55° 42′ N.	1° 17′ W.	30/6/32	11·84*	34·77*	10·0	100	,,
GB–B19	55° 40′ N.	0° 25′ W.	13/5/33	8·26	34·93	14·6	100	,,
GB–G3	56° 03′ N.	0° 38′ W.	23/5/36	8·69	34·79	8·5	100	Var. *oceanica*
				East Dogger area				
GB–C10	55° 26′ N.	4° 42′ E.	22/5/33	8·06	34·71	19·9	100	Type
GB–F7	55° 52′ N.	4° 23′ E.	23/5/35	8·14	35·00	16·3	100	,,
GB–Q12	54° 50′ N.	5° 44′ E.	20/11/36	10·40	34·65	20·3	100	,,
GB–F21	56° 53′ N.	6° 38′ E.	2/5/37	6·08	34·79	17·3	100	,,
				Off southern coast of Norway				
GB–B9	57° 40′ N.	4° 52′ E.	12/5/33	7·28	35·08	8·1	100	Var. *oceanica*
GB–G15	57° 30′ N.	4° 10′ E.	26/5/36	7·42	35·12	8·2	100	,,
				South-west Dogger Swirl area				
O–20/2	54° 24′ N.	1° 22′ E.	22/9/32	13·81	34·43	13·9	100	Type
GB–J12	53° 20′ N.	2° 40′ E.	27/10/32	11·75	34·23	16·6	100	,,
GB–J19	54° 10′ N.	5° 27′ E.	28/10/32	12·28	34·15	15·4	100	,,
GB–J22	53° 45′ N.	4° 02′ E.	29/10/32	11·89	34·72	17·6	100	,,
GB–J32–0 m.	54° 07′ N.	2° 03′ E.	31/10/32	10·74	34·49	15·9	100	,,

TABLE I (*cont.*).

St.	Lat.	Long.	Date	*T*° C. at 20 m.	*S* ‰ at 20 m.	Mean diam.	No. measured	Form
			South-west Dogger Swirl area (*cont.*)					
GB–J32–20 m.	54° 07′ N.	2° 03′ E.	31/10/32	10·73	34·52	15·5	100	Type
GB–C20	54° 19′ N.	2° 49′ E.	23/5/33	10·72	34·90	17·5	100	„
GB–G27	53° 27′ N.	2° 14′ E.	19/6/35	12·38	34·76	14·3	100	„
GB–N5	53° 52′ N.	1° 02′ E.	24/9/35	14·66	34·72	12·9	300	„
GB–N6	54° 08′ N.	1° 37′ E.	24/9/35	14·96	34·75	12·9	100	„
GB–N12	54° 36′ N.	1° 42′ E.	26/9/35	13·52	34·57	13·5	100	„
GB–O13	53° 24′ N.	1° 34′ E.	4/10/35	13·98	34·77	13·1	200	„
GB–O15	54° 03′ N.	1° 36′ E.	5/10/35	14·40	34·73	12·8	100	„
GB–O16	54° 13′ N.	2° 26′ E.	5/10/35	13·80	34·64	12·6	100	„
GB–O34	54° 35′ N.	1° 48′ E.	9/10/35	12·98*	34·59*	13·4	100	„
GB–P11	54° 30′ N.	3° 34′ E.	24/10/35	11·41	34·85	13·2	200	„
GB–P14	53° 45′ N.	4° 37′ E.	25/10/35	12·33	34·62	13·5	100	„
GB–P21	53° 15′ N.	2° 21′ E.	26/10/35	11·69	34·71	13·3	100	„
GB–Q24	53° 44′ N.	4° 09′ E.	9/11/35	11·73	34·79	13·1	100	„
GB–Q26	54° 05′ N.	4° 31′ E.	11/11/35	11·58	34·84	12·8	100	„
GB–R3	54° 55′ N.	3° 18′ E.	23/11/35	9·90	34·65	12·9	100	„
GB–R15	54° 00′ N.	1° 47′ E.	25/11/35	9·40	34·59	12·7	100	„
GB–G39	53° 43′ N.	2° 58′ E.	31/5/36	9·26	34·39	13·5	100	„
GB–J17	54° 00′ N.	3° 01′ E.	8/8/36	14·39*	34·66*	22·2	100	„
GB–P22	53° 33′ N.	3° 49′ E.	3/11/36	11·38	34·59	19·4	100	„
GB–Q18	54° 25′ N.	2° 06′ E.	21/11/36	8·88	34·65	20·2	100	„
GB–Q30	53° 36′ N.	2° 01′ E.	22/11/36	9·70	34·66	18·3	100	„
O–IV/F6	54° 32′ N.	1° 37′ E.	24/2/37	4·59*	34·80*	16·1	100	„
O–VI/F6	54° 33½′ N.	1° 35½′ E.	23/4/37	6·48*	34·76*	16·8	100	„
GB–H19	54° 21′ N.	0° 38′ E.	7/6/37	9·01	34·51	11·4	100	„
GB–L30	54° 10′ N.	3° 03′ E.	7/8/37	14·22*	34·65*	19·4	100	„
GB–L31	54° 04′ N.	2° 13′ E.	7/8/37	16·14*	34·83*	20·6	100	„
GB–M10	54° 59′ N.	1° 30′ E.	12/10/37	13·36	34·62	18·5	100	„
GB–M11–0m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·93*	20·6	100	„
GB–M11–27m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·66*	19·7	100	„
GB–M11–55m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·65*	20·2	100	„
GB–M15–0m	54° 19′ N.	0° 40′ E.	13/10/37	13·06*	34·58*	19·2	100	„
GB–M15–27m	54° 19′ N.	0° 40′ E.	13/10/37	12·94*	34·58*	20·2	100	„
GB–M15–55m	54° 19′ N.	0° 40′ E.	13/10/37	12·93*	34·58*	20·3	100	„
GB–M16	54° 23′ N.	1° 00′ E.	13/10/37	13·22	34·65	19·65	100	„
GB–M16–0m	54° 23′ N.	1° 00′ E.	13/10/37	13·24*	34·61*	19·7	100	„
GB–M16–18m	54° 23′ N.	1° 00′ E.	13/10/37	13·22*	34·65*	19·6	100	„
GB–M16–36m	54° 23′ N.	1° 00′ E.	13/10/37	13·22*	34·59*	19·6	100	„
GB–M17	54° 29′ N.	1° 19′ E.	13/10/37	14·05	34·75	18·7	100	„
GB–M18	54° 33′ N.	1° 39′ E.	13/10/37	13·56*	34·69*	17·35	100	„
GB–M19	54° 33′ N.	1° 58′ E.	13/10/37	13·48*	34·71*	17·3	100	„
GB–M21	53° 56′ N.	0° 37′ E.	14/10/37	13·77	34·74	19·5	100	„
GB–M23	53° 51′ N.	1° 43′ E.	14/10/37	14·07	34·87	19·3	100	„
GB–M24	54° 07′ N.	2° 25′ E.	14/10/37	14·36	34·85	18·8	100	„
GB–M26	53° 26′ N.	2° 11′ E.	15/10/37	14·39	34·16	19·2	100	„
GB–M37a–0m	54° 07′ N.	2° 21′ E.	17/10/37	14·18*	34·85*	19·3	100	„

TABLE I (*cont.*).

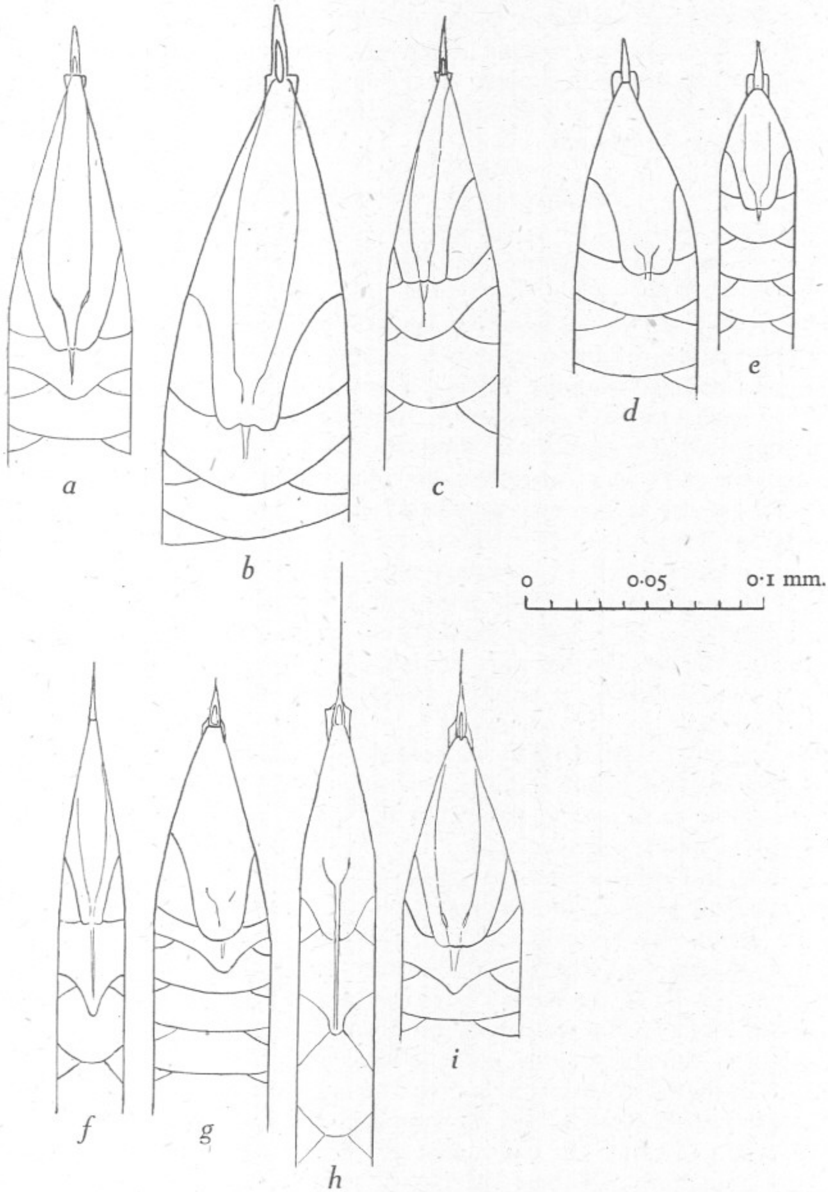
St.	Lat.	Long.	Date	T° C. at 20 m.	S ‰ at 20 m.	Mean diam.	No. measured	Form
			South-west Dogger Swirl area (*cont.*)					
GB–M 37a –18 m	54° 07′ N.	2° 21′ E.	17/10/37	14·10*	34·86*	18·9	100	Type
GB–M 37a –36 m	54° 07′ N.	2° 21′ E.	17/10/37	13·84*	34·86*	19·45	100	”
GB–N 13	53° 35′ N.	2° 57′ E.	28/10/37	13·48	34·33	19·2	100	”
GB–N 16	54° 00′ N.	4° 21′ E.	29/10/37	13·76	34·48	19·2	100	”
GB–N 25	54° 25′ N.	2° 56′ E.	30/10/37	12·99	34·84	20·2	100	”
GB–N 29	53° 48′ N.	3° 40′ E.	30/10/37	—	—	18·5	100	”
GB–P 1	53° 32′ N.	2° 20′ E.	28/11/37	9·60*	34·41*	18·4	100	”
GB–D/F 6	54° 33′ N.	1° 40′ E.	28/2/38	5·37*	34·86*	17·8	100	”
GB–E/F 5	54° 31′ N.	1° 23′ E.	13/3/38	5·97	34·86	17·4	100	”
GB–P 11	53° 20′ N.	2° 29′ E.	22/10/38	—	—	17·3	100	”
GB–P 13	54° 00′ N.	2° 34′ E.	23/10/38	13·34	34·76	17·65	100	”
GB–P 18	54° 27′ N.	2° 11′ E.	24/10/38	11·48	34·58	17·6	100	”
GB–P 27	55° 18′ N.	1° 5′ E.	25/10/38	10·44	34·83	15·6	50	”
GB–Q 8	55° 16′ N.	4° 6′ E.	11/11/38	10·67	—	17·5	100	”
GB–Q 16	56° 49′ N.	6° 38′ E.	13/11/38	11·84	34·83	16·4	100	”

St.	Lat.	Long.	Date	T° C. at 20 m.	S ‰ at 20 m.	Mean diam.	No. measured	Form
			Antarctic					
WS 67	53° 19′ 00″ S.	45° 16′ 00″ W.	20/2/27	3·64	33·80	8·5	50	Var. *oceanica*
WS 70	51° 58′ 00″ S.	55° 42′ 00″ W.	22–3/2/27	7·14	34·08	9·4	50	”
WS 472	59° 42′ 30″ S.	58° 01′ 00″ W.	12/12/29	−0·26	33·99	14·3	50	”
WS 520	52° 25′ 00″ S.	61° 20′ 00″ W.	27–8/2/30	6·33	34·11	8·4	100	”
SF 10	60° 04′ 00″ S.	10° 25′ 00″ W.	24/2/38	−0·40	—	6·7	50	”
D 161	57° 21′ 20″ S.	46° 43′ 30″ W.	14/2/27	1·43	33·80	4·1	100	Var. *semispina*
D 496	53° 17′ 45″ S.	35° 56′ 00″ W.	19/11/30	−1·10	33·91	4·2	100	”
WS 472	59° 42′ 30″ S.	58° 01′ 00″ W.	12/11/29	−0·26	33·99	6·2	100	”
SF 7	56° 45′ 00″ S.	2° 41′ 00″ E.	27/12/37	−1·20	—	4·1	50	”
SF 10	60° 04′ 00″ S.	10° 25′ 00″ E.	24/1/38	−0·40	—	4·8	100	”
			Tropical Pacific					
WS 706	5° 37′ 30″ S.	83° 58′ 00″ W.	23/7/31	19·49	35·12	5·6	100	Var. *semispina*
WS 707	5° 37′ 30″ S.	84° 31′ 30″ W	23/7/31	20·42	35·16	5·1	100	”
			Tropical Atlantic					
Da 4007	18° 22′ N.	18° 14′ W.	15/3/30	18·46	35·80	4·4	50	Type

* Depth nearest to 20 m. or that shown at left of column, except that temperatures and salinities were taken at 30 m. and 50 m. for *GB*–M 15–27 m. and 55 m., at 20 m. and 30 m. for *GB*–M 16–18 m. and 36 m., and at 20 m. and 40 m. for *GB*–M 37a–18 m. and 36 m.

RHIZOSOLENIA STYLIFORMIS AND ITS VARIETIES

The application of biometric observations to material of *Rhizosolenia styliformis*, collected beyond the area dealt with in the first part of this paper, made it abundantly clear that the specific name had been regularly applied to more than one form (Text-fig. 1). It therefore became necessary for me to attempt



Text-fig. 1. Type and varieties of *Rhizosolenia styliformis* from different sources. *a*, Type from southern North Sea (St. 4, Cruise N, 24/9/35); *b*, Type from southern North Sea; *c*, Type from semi-tropical Atlantic (St. 4007, *Dana*, 15/3/30); *d*, var. *oceanica* from west of Faeroes, 3/7/38; *e*, var. *oceanica* from Antarctic (St. 10, *Svend Foyn*, 24/1/38); *f* and *g*, var. *semispina* from tropical coast of East Pacific (St. 707, *William Scoresby*, 23/7/31); *h*, var. *semispina* from Antarctic (St. 10, *Svend Foyn*, 24/1/38); *i*, var. *semispina* from west of Faeroes, 3/7/38.

an identification of the forms I have distinguished in order to compare like with like. The somewhat confused taxonomic position revealed in the sections that follow has involved, among other things, a future consideration as to whether the species originally established as *R. styliformis* can properly be separated from *R. hebetata*.

Rhizosolenia styliformis (Brightwell)

Brightwell, T., 1858. *Quart. Journ. Micr. Sci.*, Vol. VI, pp. 93–5, pl. V.
Hustedt, F., 1930. *R. styliformis* var. *longispina*. 'Die Kieselalgen', Rabenhorst's *Kryptogamen Flora*, Bd. VII, p. 586, fig. 334.

The type of the species has been figured by Brightwell who established it from observations made on specimens taken from a tunicate attached to an oyster shell dredged from the 'Silver Pit' south of the Dogger Bank, on others found as inclusions in the bodies of *Noctiluca* collected near Gorleston and from guano taken from Callao. Brightwell writes of boiling his material in acid, and for this reason, doubtless, his figures do not show the lateral wings at the base of the apical spine to which I attach considerable importance for purposes of diagnosis. Nevertheless, the shape of the valve or calyptra resembles that form which I have found to occur alone and with great uniformity throughout the southern North Sea south of latitude 56° N. This type-form is also similar to that figured by Hustedt as *R. styliformis* var. *longispina*, except that the apical spine may be either drawn out into a fine process or blunt, the two different conditions being sometimes seen at opposite ends of the same cell.

The type is characterized by its considerable size, the fact that its valves are nearly straight-sided, and the possession of right-angled wings, which arise along the valve near its point, but end at, or very near, the origin of the eccentrically placed terminal spine (Text-fig. 1 *a*, *b*, *c*). These characters are found in all individuals from the southern North Sea, where, in the area near the south-west patch of the Dogger Bank, the species occurs regularly in its greatest profusion. Outside this area, the shape and position of the wings show variability. Samples from the western end of the English Channel and to the south-west of the British Isles nearly resemble those of the southern North Sea, but a few individuals occur in which the wings end above or below the origin of the apical spine, and the wing margins may not be quite right angled. In the Scottish material from the northern North Sea and Faeroe-Shetland areas, the proportion of these aberrant cells may be considerable, and instances in which the wings arise above the origin of the spine are particularly numerous. Of these latter individuals a certain number are to be found in which the position and even the shape of the wings is intermediate with that to be described for the variety *semispina* in the next section, and there is no doubt that the two forms are linked by a chain of morphological intermediates. Finally, in some of the smaller cells among the population taken at *Dana* St. 4007 in the subtropical Atlantic, wings are lacking.

In view of the fact that other workers have made little or no discrimination between the type and the varieties a distributional picture is difficult. From the material I have so far examined I can vouch for the presence of the type, occasionally in abundance, on the east side of the Atlantic from about 30° to 60° N. latitude, but nowhere else. Gran (1902) has recorded *R. styliformis* from the Norwegian Sea between Jan Mayen and the Norwegian coast, but the shape of the apical wings given in one of his figures suggest to me that the form found was probably not the type but my variety *oceanica*. The species has frequently been recorded from the Antarctic. However, in many of these samples, I think the organism concerned is the variety to be described below as *semispina*. It is also possible that there may have been confusion with *R. curvata* Zacharias, the shape and relation of whose wings and terminal spine are identical with that of the type I have just dealt with, so that it would not be possible to decide between the two species were only short terminal fragments available. Karsten (1905, p. 96) gives *R. styliformis* as occurring in the Antarctic, but he considers it to be a variety (*Valdiveae*) apparently synonymous with Brightwell's var. *latissima* and Castracane's *R. polydactyla* (Castracane, 1886). This larger form is now generally given specific status under the last name.

R. styliformis var. *semispina* (Hensen) Karsten

Karsten, G., 1905. *R. semispina. Wiss. Ergebn. Deutsche Tiefsee Expedition auf den Dampfer 'Valdivia'*, 1898–99, Bd. II, Pt. II, Lief. 1, p. 96, pl. X, figs. 4, 4*a* and 4*b*.
? Bailey, J. W., 1856. *R. hebetata. Amer. Journ. Sci.*, p. 5, pl. 1.
? Hensen, V., 1887. *R. semispina. Ber. Kom. der deutsches Meeres*, p. 84, pl. V, figs. 39*a*, *b*.
? Gran, H., 1902. *R. hebetata* forma *semispina. Fauna Arctica*, Bd. IV, p. 527, pl. XVII, figs. 11, 12.
Cupp, E., 1943. *R. styliformis* var. *longispina* Hust. *Bull. Scripps Inst. Oceanog.*, Vol. 5, No. 1, p. 87, fig. 488 and fig. C (5).

This second form of the species I have found to be very widely distributed. Like the type, the conical valves have rather straight sides ending in an eccentrically placed spine. The spine may be either blunt or drawn out into a fine process. Below its origin there arise on either side wing-like membranes which terminate some way up the spine. These wings commonly present an obtuse angle at their outer edge and are not rounded; they may, however, be absent altogether from some of the smaller individuals taken in warm water. Intercalary plates are numerous and arranged in two rows. The middle part of the first intercalary plate at the opposite side of the cell to the eccentrically placed spine (i.e. the 'ventral' side), is produced into a tongue extending some distance back into the next intercalary plate (Text-fig. 1 *f*, *g*, *h*, *i*).

In this variety I have classed examples from the Scottish collections in the northern North Sea and Atlantic, from the west coast of South America (*WS* 706 and *WS* 707 of the *Discovery* collections) and from the Antarctic (*Discovery* and *Svend Foyn* material). Transitional forms linking this variety to the type and found in the Scottish material have already been described in the previous section. My richest collections came from the Antarctic and in these specimens the tongue of the first intercalary plate is often very pronounced, the spine ends in a long fine process and the thick-walled cells show little variation (Text-fig. 1*h*). I have also found the variety in a number of preparations in the British Museum collections to which the authorities of the British Museum of Natural History most courteously gave me access. Below I give particulars of those examples in which it is possible to give a locality.

Slide no.	Legend	Habitat
7,987	Ascension Island per *Buccaneer*, 1886	Ascension Island
14,336	Coll. Temp. et Perag	Côtes Equatoriales d'Afrique
15,262	*R. styliformis* Tempere et Perag. Coll. Deby	Mediterranean
21,334	*R. styliformis*. St Helena from Salps	St Helena
31,060 31,061 31,063	Arafura Sea, surface Coll. Comber	Arafura Sea
31,064	Antarctic surface	Antarctic surface

From such distributional records as are available, the general impression to be gained is that the form favours water near the coast or in continental slope areas, and that it finds its optimum in cold water at high latitudes in the Antarctic.

The examples of this variety taken in the Antarctic are identical with those reported for the same area as *R. semispina* by Karsten. The variety has also been recorded as *R. styliformis* in the *Discovery Reports*. Under the title *Rhizosolenia styliformis* var. *longispina* Hustedt, Cupp figures the characteristic apical wings of the variety under discussion and the tongued first intercalary plate. It is described as 'Oceanic' and 'found off California and in Gulf of California'.

The identity of the form with that described by Karsten as *R. semispina* Hensen raises a taxonomic complication in that Hensen's *R. semispina* does not possess the characteristic lateral wings, nor does he give any record or figure showing the median tongue of the first intercalary plate. Furthermore, the apical spine and the neighbouring part of the valve are very much thicker and there is little doubt that Hensen's Baltic specimens are similar in form and structure to the fragments taken from the sea bottom off Kamschatka and figured and described by Bailey as *R. hebetata*. Gran places Hensen's *R. semispina* as *R. hebetata* forma *semispina*, but in descriptions and figures of Gran's form the apical wings and median tongue of the first intercalary plate do not appear. It has already been said that some of the smaller specimens of the variety here described have been found to lack the apical wings when found in warmer habitats. In the event of the cell diameter being reduced, it is quite possible that the median ventral tongue of the first intercalary plate might disappear. These changes would bridge the gap between the variety under discussion and the northern hemisphere forms described by Bailey, Hensen and Gran. If this chain of intermediates is established, the variety I describe as *R. styliformis* var. *semispina* and the type species itself would become varieties of the species *R. hebetata* Bailey, as this name would take precedence over Brightwell's *R. styliformis*.

R. styliformis var. *oceanica* var. nov.

Peragallo, H., 1892. *R. styliformis*. *Le Diatomiste*, p. 111, pl. XVII.
Van Heurck, 1896. *R. styliformis*. *A Treatise on the Diatomacae.*
Gran, H., 1902. *R. styliformis*. *Rep. Norw. Fish. Mar. Invest.*, Bd. II, No. 5, pp. 36–9 and 173–5, pl. I, figs. 1–9.
Hustedt, 1930. *R. styliformis*. 'Die Kieselalgen' in Rabenhorst's *Kryptogamen Flora*, p. 584, fig. 333.
Cupp, E. E., 1943. *R. styliformis*. *Bull. Scripps Inst. Oceanog.*, Vol. 5, No. 1, p. 87, fig. 48 *Aa*.

The form which I am calling var. *oceanica* has been described or figured as the type by the authorities just given above. The valves slope somewhat convexly to the eccentrically placed terminal spine. The latter is distinguished by the possession of rounded wings which run on either side from its base often for half its length (Text-fig. 1*d*, *e*). There are numerous intercalary plates arranged in two rows and the plates and valves are seldom very stoutly made. There is hardly ever any trace of the tongue-like process of the first intercalary plate which is so pronounced a feature of the variety *semispina*. Wherever I have found this form, the diagnostic value of its characters have remained sharp and clear presenting no intermediates with any other.

I have recognized this variety in the Antarctic material of the *Discovery* Expedition, in Scottish Fishery Board collections made in the Atlantic near the Faeroes and in the following slides of the British Museum of Natural History.

Slide no.	Legend	Habitat
13,067	Cl. a. M. Diat. 308	Sea of Behring
26,013	In mare H. L. Smith (452)	58° N., 32° W.
26,753	Types of Synopsis des Diatomees Belge Van Heurck	—
28,039	Coll. O'Meara	Davis Strait, 7/8/1871, lat. 45°, long. 53° 43′
28,074	Coll. O'Meara	Atlantic, lat. 58°, long. 32°
31,057	Coll. Comber	Arafura Sea, surface
7,345	P. Oberg (Cleve)	Atlantic, 10/6/1870, lat. 58°, long. 32°

It also appears in figures of Gran's collections (*loc. cit. supra*) made in August and September 1900 in the Norwegian Sea between Jan Mayen and Norway and near Bear Island, and in a figure of *R. styliformis* stated by Cupp to be 'oceanic' and 'sometimes fairly numerous' off California. So far as they go, these occurrences, taken together with my own observations, suggest a more oceanic distribution than that indicated for var. *semispina* or the type and it appears to find its optimum conditions in cold, temperate or polar water.

When the Scottish material was first measured, the fact that several varieties of the species existed was not yet appreciated. However, in view of later work giving the distribution just outlined and also because it had a strictly limited southward distribution in the North Sea, it appeared possible that its abundance relative to the other varieties of the Faeroe-Shetland area might afford an index of oceanic inflow. For this reason, although no serious big-scale effort has been attempted, I have been through the twelve Scottish stations given in Table I and have found the proportion of *oceanica* individuals in random samples of 30. These I give below:

St. no.	Date	*Oceanica* individuals	St. no.	Date	*Oceanica* individuals
1	8/4/31	1	7	30/5/34	30
2	10/5/31	4	8	19/4/35	8
3	15/4/32	12	9	16/6/36	29
4	31/8/32	3	10	26/8/37	27
5	21/5/33	30	11	3/7/38	6
6	7/6/33	17	12	27/3/39	0

These proportions suggest that the variety was relatively more abundant in the period 1933–7 than in 1931–2 and 1938–9. The reports of the Scottish Fishery Board (1932–9) indicate that the period 1931–7 was one during which an unusual influx of Atlantic water entered the northern North Sea and in these circumstances my figures hold out the hope that a more complete examination of the Scottish collections might yield interesting results.

At two stations in Scottish waters the variety was found to be forming auxospores which arose at right angles to the parent cell in the way I have observed them to do in the type. I give below some of the circumstances of their occurrence.

Position	59° 44′ N., 1° 10′ W.	60° 02′ N., 7° 50′ E.
Date	23/6/35	3/7/38
$T°$ C. at 20 m.	8·77	9·71
S ‰ at 20 m.	35·38	35·41
Diameter of parent	24 μ	24 μ
Diameter of auxospore	76 μ	44 μ

The forms I have described may be separated by the following dichotomous key:

A. Wings angular.

a. Wings usually form right angles and do not extend beyond base of apical spine. Inner edge of first intercalary plate often shows trace of tongue-like projection. — *R. styliformis*

b. Wings form obtuse angles and extend along apical spine. Inner edge of first intercalary plate generally produced into pronounced tongue-like projection. — *R. styliformis* var. *semispina*

B. Wings rounded. — *R. styliformis* var. *oceanica*

Diameter measurements of *Rhizosolenia styliformis*

All the biometric observations on the species given in my earlier paper (Wimpenny, 1936) and those for the southern North Sea, the western entrance of the English Channel, the semi-tropical Atlantic and certain stations of the north and central North Sea and the Faeroe-Shetland area, set out in Table I of this account, may be referred to the type of the species. The material from the semi-tropical Atlantic consisted of one station only and will not be further discussed at the present stage.

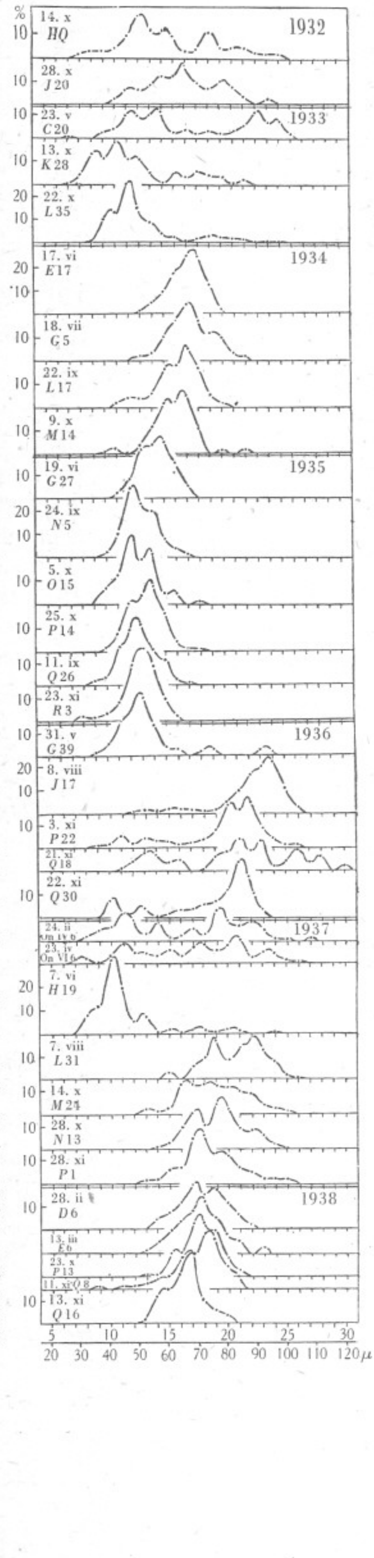
The increase in cell diameter, due to the formation of auxospores producing a new population and the continuous diminution due to fission, has been mentioned on pp. 38 and 39 of Part I of this paper. What was considered to be the newly-formed auxospore generation and the original parent stock were then shown to exist side by side in the southern North Sea. It was also pointed out that larger cells are favoured in the south and east of this area, and it was suggested that temperature may have exerted a selective effect.

In Text-fig. 2 I have plotted the numbers at different diameters for a series of representative samples of the type species taken through various seasons of 1932–9, mainly from the south-west Dogger Bank Swirl area of the North Sea. It will be seen that the narrow original parent stock of 1932–3 had disappeared by 1934 and that the wide newly-formed auxospore generation recurred each year at a steadily diminished diameter until 1937 when it also disappeared. Before its extinction, however, it must be noticed that there was a relative revival in the winter of 1936–7 and in June 1937 which may have had its origin in some external factor such as temperature or salinity. Individuals of this latter generation (Pl. V) measuring 60μ in diameter attached to an auxospore of 120μ diameter and of 40μ attached to an auxospore of 90μ were found in September (St. 5, Cruise N) and October (St. 11, Cruise P) 1935 respectively. Among the cells of the October samples there were also a considerable number with scars showing that auxospores had been attached to them. The size of generation resulting from this formation of auxospores, first evident in 1936, was comparable to that found in 1932–3, when the species was also represented by two size generations. From mid 1937 until the observations ended the species was again represented by a unimodal population consisting of individuals of the most recent generation. These observations show that on this occasion a period of three to four years elapsed between the production of auxospore generations in the southern North Sea.

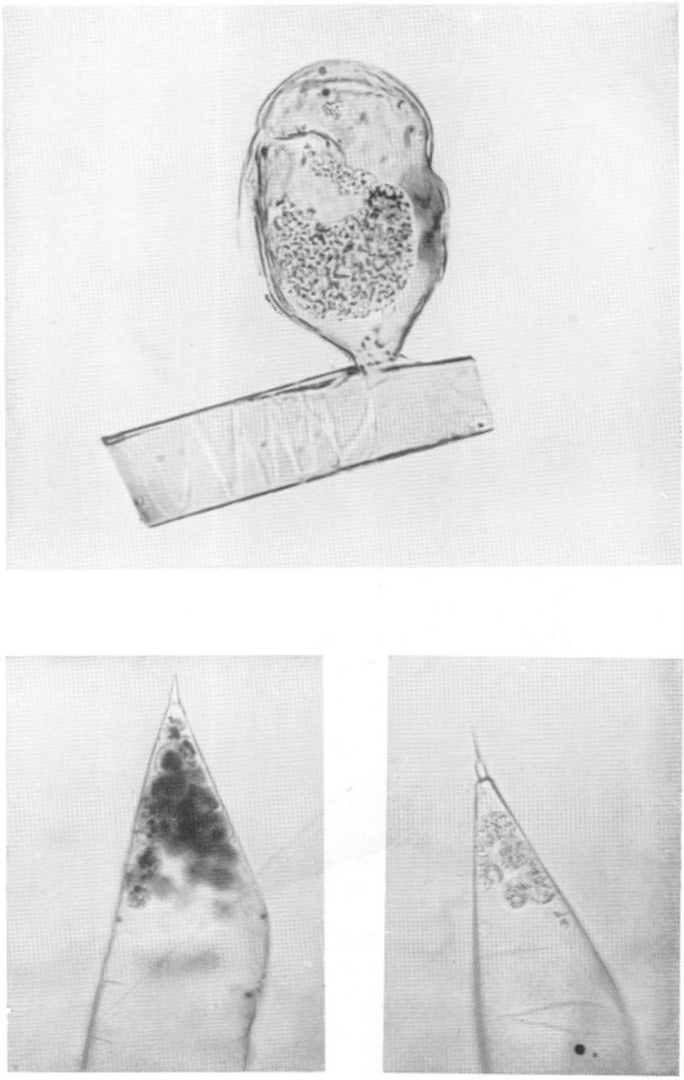
In this same area there is another internal factor which might be conceived to affect cell-diameter in these diatoms. This is the regular occurrence of microspores whenever a big flowering arises (Pl. V). Microspores were particularly numerous in the autumn and towards the end of the annual period of abundance. Their appearance is that of clear disc-shaped bodies bearing on their surfaces little extruded spheres of chromatic matter and is similar to that reported for many other species of diatom. I have only to add in respect of *R. styliformis* that I have observed the disc-shaped bodies to become fusiform and exhibit amoeba-like movement. Whereas Gross (1937) appears to think microspores a morbid or parasitic phenomenon, Karsten (1905, pp. 107–12) has described them as the agents of sexual reproduction in *Corethron* and, more recently, Braarud (1939) has found that they unite and may produce normal cells in *Chaetoceras*.

From such evidence as is available, therefore, it seems likely that microspores represent a method of sexual reproduction. However this may be, it is clear that unless cells derived from microspores immediately took up the size of microspore producers the steady size diminution ending in the production of auxospores that has just been recorded would not have been apparent.

Passing through an intermediate stage in the Firth of Forth Swirl area, the individual cells of the species were much narrower in the northern North Sea and Faeroe-Shetland area than they were in the southern North Sea. No discrimination between the varieties and type of the species was made when several of the northern North Sea and Faeroe-Shetland samples were measured, but a subsequent examination showed the type to be present in most of them. The populations were unimodal in size distribution with the exception of E 6 in 1933. Of the two modes here, however, it was found on re-examination that the smaller one was caused by the variety *oceanica*. The largest cells from this area were found early in the year, a minimum being



Text-fig. 2. Frequency distributions for cell diameters of *Rhizosolenia styliformis* taken from *George Bligh* and *Onaway* stations made between 1932 and 1938 in the south-west Dogger area of the North Sea, except Q8 and Q18, which were in the north-east Dogger area. Percentages are given on the ordinate and the diameter measurements are shown as arbitrary units along the abscissa, the corresponding values in μ being given below this.



Photomicrographs of *Rhizosolenia styliformis* Brightwell, ×215. Above: auxospore in process of formation (St. 5, Cruise N, 1935). Below: parts of cells containing microspores, from southern North Sea material.

reached in July and August, the last months in which my material showed the species is to be found in any numbers in these waters. There was, therefore, no steady fall in diameter extending over several years, but an annual diminution and a regeneration of size evident each spring. In these circumstances it appears likely that auxospore formation is annual, a state of affairs in sharp contrast to that taking place in the southern North Sea.

Still smaller individuals were represented in six samples of the type taken at the western approaches to the English Channel in the summer of 1939 (Table I). These samples were also unimodal and included one individual of 20μ diameter taken in the April collections and found to be forming an auxospore. In the June samples one or two individuals were found with diameters between 60 and 76μ. It seems likely that these represented an auxospore generation formed in April, and this appearance of the large auxospore-produced cells in the same season as their generation, taken together with the fact that the populations were even narrower than those from the Faeroe Shetland area, suggests that the process of auxospore formation takes place at a shorter interval than in the North Sea.

While it is clear that more sampling, and some *in vitro* work which was contemplated before the war, will have to be carried out before any useful picture of the external and internal factors controlling the size of this diatom can be produced, the present work sets certain problems for further elucidation.

For instance, it has been pointed out in the preceding paragraphs that in the winter of 1936–7 and early summer of 1937, there was a relative recovery in the narrower generation. This occurred at a season of low temperature and high salinity, and it remains to be shown whether either temperature or salinity is capable of affecting the normal waning of an older and narrower generation when the population is bimodal. In 1935 and 1936 the origin and development of a new wide generation took place when the salinity in the area had begun a fall which continued until 1937–8 (Wimpenny, 1944). Did a lowering of the salinity play any part in the origin and survival of the new wide generation? Again the populations of the species type are successively narrower as one proceeds from the southern North Sea, through the Firth of Forth Swirl and Scottish areas to the western entrance of the English Channel. These districts constitute a progression of increasing salinities and the question arises as to whether the salinity has any significant relation to the diameters of the various populations.

Another question concerns the cell-wall. Is its thickness affected by the supply of silica and the conditions under which it is laid down? It is easy to see that the cell-walls of cold water diatoms are thicker than those of warmer water and there may be similar seasonal and local differences. Variations in the thickness of the cell-wall would obviously affect the number of cell divisions equivalent to a given diminution of diameter.

I have put these questions in order to show that their solution will be necessary before one can hope to estimate the age, number of divisions and effect of nutrient salts on a population of *R. styliformis* as a result of considering differences in diameter. At present the chief use that can be made of these frequency observations is to help to identify populations by the noting of similar relative distributions of diameter frequencies. Useful evidence on these lines has already been obtained and more may confidently be expected to result from future work.

Summary

1. Diameter measurements of *Rhizosolenia styliformis* from the Antarctic, the subtropical Atlantic and Pacific Oceans and from the North Sea and neighbouring waters have made it appear necessary to set up two varieties, *oceanica* and *semispina*, in addition to the type of the species *R. styliformis*. The type as I describe it has been called var. *longispina* by Hustedt, but elsewhere it has often been figured as the var. *oceanica* of this paper. Var. *semispina* is synonymous with the form represented by Karsten as *R. semispina* Hensen. It differs from *R. semispina* as drawn by Hensen and its synonym *R. hebetata* forma *semispina* Gran, but is thought likely to be linked by intermediates. If this is so *R. hebetata* may have to be extended to include and suppress *R. styliformis*, as var. *semispina* is linked to the type by intermediates. Var. *oceanica* has no intermediate forms and, if *R. hebetata* is to be extended, this variety should be established as a separate species.

2. Var. *oceanica* is absent from the southern North Sea and appears to be an indicator species related to oceanic inflow.

3. Auxospore formation was observed for the type in the southern North Sea in 1935 and biometric observations suggest that a period of 3–4 years elapsed between the production of auxospore generations in that area. Outside the southern North Sea for the type, measurements give no indication of auxospore generations occurring at intervals exceeding a year. While auxospore formation has been seen in var. *oceanica* from the Shetlands area samples of June 1935 and July 1938, this phenomenon has not been observed for var. *semispina*.

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