

Extant *Ceratolithus cristatus* life-cycle observations and taxonomic simplification

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Abstract There is still limited knowledge on the taxonomy and complex life-cycle pattern of *Ceratolithus cristatus*, in which the heterococcolith-producing phase is associated with a ceratolith-bearing phase. A study of plankton samples from the surface-waters of the Maldives revealed several *C. cristatus* ceratolith-bearing specimens and a number of combination coccospheres, two of which had an association of three morphologically-distinct coccolith types—horseshoe-shaped *C. cristatus* CER *telesmus* type ceratoliths, delicate, hoop-shaped heterococcoliths and circular *C. cristatus* HET *coccolithomorpha* type planoliths. Having studied a large number of ceratoliths from these samples, we were able to demonstrate that the *cristatus* and *telesmus* ceratolith morphotypes intergrade, representing a growth sequence rather than genotypic differentiation. Based on these observations and a re-examination of other evidence, we propose that two *Ceratolithus* species occur in the modern ocean—*C. cristatus* and *C. nishidae* n. comb. In addition, our observations indicated that, in *C. cristatus*, the hoop-coccoliths and planoliths intergrade, and heterococcoliths, therefore, occur in two life-cycle phases of this species.

Keywords coccolithophores, living, Atlantic Ocean, Maldives, life-cycles, taxonomy, *Ceratolithus*, hoop-coccoliths

1. Introduction

Coccolithophores typically have heteromorphic life-cycles with two morphologically-distinct phases—one diploid and bearing heterococcoliths, the other haploid and either bearing holococcoliths or being naked (e.g. Billard, 1994; Billard & Inouye, 2004; Houdan et al., 2004). The period of change from a haploid to diploid phase, or vice versa (Young et al., 2005), can be observed when a coccolithophore cell is found bearing coccoliths characteristic of both the previous and new life-cycle stages. These ‘combination coccospheres’ provide a valuable source of information about life-cycle associations and taxonomic relationships for diverse coccolith morphotypes (e.g. Kleijne, 1991; Thomsen et al., 1991; Cros et al., 2000; Geisen et al., 2002; Frada et al., 2009; Keuter et al., 2019).

Ceratolithus cristatus Kamptner, 1950 is unusual in that it has a life-cycle that includes heterococcoliths and nannoliths (ceratoliths), but apparently no holococcoliths. A series of indirect observations have been made on this life-cycle (Alcober & Jordan, 1997; Young et al., 1998, 2003; Cros et al., 2000; Sprengel & Young, 2000), and it has been shown to involve the production of three different types of calcareous structures (Alcober & Jordan, 1997; Young et al., 1998). The nannolith-bearing phase

is represented by horseshoe-shaped ceratoliths, possibly corresponding to the haploid stage (Young et al., 2003), whereas the heterococcolith-producing, and presumably diploid, stage of *C. cristatus* is associated either with hoop-shaped, interlocking heterococcoliths, which are composed of rectangular crystal units (Norris, 1971; Manton et al., 1977; Young et al., 1998), or with overlapping coccoliths (planoliths) that have a large central opening surrounded by a collar (Kleijne, 1993; Jordan & Green, 1994; Young et al., 2003). In addition, hoop-coccoliths are commonly seen to form large, delicate coccospheres that surround the ceratoliths and the cells they embrace (Norris, 1965). The planolith coccoliths were originally considered to be a separate genus—*Neosphaera*. Alcober & Jordan (1997) observed *Ceratolithus* hoop-coccoliths on *Neosphaera* coccospheres, and inferred that *Ceratolithus* and *Neosphaera* were alternate life-cycle phases. This finding was repeated by Cros et al. (2000), whilst Sprengel & Young (2000) documented a combination coccosphere, involving all three types of structures—planoliths, hoop-coccoliths and ceratoliths—from plankton samples collected from the Canary Islands.

The basic association is thus well established; the taxonomic nomenclature, however, is confused because,

as summarised in Table 1, there are currently six types of structures associated with the species *C. cristatus*—three ceratolith types (*cristatus*, *telesmus* and *rostratus*), two planolith types (*coccolithomorpha* and *nishidae*) and the hoop-coccoliths. This results in a cumbersome terminology, especially when a formal identification is needed.

The separate Latin names reflect the taxonomic history of the group, although they are now being used informally. For the ceratoliths, *C. cristatus* was the first form to be described (Kamptner, 1950). Norris (1965, p. 22) proposed *C. telesmus* as a separate species with ceratoliths “24 to 36 μm long, horseshoe-shaped, with a narrow angle so that the tips of the arms often meet or sometimes cross at the open end”. Borsetti & Cati (1976) noted that intermediates occurred between the *telesmus* and *cristatus* forms

and suggested that they should be regarded as intraspecific taxa. Jordan & Young (1990) formalised this by recombining them as varieties. Borsetti & Cati (1976) described the morphotype *C. cristatus* forma *rostratus*, but without formally proposing it. They used the presence of a beak at the apical end to define the *rostratus*-type specimens, and many workers have recorded the morphotype as a distinctive form. So, three morphotypes are recognised, but it was not clear if they represented discrete species, or how they were combined in the life-cycle with the different planolith types. As described in Young et al. (2017), we carried out nanoplankton sampling in the Maldives during IODP Expedition 359. The assemblages included common *Ceratolithus* specimens in both the ceratolith- and planolith-bearing phases. Here, we illustrate new examples of



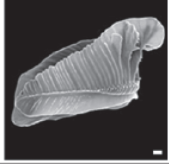
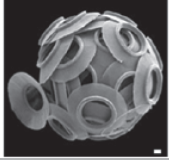

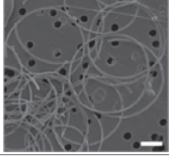
Types of structure	Typical specimens	Diagnostic features	Previous identification (from Nannotax)	Proposed identification
<i>cristatus</i> -type ceratolith		Typical ceratoliths, horseshoe-shaped	<i>Ceratolithus cristatus</i> CER <i>cristatus</i> type	<i>Ceratolithus cristatus</i> CER
<i>telesmus</i> -type ceratolith		Ceratoliths with long delicate arms that curve together to almost touch	<i>Ceratolithus cristatus</i> CER <i>telesmus</i> type	<i>Ceratolithus cristatus</i> CER
<i>rostratus</i> -type ceratolith		Ceratoliths with anterior beak	<i>Ceratolithus cristatus</i> CER <i>rostratus</i> type	<i>Ceratolithus nishidae</i> CER
<i>coccolithomorpha</i> -type planolith		Planoliths with wide central opening	<i>Ceratolithus cristatus</i> HET <i>coccolithomorpha</i> type	<i>Ceratolithus cristatus</i> HET
<i>nishidae</i> -type planolith		Planoliths with narrow central opening	<i>Ceratolithus cristatus</i> HET <i>nishidae</i> type	<i>Ceratolithus nishidae</i> HET
hoop coccolith		Delicate hoop-coccoliths produced by <i>Ceratolithus</i>	<i>Ceratolithus cristatus</i> HET hoops type	<i>Ceratolithus</i> hoop

Table 1: Taxonomic revision of *Ceratolithus* structures. Scale-bars = 1 μm

C. cristatus combination coccospheres from the Maldives that involve various morphotypes, and we provide additional documentation of *C. cristatus* ceratolith specimens. We discuss the main morphological features by comparing the Maldives ceratoliths with several other specimens that were acquired from diverse environments, using these to suggest taxonomic revisions in order to simplify the nomenclature.

2. Materials and methods

In the Maldives, plankton sampling was undertaken during IODP Expedition 359 in October–November 2015, as documented in Young et al. (2017). Samples were collected using a WildCo Beta 8.3-L van Dorn-style plankton sampling bottle from ~15 m below the sea surface. Two litres of sea-water (per filter) were: 1) filtered onto 25-mm-diameter, 0.8- μ m-pore-sized Whatman Nuclepore polycarbonate, track-etched filters and 0.8- μ m Sartorius cellulose nitrate filters; 2) oven-dried at 40°C; and 3) stored in a 47-mm-diameter Millipore plastic Petri dish. The polycarbonate filters were subsequently mounted on aluminium stubs and received gold-palladium coatings, using a Leitz EM ACE2000 sputter-coater. Imaging was initially carried out onboard the ship, using a Hitachi TM3000 scanning electron microscope (SEM), and then using a Jeol JSM-6480LV SEM at University College London (Department of Earth Sciences) to confirm the initial observations and obtain high-resolution micrographs. The cellulose filters were used for light microscope (LM) observation and imaging (Young et al., 2017).

Combination coccospheres were found in Samples Plkt-38 (4.944°N, 73.074°E) and Plkt-45 (4.766°N, 73.135°E), which were collected on 12 and 18 November, 2015, respectively. Plkt-26, Plkt-29, Plkt-32 (4.850°N, 73.283°E) and Plkt-41 (4.777°N, 72.983°E), which were retrieved on 29 October and 3, 6 and 15 November, 2015, respectively, were examined using electron and light microscopy. Plkt-36 (4.933°N, 73.071°E), which was collected on 10 November, 2015, was examined only in the LM. In order to investigate the ceratolith morphology and size variation in *C. cristatus*, ~60 ceratolith specimens were imaged at random from this sample, using a QImaging MicroPublisher 5.0 RTV digital camera.

Additional observations on ceratolith morphology were made using images of specimens from diverse environments (Figure 1, with information on the studied

samples given in Table 2), including specimens from the North and South Atlantic, Pacific and NW Mediterranean. The water samples came from multiple cruises, and were typically collected using CTD rosette samplers, with 12 x 5-L Niskin bottles, concentrated by vacuum filtration onto Millipore-membrane filters that were then cut up and mounted on aluminium stubs. These were subsequently sputter-coated with gold-palladium. Examination of these samples was performed by SEM at the Natural History Museum, London. For measurements, the image-analysis software programme ImageJ (Schneider et al., 2012) was used.

3. Results

3.1 Ceratolith life-cycle observations and morphology in the Maldives

Seven life-cycle associations of *C. cristatus* were documented by SEM from two samples—Plkt-38 and Plkt-45. In Plkt-38, two *telesmus*-type ceratoliths with delicate hoop-coccoliths and one bare ceratolith specimen with no coccoliths were recorded. Other observations included several hoop-coccoliths with *coccolithomorpha*-type planoliths or no other *Ceratolithus* morphotypes at all. The association involving all three types (Plate 2, fig. 1) consisted of a ceratolith in the middle of a large collapsed coccosphere composed predominantly of hoop-coccoliths and six *coccolithomorpha*-type circular planoliths, which interlocked with the hoop-coccoliths. The planoliths from this specimen were 0.74–1.29 μ m thick. The hoop-coccoliths were 0.13–0.28 μ m thick and the ceratolith was 8.4 μ m long. Plkt-45 contained four combination coccospheres, one of which simultaneously bore all three distinct coccolith types. This specimen (Plate 1, fig. 1a) was well preserved and had one *telesmus*-type ceratolith, 26 circular planoliths and numerous delicate hoop-coccoliths. These overlapping, collar-bearing planoliths with a large central opening were located at the periphery of the coccosphere, surrounding the delicate hoop-coccoliths, which surrounded the ceratolith. The planolith rims were 1.37–2.21 μ m thick, the hoop-coccoliths from this specimen were 0.11–0.24 μ m thick and the length of the *telesmus*-type ceratolith was estimated to be 14.2 μ m. All other encountered horseshoe-shaped ceratoliths were associated with hoop-coccoliths, except for one specimen that bore no associated coccolith types at all. In addition, a coccosphere with *coccolithomorpha*-type planoliths and a few

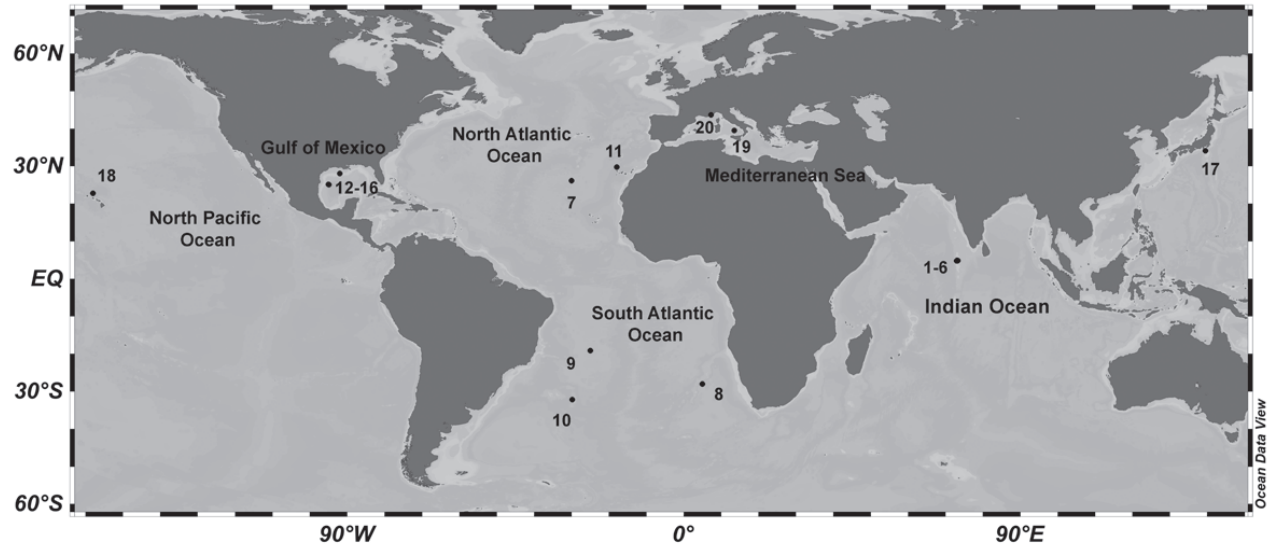


Figure 1: Map of sampling stations from which the *C. cristatus* specimens examined in this study were collected. Details of all samples analysed can be found in Table 2. The map was generated using Ocean Data View software v.4.7.10 (Schlitzer, 2017)

SEM													Distance between arms (µm)	Image code	Sampling date			
Study area	Station	Sample	Coordinates		Depth (m)	Ceratolith length (µm)			Ceratolith width (µm)									
			Latitude (°N)	Longitude (°E)		telesmus-type	cristatus-type	rostratus-type	(side-view images only)									
						telesmus-type	cristatus-type	rostratus-type	telesmus-type	cristatus-type	rostratus-type							
Indian Ocean	Maldives	1	Pikt-26	4.85	73.283	15	19.18	-	-	-	-	6.632	359-P26-399	29/10/2015				
		2	Pikt-29	4.85	73.283	15	19.11	-	-	3.088	-	6.518	359-P29-528	03/11/2015				
							20.85	-	-	-	-	6.657	359-P29-533					
							20.18	-	-	-	-	6.138	359-P29-533					
							-	9.29	-	-	-	5.975	359-P29-534					
		3	Pikt-32	4.85	73.283	15	20.34	-	-	6.03	-	-	359-P29-547	06/11/2015				
							18.90	-	-	9.773	-	-	359-P29-548					
							22.73	-	-	6.408	-	-	359-P32-582					
							19.26	-	-	-	-	5.993	359-P32-586					
							18.64	-	-	-	-	6.267	359-P32-587					
							22.83	-	-	-	-	6.6	359-P32-598					
							19.07	-	-	-	-	6.621	359-P32-603					
							18.89	-	-	-	-	6.604	359-P32-605					
							4	Pikt-38	4.944	73.074	15	8.41	-		-	6.447	-	-
22.91	-											-	8.13		-	-	359-P38-691	
5	Pikt-41	4.777	72.983	15	19.71	-	-	-	-	6.473	359-P38-694	15/11/2015						
					19.65	-	-	-	-	6.968	359-P41-716							
					20.21	-	-	8.082	-	-	359-P45-553		24/11/2015					
					14.20	-	-	4.706	-	-	6.578			359-P45-567				
6	Pikt-45	4.766	73.135	15	-	-	-	5.155	-	5.765	359-P45-568							
Atlantic Ocean	N Atlantic	7	11290/2/11	26.16	-30.00	35	-	-	23.57	-	10	181-89	10/11/2008					
	S Atlantic	8	AMT16 CTD8	-28	5	0	-	16.76	-	-	7.252	232-19	25/05/2005					
		9	AMT18 CTD75/4	-19.12	-25.00	53	-	-	20.62	-	7.086	305-063	26/10/2008					
		10	AMT18 CTD089	-32.18	-29.83	0	-	15.73	-	-	5.296	-	280-23B	02/11/2008				
	Canary Islands	11	P233b-2	29.75	-17.93	25	-	-	20.85	-	6.749	109-P233B34	24/09/1997					
							-	-	21.32	-	8.43	113-20						
							-	-	18.98	-	4.838	113-29						
							-	-	19.82	-	6.35	115-04						
							-	-	17.71	-	5.774	115-08						
	Gulf of Mexico	12	89-G-10 Stn 12	25.06	-94.89	10	13.21	-	-	5.247	-	-	CSF0023	10/09/1989				
-							-	-	-	-	9.392	CSF0018	13/09/1989					
-							13.71	-	-	-	9.323	132-31						
-							13.83	-	-	-	9.453	CSF0019	13/09/1989					
-							12.68	-	-	-	10.364	CSF0110	05/07/1992					
Pacific Ocean	Miyake Island	17	Miyake Jima 4	34.11	139.5	0	-	14.84	-	-	8.253	129-07	01/11/1999					
	Hawaii	18	HOTS169 Stn 2	22.75	-158.0	0	-	-	16.83	-	5.675	219-22	01/09/2005					
Mediterranean Sea	Gulf of Naples	19	Gulf of Naples	39.50	13.5	10	-	-	19.68	-	6.929	-	275-11	24/11/2006				
							-	13.68	-	-	7.734	-	276-41					
							-	14.25	-	-	5.759	-	276-42					
							-	-	19.77	-	7.018	-	276-43					
							-	-	18.92	-	8.524	-	276-46					
	Villefranche	20	StnD 13/9/07	43.68	7.31	30	-	-	20.63	-	8.562	-	276-48					
							-	-	21.20	-	9.133	-	284-28					
							-	-	19.86	-	7.794	-	269-07					
							-	-	19.50	-	8.344	-	269-01					
							-	-	-	-	-	-	-					

Table 2: General information on all studied sites and morphometric measurements of *C. cristatus* (*telesmus*-, *cristatus*- and *rostratus*-type) ceratoliths from diverse environments

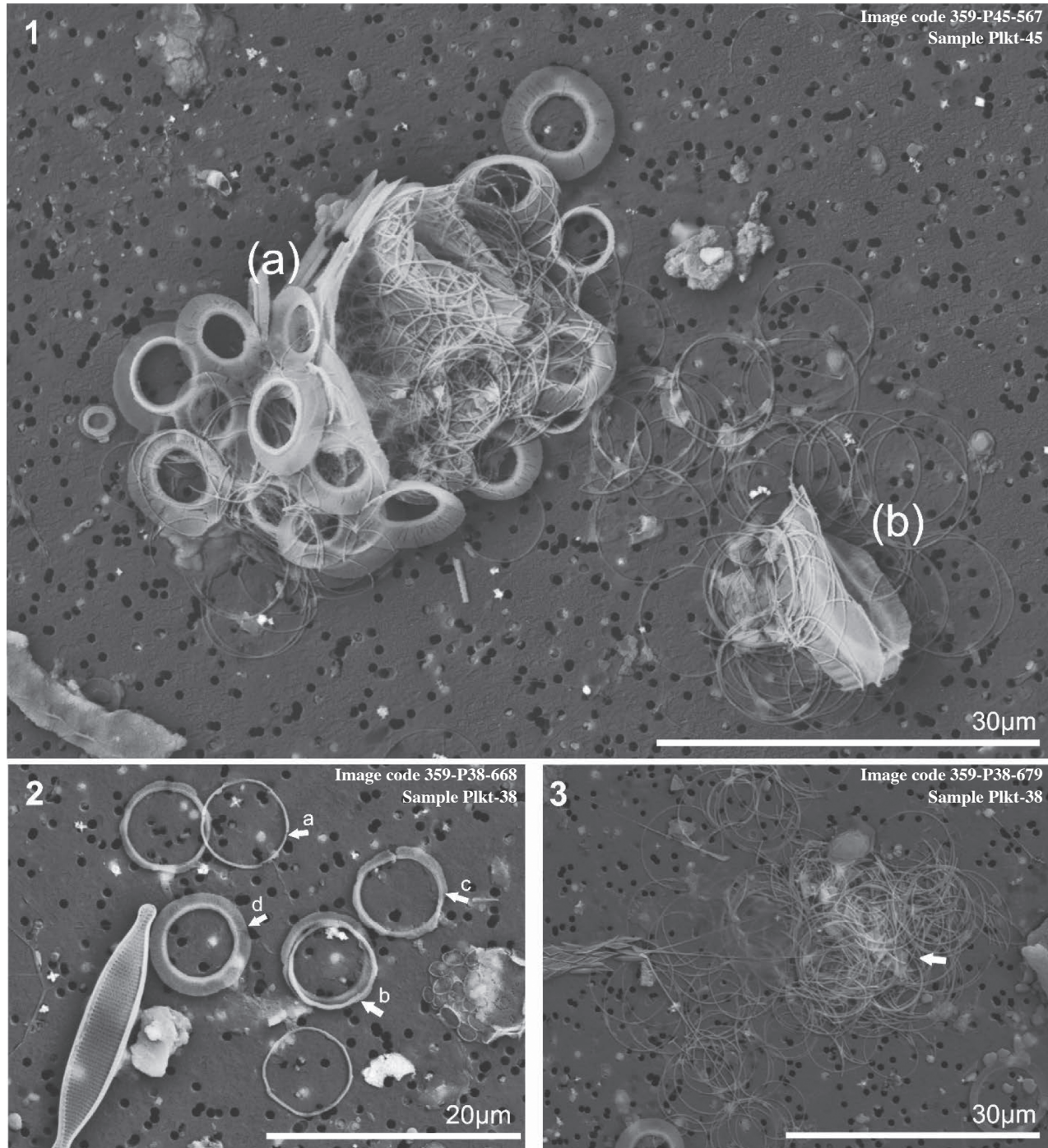
hoop-coccoliths was noted (Plate 2, fig. 2).

No combination coccospheres were documented from Plkt-26, Plkt-29, Plkt-32 or Plkt-41. Plkt-26 contained one *telesmus*-type ceratolith, 19.2 µm long, two *Neosphaera coccolithomorpha* coccospheres and one specimen involving hoop-coccoliths and a few planoliths (Plate 2, fig. 3).

Five *telesmus*-type and one *cristatus*-type ceratoliths were observed in Plkt-29, with the *telesmus*-type specimens being 18.9–20.8 µm long. The *cristatus*-type ceratolith was 9.3 µm long, and occurred with a few hoop-coccoliths and one *coccolithomorpha*-type planolith. Plkt-32 included six *telesmus*-type ceratoliths, 18.6–22.8 µm in length, two *N.*

Plate 1

Electron micrographs showing *C. cristatus* life-cycle patterns, Maldives



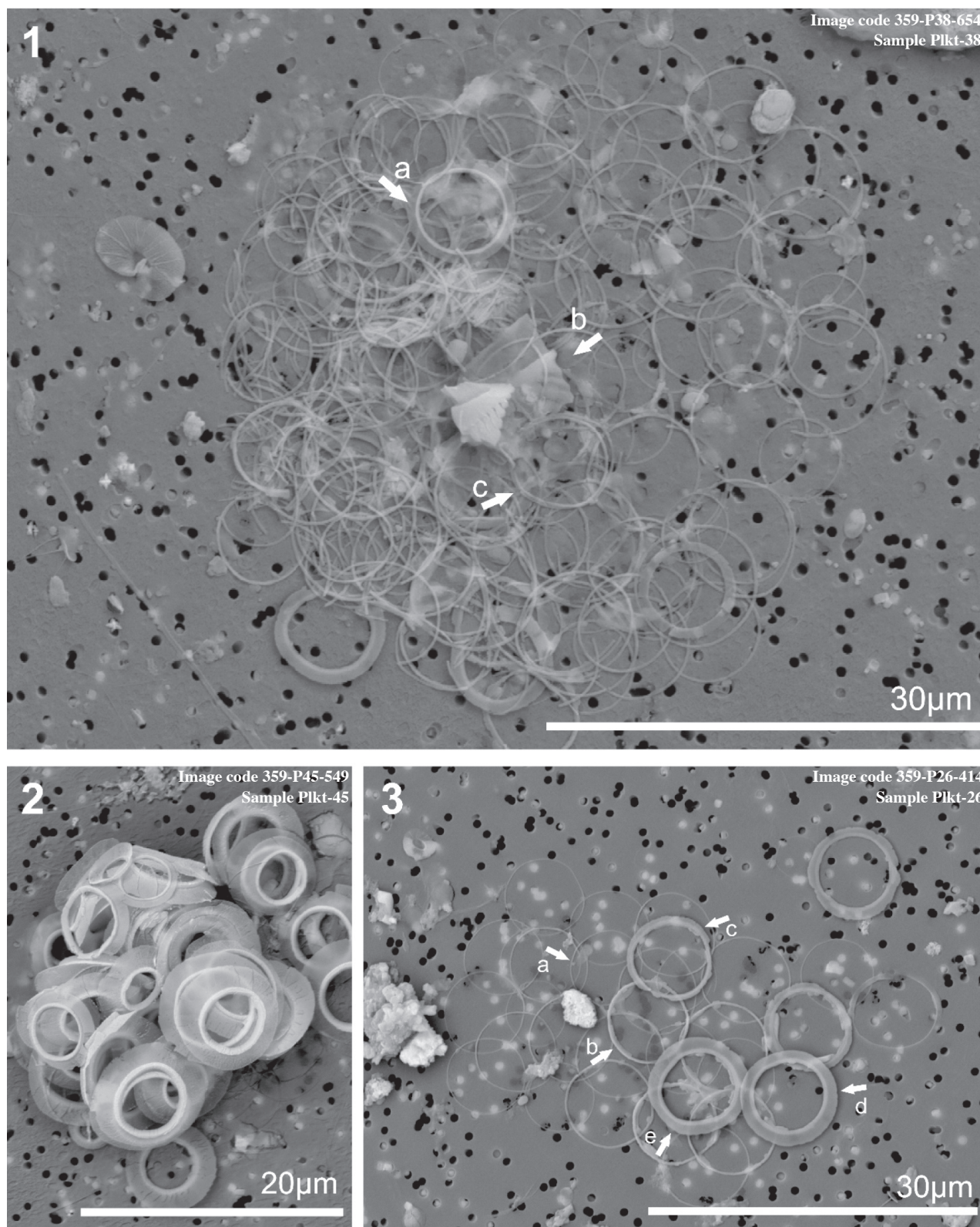
1. (a) *C. cristatus* (*telesmus*-type) ceratolith surrounded by a mass of delicate hoop-coccoliths and 26 *N. coccolithomorpha* planoliths
(b) *C. cristatus* (*telesmus*-type) ceratolith with only hoop-coccoliths
2. Different biomineralisation stages between (a) hoop-coccoliths or *coccolithomorpha* planolith protococcolith rings and (d) a fully-developed planolith. Stages (b) and (c) are transitional between (a) and (d)
3. Disintegrated coccosphere of numerous hoop-coccoliths covering a possible ceratolith specimen (see arrow)

coccolithomorpha planolith-bearing coccospheres, and no hoop-coccoliths. Only one *telesmus*-type ceratolith (19.6 μ m long) and two coccospheres, composed of *coccolitho-*

morpha-type planoliths, were observed in Plkt-41. Hoop-coccoliths were not documented in this sample using the SEM.

Plate 2

Electron micrographs showing *C. cristatus* life-cycle patterns, Maldives



1. Collapsed coccosphere composed of (a) *N. coccolithomorpha* planoliths, (b) a *C. cristatus* (*telesmus*-type) ceratolith and (c) several hoop-coccoliths, with the hoop-coccoliths and planoliths being equally sized
2. Monomorphic, multilayered coccosphere composed of *N. coccolithomorpha* var. *coccolithomorpha* planoliths and a few hoop-coccoliths
3. Biom mineralisation stages, showing the gradual transition from (a) hoop-coccoliths to (e) a well-developed *coccolithomorpha* planolith

3.2 Morphological variation in ceratoliths from the Maldives

The Maldives samples contained common ceratoliths, which showed a range of morphologies from simple horseshoe-shaped forms to elongate forms in which the arms curved toward each other. These corresponded to typical *C. cristatus* CER *cristatus* type and *C. cristatus* CER *telesmus* type. To test whether this variation represented a mix of two species or variation within a single species, we collected LM images of every ceratolith found in the preparations of three samples (Plkt31, Plkt36 and Plkt41). This gave a total of 98 images, of which 41 were specimens in side view and 57 in plan view. We measured the length of all specimens, and the maximum width of the specimens seen in plan view, and subjectively assigned the specimens to typical *cristatus* (simple horseshoe shape), typical *telesmus* (arms nearly touching or even crossing) or intermediate categories.

Ceratolith length ranged from 7 to 26 μm , with a broadly unimodal distribution, and a peak at 15–18 μm (Figure 2b). Specimen width showed a lower degree of variation (5–7 μm), did not correlate with length, and there was no obvious clustering of specimens on the bivariate length/width plot (Figure 2a). Specimens <11 μm long almost always showed *cristatus* morphology, whilst those >18.0 μm long predominantly showed typical *telesmus* morphology. Intermediate-length specimens (11–18 μm) were a mix of *cristatus*, *telesmus* and intermediate morphologies. These results suggest that all the specimens formed a single population, but with the longer forms having more curved rays; that is, that we are essentially seeing a growth sequence from shorter (*cristatus*) to longer (*telesmus*) forms. This is supported by comparisons of specimens in plan view (Plate 3), which show a complete intergradation of the two morphotypes. The fact that ceratolith width did not correlate with length, but rather was similar for all lengths, again supports the interpretation that length variation represents a growth sequence, where maximum width is attained in the early growth stage. These observations suggest that, in this population, the *telesmus* and *cristatus* morphotypes intergrade and are not the result of genotypic variation.

3.3 Ceratolith morphology in other environments

We reviewed SEM images of *Ceratolithus* specimens that

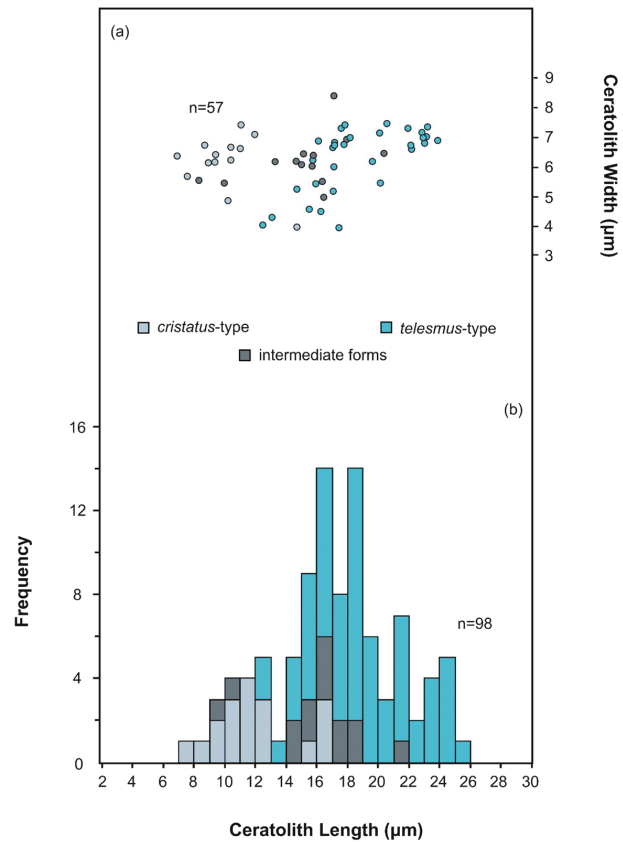


Figure 2: (a) Scatter plot of ceratolith length vs width, showing no significant correlation. (b) Frequency distribution of ceratolith length, showing a broadly unimodal distribution

were collected during the analysis of water samples from other environments in our previous research (Figure 1, Table 2). In the North Atlantic Ocean and the Canary Islands, the ceratoliths (10 in total) were frequently of the *rostratus* type (eight specimens), with lengths ranging from 17.7 to 21.3 μm , and less regularly of the *cristatus* type (two specimens) that averaged 16.2 μm in length. No *telesmus*-type ceratoliths were documented in any of the studied Atlantic sites. In the Gulf of Mexico, five *cristatus*-type ceratoliths, with an average length of 13.7 μm , were observed, but no *rostratus*- or *telesmus*-type ceratoliths. Only two *C. cristatus* ceratolith images were obtained from the Pacific Ocean, one of which was of the *cristatus* type, 14.8 μm long, and the other of the *rostratus* type, 16.8 μm long. In the NW Mediterranean Sea, nine *rostratus*- and two *cristatus*-type ceratoliths were identified with the SEM. Specimens of the *rostratus* type were 16.8–21.2 μm long, whereas the *cristatus*-type ceratoliths averaged 14.0 μm in length. No *telesmus*-type specimens were encountered in the Mediterranean water samples.

Light micrographs of *Ceratolithus*

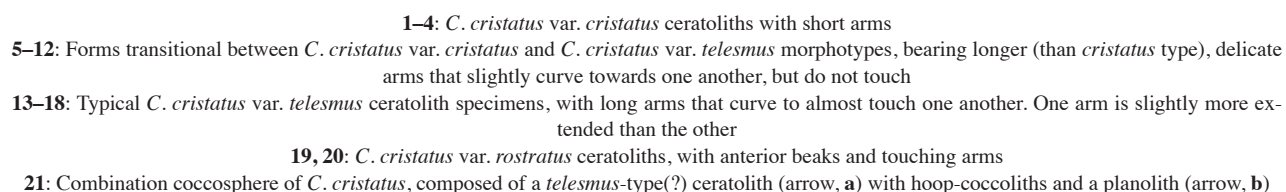
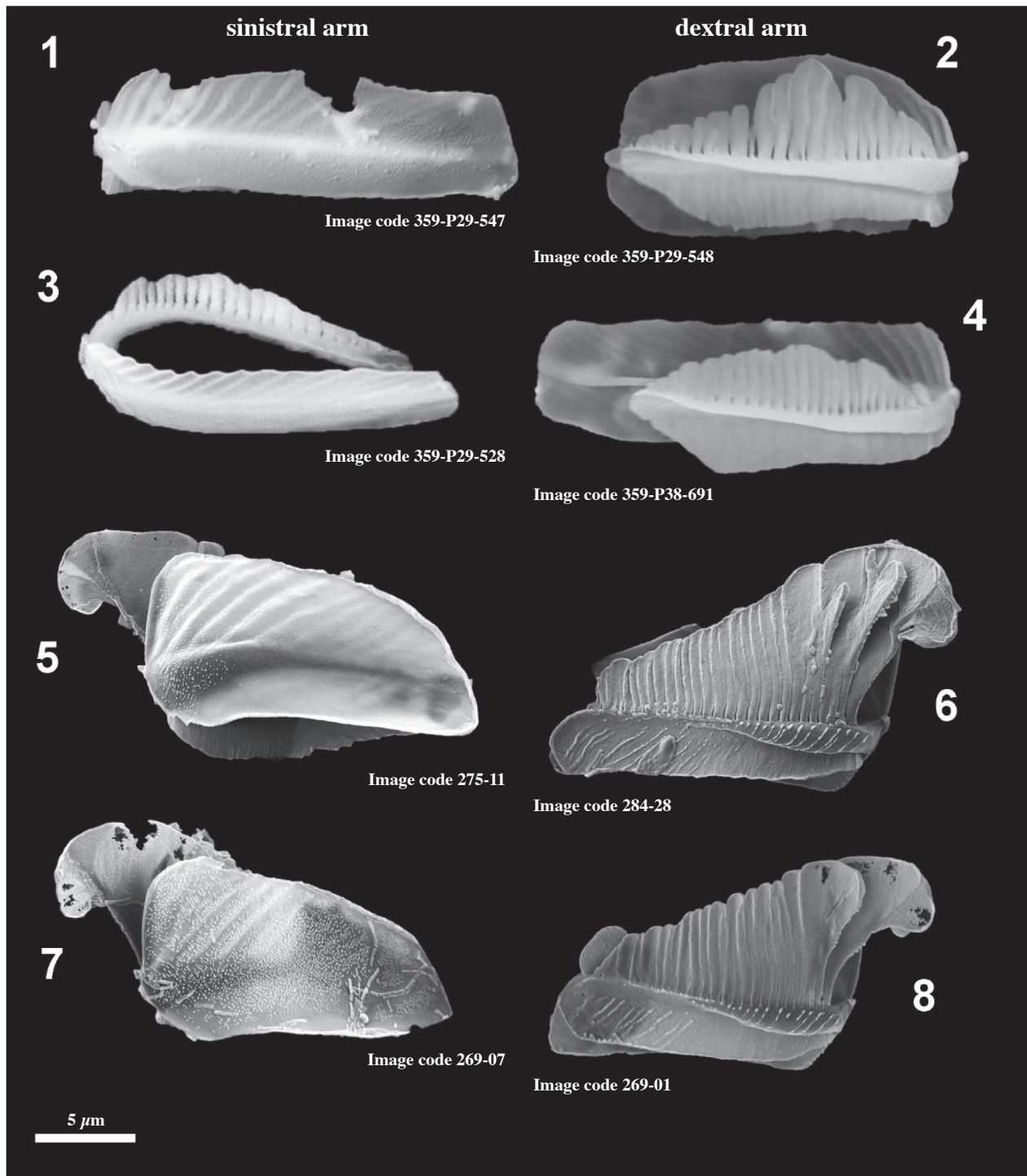


Plate 4

Ceratolith morphology in side view



3.4 Differentiation of the *rostratus* morphotype

From our SEM ceratolith side-view images, we observed that, in the *rostratus*-type ceratoliths, the ceratolith has a triangular shape in side view (e.g. Plate 4, figs 7, 8), with the height of the ceratolith increasing continuously to-

wards the apical region, as opposed to the more parallel-sided form of *C. cristatus* (including both *telesmus*- and *cristatus*-type ceratoliths) (e.g. Plate 4, figs 1, 2, 4). We thus deem ceratolith shape to be an important and widely applicable taxonomic criterion in the *Ceratolithus* identification process. The high sides of *rostratus*-type ceratoliths

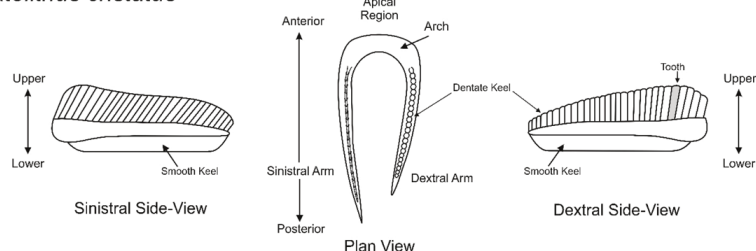
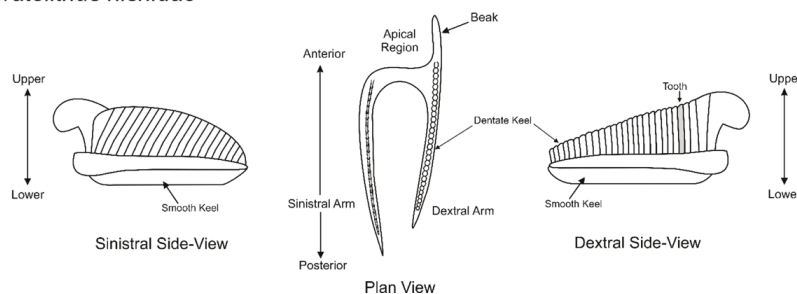
Ceratolithus cristatus*Ceratolithus nishidae*

Figure 3: Schematic representation and proposed terminology of *C. cristatus* and *C. nishidae* ceratoliths, redrawn from Young et al. (1997)

mean that they typically fall over and are thus seen predominantly in side view. However, we did have one good plan-view light micrograph of the *rostratus* type (Plate 3, fig. 19) from a sample from the Canary Islands (P233b), in which many *rostratus*-type specimens were seen in both the SEM and LM. This specimen showed how the beak extends beyond the arch, giving a very different form to that of the typical *cristatus* type. These observations reinforce the case for considering the *rostratus*-type ceratoliths to be distinctly different from the *cristatus* type.

It is also noteworthy that, in many *rostratus* specimens, the arms curve together, away from the arch, as in the ‘*telesmus*’ morphotype. Because this type of arm curvature occurs in different morphotypes, it should not be used to distinguish among taxa.

4. Discussion and conclusions

4.1 Taxonomic revision of *Ceratolithus*

Young et al. (2003) proposed the current scheme, in which only one formal taxon—*Ceratolithus cristatus*—is recognised, but with several different coccolith/coccosphere types being informally named, including *C. cristatus* CER *cristatus* type, *C. cristatus* CER *telesmus* type, *C. cristatus* CER *rostratus* type, *C. cristatus* HET *coccolithomorpha* type and *C. cristatus* HET *nishidae* type (Table 1). This scheme is obviously awkward, but has been a necessary compromise, given the uncertainty of the life-cycle asso-

ciations. Our observations have led us to the following conclusions:

1) The *telesmus* and *cristatus* morphotypes intergrade, with the *telesmus* form simply representing a larger, better developed, morphotype. This is in accordance with the previous conclusions of Borsetti & Cati (1976) and Jordan & Young (1990), and is supported by our observations from the Maldives samples;

2) The *coccolithomorpha*-type planoliths are associated with *cristatus/telesmus*-type ceratoliths, whereas the *nishidae*-type planoliths are associated with *rostratus*-type ceratoliths. The *coccolithomorpha*–*cristatus/telesmus* association is based on our observations, whilst the *nishidae/rostratus* association is based on the observations

of Cros et al. (2000) and Sprengel & Young (2000); and
3) The combination of differences in the planolith and ceratolith morphologies supports the separation of these two pairs of associations into discrete species. The difference in planolith morphology is very strong and consistent. The difference in the ceratolith form is subtler, and may not be easy to observe in smaller specimens, but our observations on the differences in their profiles support this separation. It follows that the correct name for the *cristatus*–*telesmus/coccolithomorpha* association is *C. cristatus*, whilst the correct name for the *rostratus/nishidae* association is *C. nishidae*. The latter combination has not yet been formally proposed, and so is proposed here.

4.2 Life-cycle observations and hoop-coccoliths

Our life-cycle associations, supported by the documentation of similar *Ceratolithus* coccospheres by Sprengel & Young (2000), confirm the interpretation of Alcober & Jordan (1997) that *Ceratolithus* produces two types of coccoliths in addition to the ceratoliths, and that the two typical cell types (Figure 4, Plate 5) are: 1) cells bearing both ceratoliths and an outer coccosphere of delicate hoop-coccoliths; and 2) cells with a coccosphere of more robust planoliths.

This is anomalous, in terms of coccolithophore life-

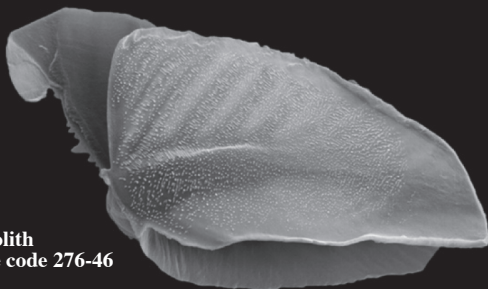
Plate 5

Differentiation between *C. nishidae* (former *rostratus* type) and *C. cristatus* (former *telesmus* and *cristatus* types) biomineralisation modes during all distinct life-cycle phases

A *C. nishidae* former *rostratus* type

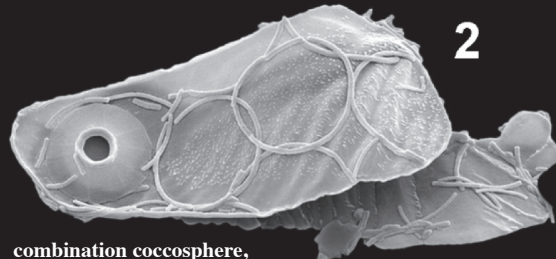
1

ceratolith
image code 276-46



2

combination coccosphere,
with hoop-coccoliths and a planolith
image code 115-12



3

HET coccosphere
composed of
N. coccolithomorpha var.
nishidae planoliths
image code 109-P233-B315



4

well-preserved
combination
coccosphere,
bearing all discrete
coccolith types
image code 113-20



5 μm

B *C. cristatus* former *telesmus* and *cristatus* types

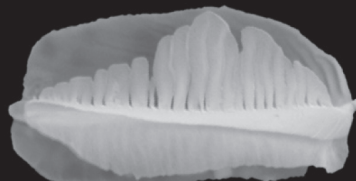
1

ceratolith
(former *cristatus* type)
image code 132-31



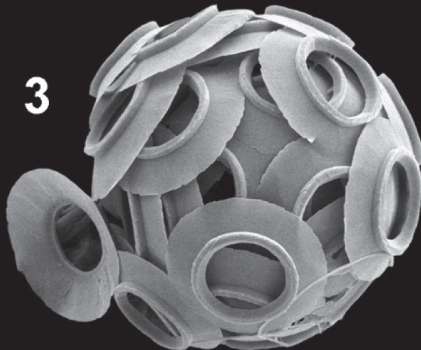
2

ceratolith
(former *telesmus* type)
image code 359-P29-548



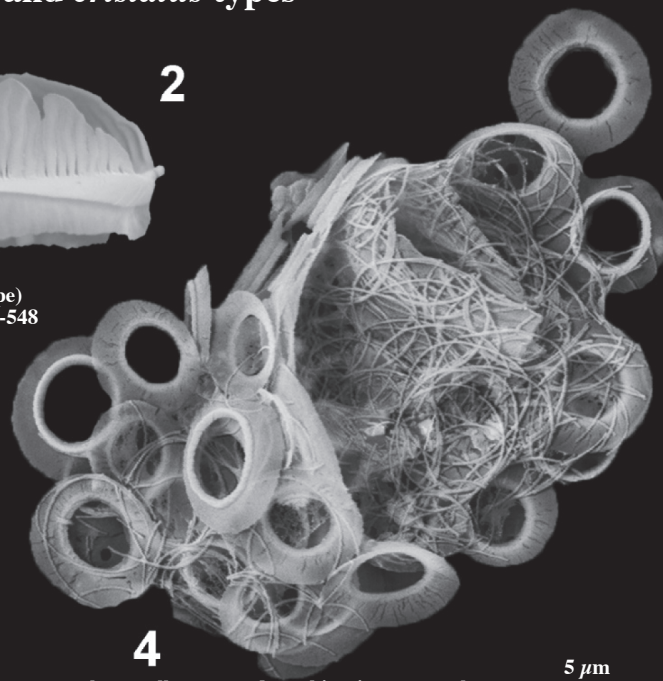
3

HET coccosphere, bearing
N. coccolithomorpha var. *coccolithomorpha*
planoliths
image code CSF0110



4

complete, well-preserved combination coccosphere,
bearing all morphologically-distinct coccolith types
of the different life-cycle stages
image code 359-P45-567



5 μm

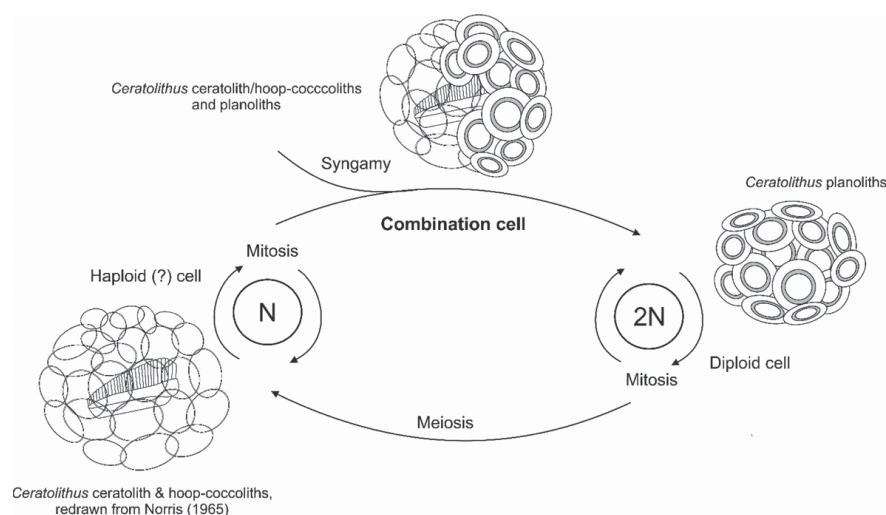


Figure 4: Schematic representation of the most plausible case for the *Ceratolithus* life-cycle

cycles, because both the hoop-coccoliths and the planoliths are heterococcoliths and, in all other known coccolithophore life-cycles, heterococcoliths are exclusively formed during the diploid life-cycle phase. Young et al. (1998, p. 91) speculated that the hoop-coccoliths might be “special heterococcoliths produced during, or prior to, phase changes”. However, this is not a tenable explanation for the anomaly of heterococcoliths occurring in two phases of the life-cycle because the association of hoop-coccoliths with ceratoliths is very common (Norris, 1965; Alcober & Jordan, 1997; I. Probert, pers. comm., 2019; our observations).

This anomaly is further highlighted by our observation of intermediates between the hoop-coccoliths and the *coccolithomorpha*-type planoliths (Plates 1, 2) from the Maldives. These intermediates resemble hoop-coccoliths with enlarged rims, or incomplete planoliths. It appears that hoop-coccoliths and planoliths are not the products of discrete biomineralisation processes, but rather are directly homologous. That is, they are both formed by the same process, but in some cases, growth stops at the hoop-coccolith stage, whilst in others, it progresses to form the larger planoliths. If this is the case, then it follows that similar biomineralisation processes occur in both the ceratolith- and hoop-coccolith-bearing cells, and in the planolith-bearing cells. So, either both cell types form during the diploid life-cycle phase or, in *Ceratolithus*, heterococcoliths are formed during both the haploid and diploid life-cycle phases. In either case, this is significantly different from any other known coccolithophore life-cycle and so may be a relevant model for understanding other fossil

nannoliths. Clearly, observations of cultured specimens would be of great interest.

5. Systematic taxonomy: Proposal of new combination

Ceratolithus nishidae (Kleijne, 1993) comb. nov.

Basionym: *Neosphaera coccolithomorpha* var. *nishidae* Kleijne, 1993: p. 193, pl. 3, fig. 4.

Synonym: *Ceratolithus cristatus* forma *rostratus* Borsetti & Cati, 1976 (invalid).

Differential diagnosis: The ceratoliths of *C. nishidae* are similar to those of *C. cristatus*, but the anterior ends of the rodded keels in the former are significantly higher and extend beyond the arch, especially on the right arm, frequently forming a pronounced beak or rostrum. The planoliths of *C. nishidae* are significantly smaller than those of *C. cristatus* (4–7 μm vs 6–10 μm) and have a much smaller central opening (0.15–0.3x coccolith diameter vs 0.4–0.5x). The hoop-coccoliths are similar in the two species.

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