'MIDDLE' CRETACEOUS MORPHOLOGICAL DIVERSITY WITHIN THE GENUS *CERATOLITHINA* MARTINI, 1967

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Abstract: During the course of a study of the 'Middle' and Upper Cretaceous of the Indian Ocean, a wide variety of *Ceratolithina* Martini, 1967 morphologies and size-ranges was observed with the light-microscope in an apparently expanded Upper Albian to Upper Cenomanian sequence from Deep Sea Drilling Project (DSDP) Site 258. Site 258 is presently situated at 33°47.69'S, 112°28.42'E on the northern flank of the Naturaliste Plateau, off SW Australia. Such variety and relatively frequent abundance of *Ceratolithina* seems not to have been recorded elsewhere. Three new species, *Ceratolithina copis*, *Ceratolithina duplex* and *Ceratolithina naturalisteplateauensis*, and three new subspecies, *Ceratolithina cruxii* subsp. *capitanea*, *Ceratolithina duplex* subsp. *gemina* and *Ceratolithina hamata* subsp. *falcata* are described. Preservational implications are discussed. A lineage is conjectured.

Provenance

Martini (1967) originally reported *Ceratolithina hamata* from the Albian of NW Germany. Perch-Nielsen (1988) described *Ceratolithina bicornuta* and *Ceratolithina cruxii* from the Albian of SE England. Both these localities lie within the boreal palaeobiogeographical region. Although few in number, other reports of *Ceratolithina* also appear to be restricted to relatively high northern palaeolatitudes (*e.g.* the North Sea and UK area: Crux, 1991; Varol & Girgis, 1994; Jeremiah, 1996). Burnett (*in* Gale *et al.*, 1996) also recorded *Ceratolithina* at particular horizons in marls from the Mont Risou section of the Hautes-Alpes (SE France). This latter location contains palaeobiogeographically mixed nannofloras (*e.g.* the co-occurrence in the section of *Nannoconus* spp. with *Repagulum parvidentatum*, *Seribiscutum primitivum* and *Calculites anfractus*) and is believed by Burnett (*op. cit.*) to have occupied a position close to the edge of the boreal region during the Albian to Cenomanian which experienced alternating boreal and tethyan influences. DSDP Site 258 was located at 57.4°S in the Albian-Cenomanian (according to an ATLAS™ palaeogeographical projection for this interval), and contains nannofloras characteristic of the austral palaeobiogeographical realm, *i.e.* it is a high southern palaeolatitude site. The author is unaware of any reports of this genus from low-latitude sequences. It seems likely, therefore, that *Ceratolithina* was a predominantly high-latitude, bipolar genus, which may indicate that it thrived in relatively cool oceanic conditions (although the global temperature gradient during the Albian-Cenomanian is believed to have been much lower than it is now, the poles being ice-free).

Thierstein (1974) logged the nannofossils for Leg 26 of the DSDP but made no mention of *Ceratolithina* at any of the sites. Bown (pers. comm., 1996) found *C. bicornuta* in Albian sediments at Sites 257 and 259, and *C. bicornuta* and *C. hamata* in the Albian of Site 258. This study has shown that at DSDP Site 258, *Ceratolithina* was unusually frequent in soft, laminated clays and shales in which the attendant nannofloras were mainly poorly-preserved and of low abundance. Both Martini (1967) and Perch-Nielsen (1988) first identified the species of this genus from clay lithologies, and other reports (*op cit.*) are also mainly from this lithology. This may constitute evidence to suggest that *Ceratolithina*: (i) is more resistant to corrosion than other nannofossils, thus allowing it to become apparently relatively abundant, or more easily observed, in poorly-preserved material (although the Gault Formation, from which Perch-Nielsen (1988) described *C. cornuta* and *C. cruxii*, contains rather well-preserved nannofloras); and/or (ii) may have preferred to inhabit deeper-water and/or restricted-circulation environments.

Ceratolithina morphology

Ceratolithina possesses only a few morphological components (Figure 1). A rod is common to all species, and this tends to be rounded at the ends. The rod supports horns (scythe-like), rectangular blade-like structures, and triangular to concave-triangular sail-shaped structures. Where a species possesses more than one of these features, they may or may not lie in the same plane. Herein, the anterior end is designated as the end of the central rod which bears the bulk of the largest feature(s), whilst the posterior end of the rod may bear smaller horns or blades, or may not bear any feature. In the light-microscope, members of the genus appear to act as a single crystal. It has low birefringence for such a relatively thick form, suggesting that the *c*-axis is not in the plane of the nannolith. Light-microscope observations have shown that the *c*-axis lies at 45° to the rod. This crystallographic structure is significantly different to the Tertiary genera *Amaurolithus* and *Ceratolithus*, in which the *c*-axis is perpendicular to the plane of the nannolith in the former, and in the plane of the nannolith but perpendicular to the arms in the latter (J. Young and P. Bown, pers. comms, 1997).

The genus has been described as being morphologically similar to the genera *Amaurolithus* and *Ceratolithus* (*e.g.* Martini, 1967; Crux & Lord, 1982), both of which first appeared in the Neogene. However, it is unlikely that *Ceratolithina* is related to either of these taxa because (i) *Ceratolithina* has not been observed in the Cretaceous stratigraphically higher than the Cenomanian/Turonian boundary interval (herein and pers. obs.), so that there is no direct evidence for descendancy, (ii)

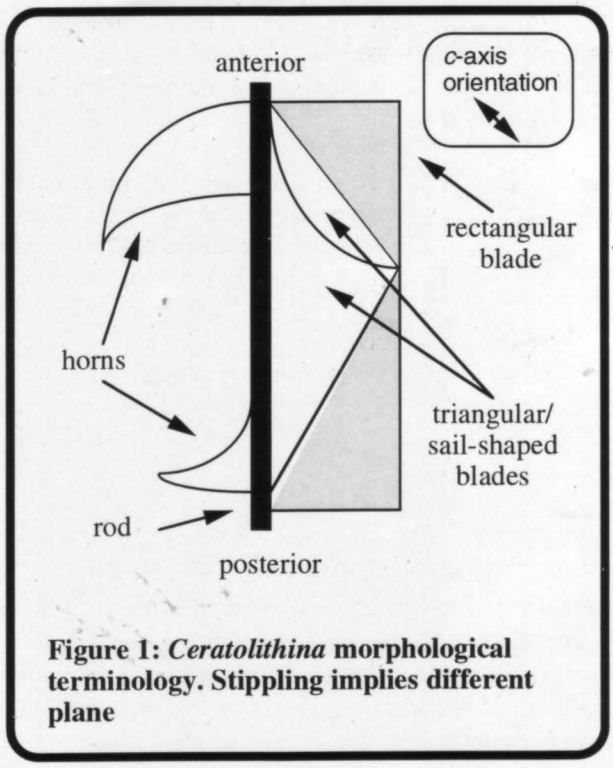

Figure 1: *Ceratolithina* morphological terminology. Stippling implies different plane

Ceratolithina has a much less complex morphology than the younger genera (compare Figure 1 herein to Perch-Nielsen, 1985a, p.454, fig.15), and (iii) the two younger genera are low-latitude, open-ocean taxa (Perch-Nielsen, 1985a, p.457). This is in agreement with Perch-Nielsen's (1979, 1985a) view. She suggested that the Neogene forms evolved from the Miocene genus *Triquetrorhabdulus* (this was prior to her description (1988) of *Triquetrorhabdulus? shetlandensis* from the Valanginian of the northern North Sea but which she believes is not related to the Miocene forms either). Indeed, Raffi & Flores (1995) have observed forms intermediate between *Triquetrorhabdulus* and *Amaurolithus*.

It has also been speculated that *Ceratolithina* is related to the Campanian-Maastrichtian genus *Ceratolithoides* Bramlette & Martini, 1964 (*e.g.* Martini, 1967; Crux & Lord, 1982). This relationship also seems unlikely, since (i) *Ceratolithoides* morphology is substantially different, early forms of *Ceratolithoides* having a conical morphology which evolves into a flattened arrowhead-shape with bilateral symmetry, (ii) *Ceratolithoides* is a well-documented low-latitude taxon, and, again, (iii) there is no evidence that *Ceratolithina* lived beyond the Cenomanian, or that *Ceratolithoides* first occurred below the Campanian. Again, this is in agreement with Perch-Nielsen's (1979, 1985a, b) view.

Ceratolithina diversity and taxonomy

Only three species have previously been assigned to *Ceratolithina*. The diversity identified in this study centred around the shape, size, number and orientation of blades attached to the central rod (Figure 2), and the fact that distinct biostratigraphical distributions could be defined (Figure 3) using these morphological features. 'Twinning' was also encountered.

Family: *Incertae sedis*
Genus: *Ceratolithina* Martini, 1967
Type Species: *Ceratolithina hamata* Martini, 1967

Ceratolithina copis sp. nov.
Figure 2e; Plate 1, Figures 24-26, 29-31

Holotype: Plate 1, Figure 26.
Stratigraphical horizon: 258-15-6, 95-96cm, CC9c, Lower Cenomanian.
Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.
Derivation of name: Latin *copis* = cleaver, referring to the appearance of its blade.
Diagnosis: A rod bearing a relatively large, rectangular to subtrapezoid blade, with or without a second, smaller blade.
Description: A number of different morphologies are attributed to this new species (see Figure 2e). In **type A**, the rectangular blade is positioned at the anterior end of the rod and extends down to around three-quarters of the length of the rod. Another, much narrower blade lies on the opposite side to the first, apparently in the same plane, and extends down almost the entire length of the rod. A third, very narrow blade lies apparently perpendicularly to the second blade. **Type B** has a rectangular blade which is attached to the middle portion of the rod, with a single, much narrower but longer blade lying on the opposite side, and also attached to the middle portion of the rod. **Type C** has a rod with a trapezoid to subtrapezoid blade on one side, with or without a second, narrower blade on the opposite side. It is possible that etching along the margins of the trapezoid blade caused the curved outline illustrated in Figure 2e. ***?C. copis*** may have been modified by etching of the blades.

Ceratolithina cruxii Perch-Nielsen, 1988 subsp. *cruxii*
Figure 2c; Plate 1, Figures 8-11, 15-18

1988 *Ceratolithina cruxii* Perch-Nielsen: p.30, pl.1, figs 5-7.

Holotype: Perch-Nielsen, 1988, pl.1, fig.5.
Stratigraphical horizon: Bed VII, CC8b, niobe Ammonite Zone, Middle Albian.
Type locality: Copt Point, Folkestone, Kent, SE England.
Definition: Nannofossil with a straight to very slightly curved horn and one or more lateral blade(s).
Remarks: Two types were distinguished in this study. **Type A** has a sail-shaped blade attached to almost the entire length of the rod, with a second, narrow, rectangular blade attached to almost the entire length, but on the opposite side of the rod. **Type B** has a narrow, triangular blade attached to almost the entire rod-length, and may or may not possess a second, rectangular blade. Variants of both types also occur with a much elongated rod, the triangular blade being attached to only the anterior portion of this.

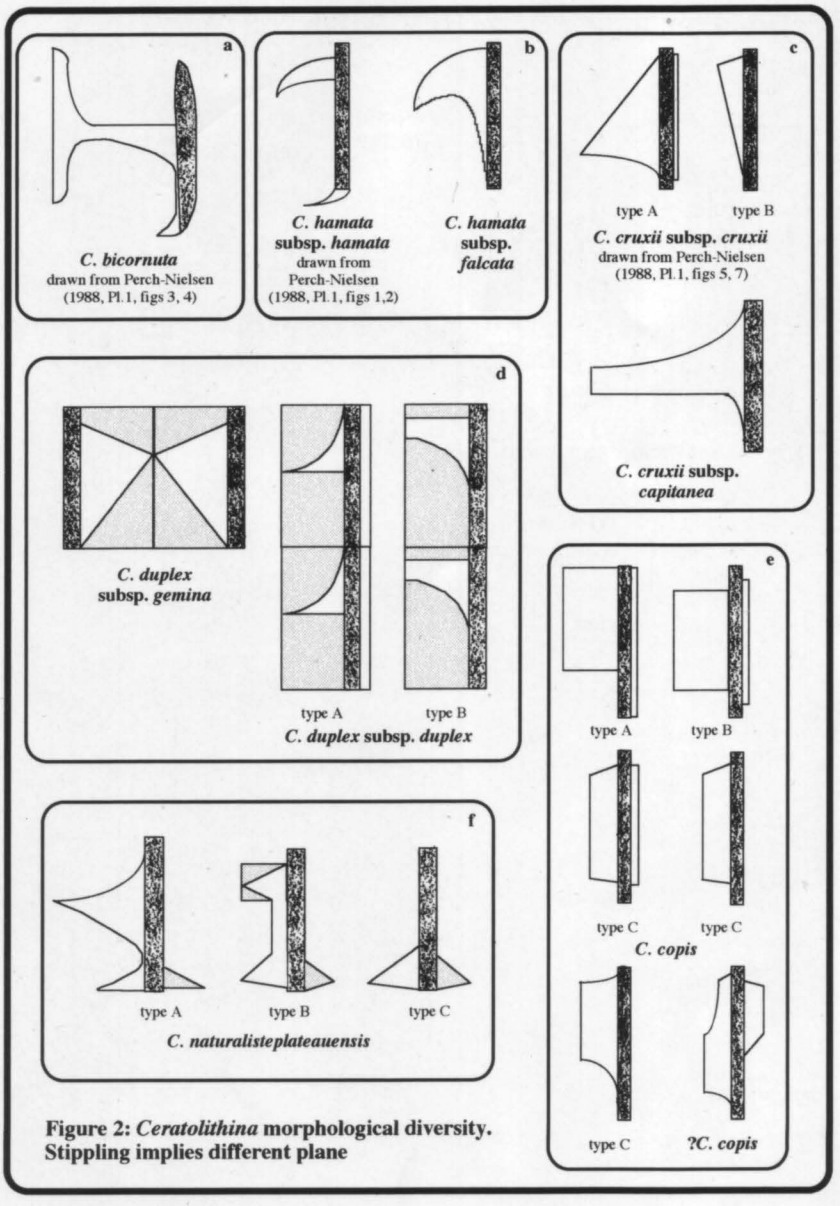

Figure 2: *Ceratolithina* morphological diversity. Stippling implies different plane

Ceratolithina cruxii* Perch-Nielsen, 1988 subsp. *capitanea subsp. nov.
Figure 2c; Plate 1, Figure 4

Holotype: Plate 1, Figure 4.
Stratigraphical horizon: 258-16-1, 144cm, CC9b, Upper Albian-Lower Cenomanian.
Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.
Derivation of name: Latin *capitaneus* = chief in size, large, referring to the size of the taxon.
Diagnosis: A large form (see plate) composed of a rod bearing a single, lateral blunt-sail-shaped blade attached down the entire length of the rod.

Ceratolithina duplex sp. nov.* subsp. *duplex subsp. nov.
Figure 2d; Plate 1, Figure 27

Holotype: Plate 1, Figure 27.
Stratigraphical horizon: 258-16-5, 36-37cm, CC9b, Upper Albian-Lower Cenomanian.
Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.
Derivation of name: Latin *duplex* = double, referring to the characteristic 'stacked twinning' observed in the taxon.
Diagnosis: Each individual comprises a rod bearing a rectangular blade which extends down the entire length of the rod. In a similar orientation but in a different plane, the rod bears a sail-shaped to blunt-ended sail-shaped blade, which is attached to approximately half of the length of the rod. These individuals are 'twinned' in such a way that one individual is sutured to its neighbour along the anterior/posterior ends (see Figure 2d). The sutures between the individuals may not be obvious in specimens which are poorly-preserved, wherein the form appears to have a single rectangular blade and a complex double-sail-shaped blade.
Description: Two types were distinguished within the concept of this subspecies (see Figure 2d). **Type A** individuals have a sail-shaped blade attached from the anterior end of the rod to half-way down the rod, and a second, much narrower rectangular blade in an opposite orientation to the first two, and extending down the entire length of the rod. **Type B** individuals possess a blunted sail-shaped blade attached to the anterior end of the rod, and apparently lack a third blade.

Ceratolithina duplex sp. nov.* subsp. *gemina subsp. nov.
Figure 2d; Plate 1, Figure 28

Holotype: Plate 1, Figure 28.
Stratigraphical horizon: 258-15-1, 141-142cm, CC10a, Lower-Upper Cenomanian.
Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.
Derivation of name: Latin *geminus* = twin, referring to the habit of 'mirror-image twinning' observed between individuals.
Diagnosis: Individuals are composed of a rod bearing a relatively large, rectangular blade which extends down the entire length of the rod. In a similar orientation but in a different plane, a sail-shaped blade is attached to the rod for almost the entire length of the rod. 'Twinning' in this subspecies differs from that observed in *Ceratolithina duplex sp. nov.* subsp. *duplex subsp. nov.* in that individuals are sutured along the lateral axis opposite to the rod, forming a mirror image of one another (see Figure 2d).

Figure 3: *Ceratolithina* distribution, Indian Ocean DSDP Site 258
*data from Bown (pers. comm., 1996)

SAMPLE	TAXA: *Ceratolithina bicornuta*	*Ceratolithina copis* type A	*Ceratolithina copis* type B	*Ceratolithina copis* type C	*?Ceratolithina copis*	*Ceratolithina cruxii capitanea*	*Ceratolithina cruxii cruxii* type A	*Ceratolithina cruxii cruxii* type B	*Ceratolithina duplex duplex* type A	*Ceratolithina duplex duplex* type B	*Ceratolithina duplex gemina*	*Ceratolithina hamata falcata*	*Ceratolithina hamata hamata*	*Ceratolithina naturalisteplateauensis* type A	*Ceratolithina naturalisteplateauensis* type B	*Ceratolithina naturalisteplateauensis* type C	MARKER SPECIES: *Corollithion kennedyi*	*Eiffellithus turriseiffelii*	*Lithraphidites acutus*	*Microstaurus chiastius*	*Tranolithus orionatus*	NANNOFOSSIL ZONE after Sissingh (1977, 1978) & Perch-Nielsen (1985)	STAGE *sensu* Burnett (1996) & after Jeremiah (1996)
14-1, 40-41cm	barren & no *Ceratolithina* above this level																					CC10B	
14-1, 141-142cm				F								R	F	R	R	R		F		F	C		
15-1, 141-142cm		R		F		R		R		R	R	R	R	F	F	R		C	F	F	C	CC10A	
15-2, 33-35cm								R				R		R	F		R	F	R	R	F		
15-3, 35-36cm			R	F			R	F	R			F	F	F	F		R	F		R	R	CC9C	CENOMANIAN
15-4, 102-103cm		R		R			R	F										F		R	F		
15-5, 43-44cm		R			F		R	R							R			F			F		
15-6, 95-96cm		R		F				R	R			R			F		R	F		R	F		
16-1, 144cm		R		R		R		R				R			F			C		F	R		
16-2, 114-115cm							R	R										R			F		
16-3, 31-32cm		R					R		R			R						F			F		
16-4, 45-46cm								R	R			R						F			F		
16-5, 36-37cm		F		R		R	R	R	R			F						R		R	F		
16-6, 15-16cm		R		R				F				F									R		
17-1, 27-28cm		R					R	F	F			R			R			R			F		
17-2, 38-39cm							R	F	R			F									R	CC9B-9A	ALBIAN/CENOMANIAN BOUNDARY
17-3, 63-64cm			R	R			R	R				F											
17-4, 45-46cm		R		F			F					F						F			F		
17-5, 110-111cm							R					R						F			F		
18-1, 66-67cm																		F			R		
18-2, 104-105cm																		F			F		
18-3, 116-117cm																		F			C		
18-4, 124-125cm																		F			C		
*18-4, 143cm																		F			C		
*19-CC																					F		
*20-1, 87cm																					F		
*20-1, 128cm																					R		
*21-1, 97cm																					F		
*21-1, 138cm																					R		
*21-2, 61cm																					F		
*21-2, 124cm																					F		
*21-3, 5cm																					R		
*21-3, 140cm																					R	CC8B	MIDDLE-UPPER ALBIAN
*22-1, 86cm	R																						
*22-1, 130cm	R																						
*22-3, 28cm																					R		
*22-3, 92cm	R																				R		
*22-5, 48cm																							
*22-5, 81cm	R																						
*22-5, 112cm	R																				R		
*23-1, 147cm	no *Ceratolithina* below this level																					CC8A	LR. ALB.

no *Ceratolithina* recorded

Ceratolithina hamata* Martini, 1967 subsp. *hamata
Figure 2b; Plate 1, Figures 5, 6

1967 *Ceratolithina hamata* Martini: p.295-296, pl.30, figs 1-3.
1988 *Ceratolithina hamata* Martini: Perch-Nielsen, pl.1, fig.1, ?*non* pl.1, fig.2.

Holotype: Martini, 1967, pl.30, figs 1, 2.
Stratigraphical horizon: At 346m in the Konrad 2 Borehole, *minimus* Clay, Middle Albian.
Type locality: Salzgitter-Watenstedt, NW Germany.
Derivation of name: Latin *hamatus* = hooked.
Description: Fish-hook-shaped form in which two horns of different size and curvature extend laterally and in the same orientation from a rod. The rod extends beyond the anteriorally-positioned horn, forming an apical spur.

Ceratolithina hamata* Martini, 1967 subsp. *falcata subsp. nov.
Figure 2b; Plate 1, Figure 7

?1988 *Ceratolithina hamata* Martini, 1967: Perch-Nielsen, pl.1, ?fig.2, *non* pl.1, fig.1.

Holotype: Plate 1, Figure 7.
Stratigraphical horizon: 258-14-1, 141-142cm, CC10a, Lower-Upper Cenomanian.

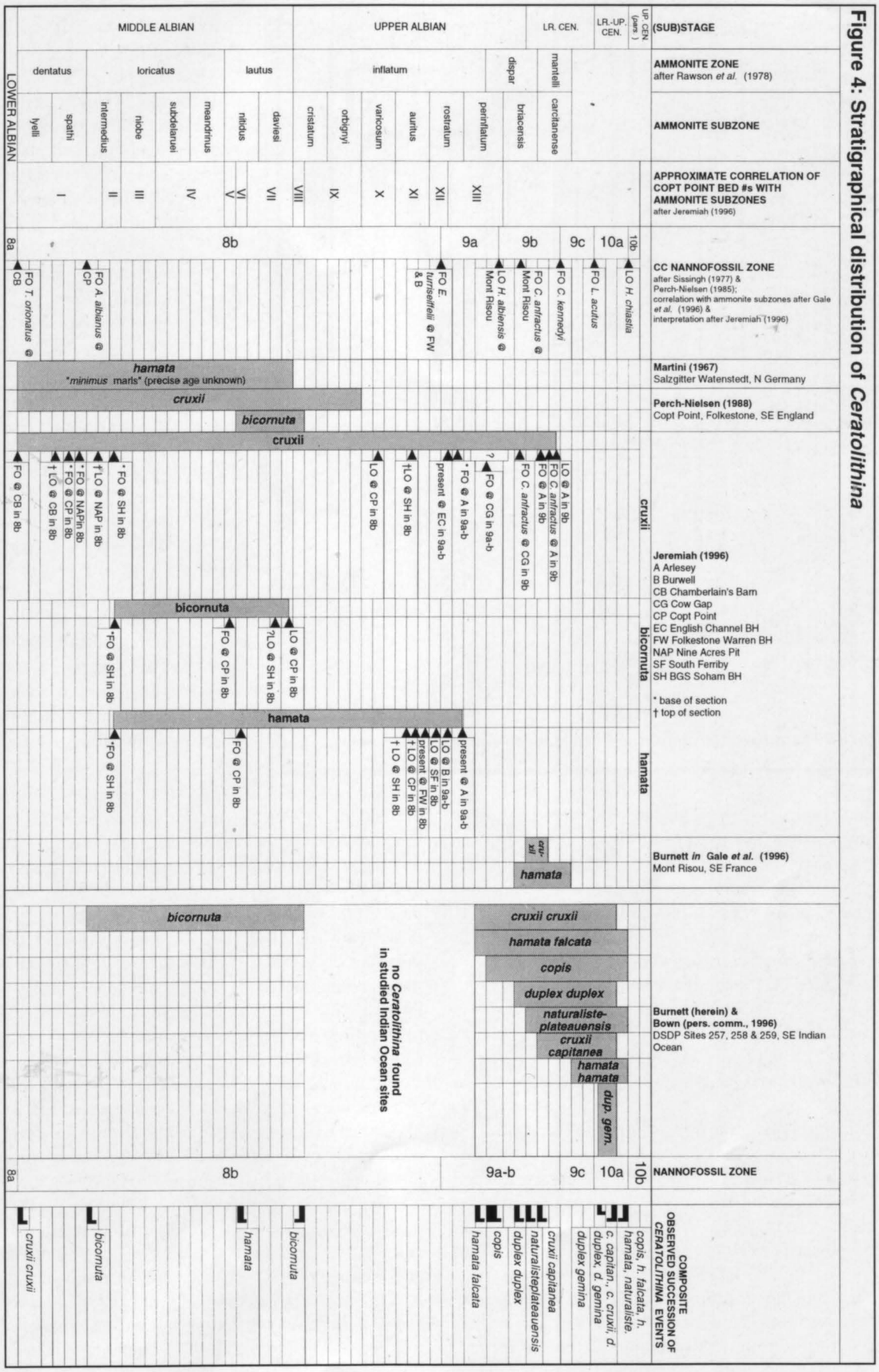

Figure 4: Stratigraphical distribution of *Ceratolithina*

Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.

Derivation of name: Latin *falcatus* = sickle-shaped, referring to the appearance of the single horn.

Diagnosis: A rod bearing a single, moderately-sized horn, situated at the anterior end of the rod.

Remarks: Since this form shows no evidence of having possessed two horns, it is considered to be sufficiently

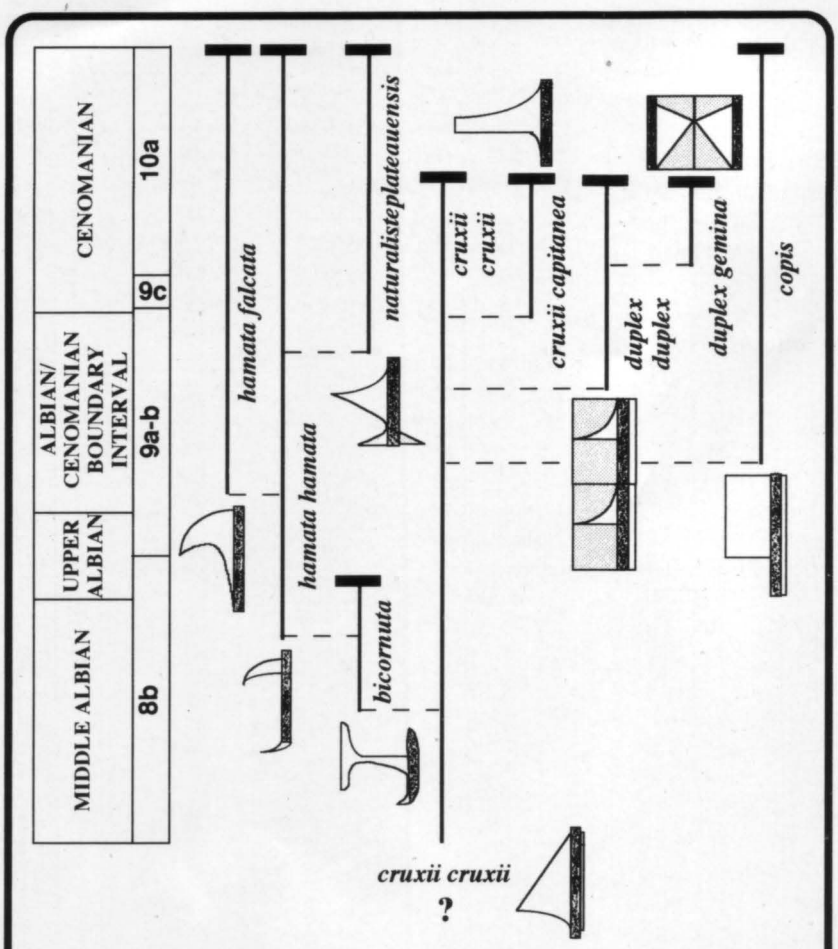

Figure 5: Tentative *Ceratolithina* lineage, based on published data

differentiated from *C. hamata* subsp. *hamata* to warrant subspecies status. The form illustrated by Perch-Nielsen (1988, pl.1, fig.2) may be a broken *C. hamata* subsp. *hamata*, and is thus not designated as the holotype. This subspecies may possess an elongated rod.

Ceratolithina naturalisteplateauensis sp. nov.
Figure 2f; Plate 1, Figures 12-14, 19-23

Holotype: Plate 1, Figure 13.
Paratypes: Plate 1, Figures 14, 19, 20, 21.
Stratigraphical horizon: 258-15-3, 35-36cm, CC9c, Lower Cenomanian.
Type locality: DSDP Site 258, Naturaliste Plateau, SE Indian Ocean.
Derivation of name: After the Naturaliste Plateau upon which Site 258 was drilled.
Diagnosis: A rod bears two horns positioned at the anterior and posterior ends of the rod but apparently joined (see Figure 2f). The larger anterior horn (or possibly a blade) is triangular in outline, joined to the rod below the end of the rod thus forming a small, apical spur. The smaller posterior horn is attached to the opposite end of the rod. A second small, posterior horn lies in an opposite orientation to the first posterior horn but in a different plane, such that it is often hidden from view in the light-microscope.
Description: Three types were distinguished which may or may not reflect preservational effects (see Figure 2f). **Type A** is used to define the taxon (see diagnosis). **Type B** has a more-pronounced join between the similarly-oriented horns, which are also of similar size. At the anterior end of the form, a small, rectangular blade lies in the same orientation but in a different plane to the anterior horn. In **type C**, only the two, small, ?posterior horns are present.

Biostratigraphy and lineage speculations

Figure 3 shows the biostratigraphical distributions of *Ceratolithina* and the marker-taxa in Site 258, Naturaliste Plateau, SE Indian Ocean. *Ceratolithina* was identified between samples 17-5, 110-111cm and 14-1, 141-142cm, an interval interpreted as lying within NF Subzones CC9a-b to CC10a and therefore equivalent to the Albian/Cenomanian boundary interval to the Upper Cenomanian, according to Burnett (1996). The addition of data from samples stratigraphically below this interval (18-4, 143cm to 23-1, 147cm, CC8b-9a: Bown, pers. comm., 1996) provides a complete view of this genus at this site. *Ceratolithina* has also been recorded at Sites 247 and 249 in the SE Indian Ocean (Bown, pers. comm., 1996). An interesting phenomenon is the absence of *Ceratolithina* between cores 21-3 and 18-1. If this taxon is a cooler-water form, then it is possible that this absence is due to a warming episode at 57.4°S during the Middle Albian-Early Cenomanian. Burnett *et al.* (in press) show some evidence to support this. They describe poleward excursions of coccolith taxa, defined as intermediate-latitude-preferring, at high southern latitudes for this interval in the Indian Ocean. There is no evidence at present to support warming as a cause for the absence of *Ceratolithina* from the Cenomanian of the North Sea.

In order to surmise a lineage for *Ceratolithina*, it was first necessary to determine the reported first and last occurrences (FOs/LOs) of each taxon. Figure 4 sets these out. Martini (1967) described *hamata* (subsp. *hamata*) from the '*minimus* Marls' which are of Middle Albian age. Perch-Nielsen (1988) reported *cruxii* (subsp. *cruxii*) and *bicornuta* from the Gault Clay Formation, with the FO of *cruxii* (subsp. *cruxii*) at the base of the Middle Albian, and the range of *bicornuta* spanning the Middle-Upper Albian boundary. Crux (1991, p.214) lumped *hamata* and *cruxii* together in his range-chart, so his data is omitted from Figure 4. Jeremiah (1996) examined numerous sections, and Figure 4 shows the FOs and LOs of the species in each section, such that composite ranges can be worked out from his data. Thus, he is in agreement with Perch-Nielsen on the FO of *cruxii* (subsp. *cruxii*) at the base of the Middle Albian and also the base of CC8b (FO of

Tranolithus orionatus); he found the FO of *bicornuta* slightly stratigraphically lower than Perch-Nielsen did, if it is true that his record of this taxon in the BGS Soham Borehole is from a displaced sample (Jeremiah, 1996, fig.7 note), but he also found its LO to be lower, placing it at the top of the Middle Albian rather than the base of the Upper Albian. He placed the FO of *hamata* (subsp. *hamata*) just above his FO of *bicornuta* at Copt Point (again, if the Soham Borehole sample is displaced), in the Middle Albian. Bown (pers. comm., 1996), however, found *bicornuta* to first occur with *Axopodorhabdus albianus* in Sites 257 and 259, which places its FO lower in the Middle Albian than either Perch-Nielsen or Jeremiah believed. He also found that the LO of *bicornuta* in the SE Indian Ocean heralded the period of *Ceratolithina*-free sedimentation postulated above as being a warming episode. Burnett (*in* Gale *et al.*, 1996) recorded *cruxii* subsp. *cruxii* and *hamata* subsp. *hamata* around the Albian/Cenomanian boundary, whilst the data presented herein provides LOs for the taxa. The stratigraphical positioning, and the abrupt nature, of these LOs appears to indicate a link between the extinction of the genus and the Cenomanian-Turonian Oceanic Anoxic Event.

Based on these ranges, and on gross morphological characteristics of the species and subspecies, a putative lineage has been drawn (Figure 5). Perch-Nielsen (1988) speculated that *C. cruxii* might have been the ancestor to *C. hamata* and this appears to be the case, possibly via *C. bicornuta*. *C. hamata* gave rise to *C. hamata* subsp. *falcata*, and probably also to *C. naturalisteplateauensis*, although this latter form might just as easily have come from *C. cruxii*. *C. cruxii* is believed to have given rise to *C. copis*, *C. duplex* and *C. cruxii* subsp. *capitanea*.

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Calculites anfractus (Jakubowski, 1986) Varol & Jakubowski,1989

Ceratolithina Martini, 1967

C. bicornuta Perch-Nielsen, 1988

C. copis

C. cruxii Perch-Nielsen, 1988 subsp. *cruxii*

C. cruxii Perch-Nielsen, 1988 subsp. *capitanea*
C. duplex sp. nov. subsp. *duplex*
C. duplex sp. nov. subsp. *gemina*
C. hamata Martini, 1967 subsp. *hamata*
C. hamata Martini, 1967 subsp. *falcata*
C. naturalisteplateauensis
Ceratolithoides Bramlette & Martini, 1964
Ceratolithus Kamptner, 1950
Nannoconus Kamptner, 1931
Repagulum parvidentatum (Deflandre & Fert *in* Deflandre, 1954) Forchheimer, 1972
Seribiscutum primitivum (Thierstein, 1974) Filewicz *et al. in* Wise & Wind, 1977
Triquetrorhabdulus Martini, 1965

PLATE 1

Light photomicrographs appear at 940x actual size, all with crossed-polars.
SEM photomicrographs appear at 7500x actual size.
Negatives, slides and material are stored in the Micropalaeontology Unit, UCL.

Figs 1-3: *Ceratolithina bicornuta*
Sample DSDP 259-15-1, 124cm; CC8b, Middle-Upper Albian. **1**: Neg.# UCL-5601-34; **2**: Neg.# UCL-5601-32; **3**: Neg.# UCL-5601-31.

Fig.4: *Ceratolithina cruxii* subsp. *capitanea*
Holotype. Sample 258-16-1, 144cm; CC9b, Upper Albian-Lower Cenomanian. Neg.# UCL-5601-16.

Figs 5, 6: *Ceratolithina hamata* subsp. *hamata*
Sample 258-17-4, 45-46cm; CC9b, Upper Albian-Lower Cenomanian. **5**: Neg.# UCL-5601-29; **6**: Neg.# UCL-5601-28.

Fig.7: *Ceratolithina hamata* subsp. *falcata*
Holotype. Sample 258-14-1, 141-142cm; CC10a, Lower-Upper Cenomanian. Neg.# UCL-5601-30.

Figs 8-11, 18: *Ceratolithina cruxii* subsp. *cruxii* type A
8: Sample 258-17-2, 38-39cm; CC9b, Upper Albian-Lower Cenomanian; Neg.# UCL-5601-8; **9**: Sample 258-17-4, 45-46cm; CC9b; Neg.# UCL-5601-6; **10**: Sample 258-16-3, 31-32cm; CC9b; Neg.# UCL-5601-14; **11**: Sample 258-16-5, 36-37cm; CC9b; Neg.# UCL-5601-3; **18**: Sample 258-15-3, 35-36cm; CC9c, Lower Cenomanian; Neg.# UCL-5601-4.

Figs 12-14, 19-23: *Ceratolithina naturalisteplateauensis*
12: Sample 258-15-1, 141-142cm; CC10a, Lower-Upper Cenomanian; Neg.# UCL-5601-27; **13**: Holotype. Sample 258-15-3, 35-36cm; CC9c, Lower Cenomanian; Neg.# UCL-5601-20; **14**: Paratype. Sample as for 13; Neg.# UCL-5601-18; **19**: Paratype. Sample as for 13; Neg.# UCL-5601-35; **20**: Paratype. Sample as for 13; Neg.# UCL-5601-19; **21**: Paratype. Sample as for 13; Neg.# UCL-100ASA-22; **22**: Sample as for 12; Neg.# UCL-5004-6; **23**: Sample as for 12; Neg.# UCL-5004-5.

Figs 15-17: *Ceratolithina cruxii* subsp. *cruxii* type B
15: Sample 258-17-1, 27-28cm; CC9b, Upper Albian-Lower Cenomanian; Neg.# UCL-5601-9; **16**: Sample 258-15-3, 35-36cm; CC9c, Lower Cenomanian; Neg.# UCL-5601-21; **17**: Sample 258-17-3, 63-64cm; CC9b; Neg.# UCL-5601-7.

Figs 24, 25, 29, 30: *Ceratolithina copis* type C
24: Sample 258-16-5, 36-37cm; CC9b, Upper Albian-Lower Cenomanian; Neg.# UCL-5601-12; **25**: Sample 258-17-1, 27-28cm; CC9b; Neg.# UCL-5251-28; **29**: Sample as for 25; Neg.# UCL-5251-22; **30**: Sample 258-17-4, 45-46cm; CC9b; Neg.# UCL-5601-5.

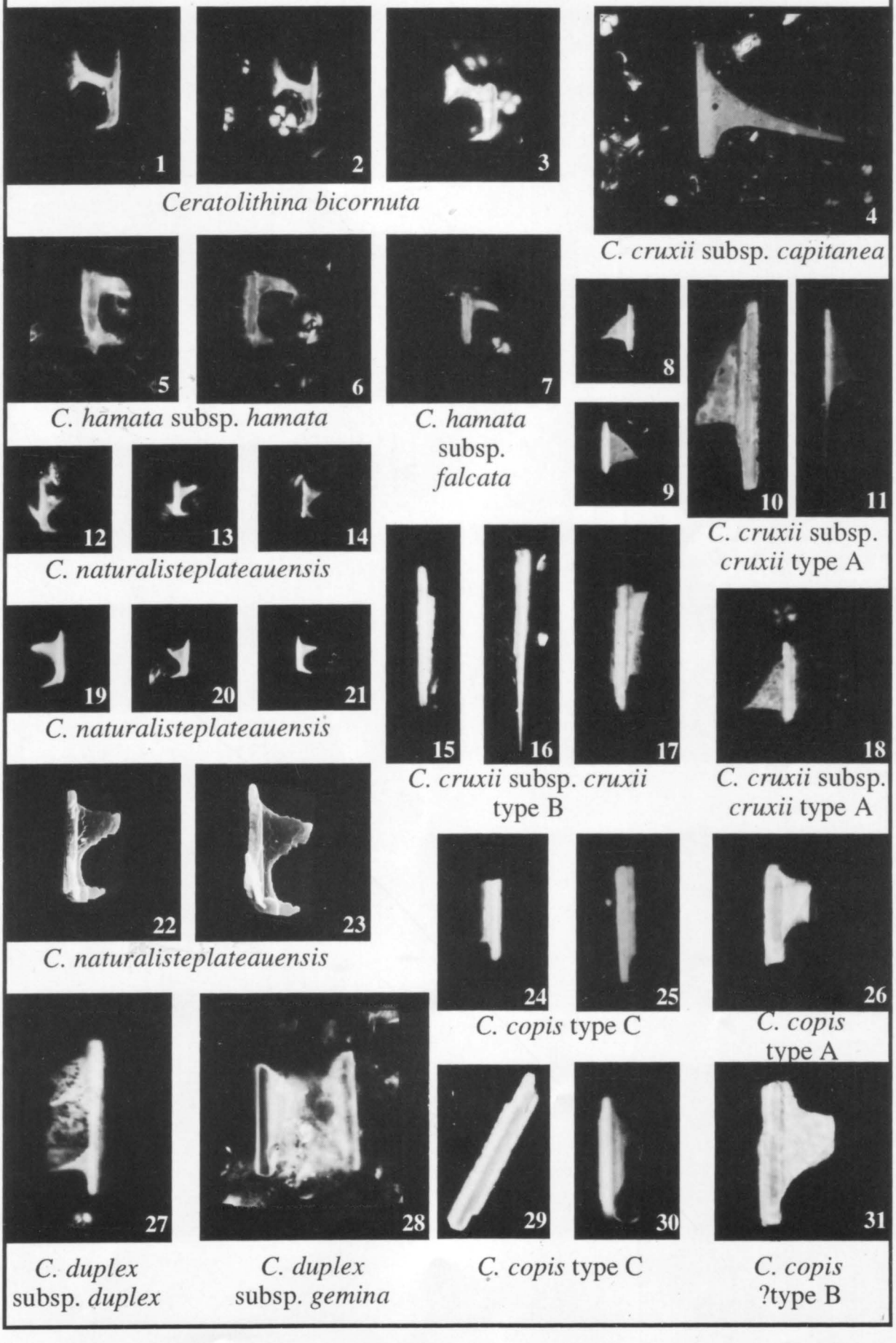
Fig.26: *Ceratolithina copis* type A
Holotype. Sample 258-16-6, 15-16cm; CC9a-b, Albian/Cenomanian boundary interval; Neg.# UCL-5250-35.

Fig.27: *Ceratolithina duplex* subsp. *duplex*
Holotype. Sample 258-16-5, 36-37cm; CC9b, Upper Albian-Lower Cenomanian; Neg.# UCL-5601-10.

Fig.28: *Ceratolithina duplex* subsp. *gemina*
Holotype. Sample 258-15-1, 141-142cm; CC10a, Lower-Upper Cenomanian; Neg.# UCL-5250-27.

Fig.31: *Ceratolithina copis* ?type B
Sample 258-15-5, 43-44cm; CC9c, Lower Cenomanian; Neg.# UCL-5250-15.

PLATE 1


1
2
3
Ceratolithina bicornuta
4
C. cruxii subsp. capitanea
5
6
C. hamata subsp. hamata
7
C. hamata subsp. falcata
8
9
10
11
C. cruxii subsp. cruxii type A
12
13
14
C. naturalisteplateauensis
15
16
17
C. cruxii subsp. cruxii type B
18
C. cruxii subsp. cruxii type A
19
20
21
C. naturalisteplateauensis
22
23
C. naturalisteplateauensis
24
25
C. copis type C
26
C. copis type A
27
C. duplex subsp. duplex
28
C. duplex subsp. gemina
29
30
C. copis type C
31
C. copis ?type B