NORTH SEA LITUOLID FORAMINIFERA WITH COMPLEX INNER STRUCTURES: TAXONOMY, STRATIGRAPHY AND EVOLUTIONARY RELATIONSHIPS

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**Abstract:** The taxonomic, stratigraphic and inferred phylogenetic relationships of North Sea lituolid foraminifera with complex inner structures (i.e., the Subfamilies Cyclamininae and Spiropamininae of the Family Lituolidae) are reviewed. Five essentially Cenozoic evolutionary lineages are recognised, four (Subfamily Cyclamininae) appearing to have originated from *Haplophragmoides* or *Velerinitoides* (Subfamily Haplophragmoidinae), one (Subfamily Spiropamininae) from *Eratidos* (Subfamily Ammomarginulininae), and perhaps ultimately from *Spiroplectammina* (Subfamily Spiroplectammininae, Family Textulariidae). Selective synonymsies, taxonomic notes and detailed documentations of North Sea distributions are appended.

The evolution (and extinction) of the various complex lituolid species appears to be related to evolving palaeoenvironmental conditions mediated by tectono-eustasy. The most important time in terms of evolution was the late Palaeocene.

Further work is recommended on the taxonomic and phylogenetic relationships between certain problem species, and on areas outside the North Sea. Further work is also recommended on the controls on the development of alveolar wall structure and cribrate apertures (i.e., whether evolutionary or environmental). Investigation of variations in these aspects of morphology along coeval transects from the margin to the centre of a basin would be highly instructive in this regard. Variations in other aspects of morphology with depth could also be investigated by this means. Investigation of possible temporal variations in depth distributions would have to be based around analyses of transects from successive time-slices.

**Abstrakt:** Autorzy przedstawiają rewizję otwornic aglutynujących z rodziny Lituolidae (podrodzina Cyclamininae i Spiropamininae) biorąc pod uwagę cechy taksonomiczne, zasięgi stratygraficzne oraz określając ważne relacje filogenetyczne. Wyróżniono pięć głównych linii ewolucyjnych, z których cztery (dotyczącyclamininae) rozpoczęły rodaj *Haplophragmoides* lub *Velerinitoides* (podrodzina Haplophragmoidinae), a piąty (podrodzina Spiropamininae) jest prawdopodobnie rodajem *Eratidos* (podrodzina Ammomarginulininae) lub *Spiroplectammina* (podrodzina Spiroplectammininae).

Ewolucja poszczególnych gatunków w obrębie rodziny Lituolidae była związana ze zmieniającymi się warunkami paleosrodowiska, stymulowanymi przez procesy eustatyczne i tektoniczne. Najszybsze zmiany ewolucyjne w tej rodzinie zachodziły w późnym paleocenie.

Autorzy rekomендują kilka gatunków otwornic w rodzinie Lituolidae do dalszych badań taksonomicznych i filogenetycznych, które uwzględniałyby zespoły mikrofauny pochodzące również z osadów spoiw basenu Morza Północnego.

Autorzy proponują zwrócić uwagę na zmiany alveolarnych struktur ścin skorupki oraz na zmiany w kształcie i obecności sitkowaty otworów skorupki, określając czy zmiany te powstały na drodze ewolucyjnej czy związane są siłą ze zmianami środowiska. Pomoc temu mogą badania zespołów lituolidów z osadów tego samego wieku ale pochodzących z różnych części basenu. Powinni one być badane w kolejnych sekwencjach osadów odpowiadającym jak najmniej tym jednostkom chronostratygraficznym.

Przedstwiono szczegółowy opis otwornic z rodziny Lituolidae, pochodzących z osadów Morza Północnego, zawierający systematykę oraz cechy taksonomiczne.

**Key words:** North Sea, lituolid agglutinated foraminifera, complex structures, taxonomy, stratigraphy, evolution.

*Manuscript received 29 January 1997, accepted 5 February 1997*
INTRODUCTION

Assemblages of deep-water agglutinated foraminifera (DWAF) are a characteristic feature of the Cenozoic stratigraphic succession of the North Sea Basin, especially the uppermost lower Palaeocene–upper Miocene of the deeper parts of the Central and South Viking Grabens (Figs. 1, 2). The North Sea at this time was characterised by a series of tectono-eustatically-mediated sea-level low-stands resulting in rapid sedimentation, an excess of runoff, water-mass stratification, restricted circulation (exacerbated by basin isolation), and reduced oxygenation and enhanced carbon dioxide saturation of bottom and pore waters. These conditions favoured the sustenance and/or preservation of the agglutinated foraminifera at the expense of their calcareous counterparts (e.g., Jones, 1996, pp. 12–13, 17, 19, and references therein).

The DWAF assemblages are themselves characterised by a group of complex lituolids (Family Lituolidae, Subfamilies Cyclammininae and Spirospamininae) whose evolutionary history records their adaption to palaeoenvironmental conditions mediated by tectono-eustasy (cf. Seiglie, 1987). The first appearance of DWAF assemblages in the Central North Sea was during the latest early Palaeocene (approximately 61 Ma), but that of the complex lituolids (e.g., Cyclammina (Reticulophragmium) sp. 1) was not until the late Palaeocene (approximately 56.5 Ma) (Fig. 2). The proliferation of complex lituolids (e.g., Cyclammina (Reticulophragmium) sp. 1) within the late Palaeocene appears to correlate with the transgressive and highstand systems tracts (TSTs and HSTs) of Global Third-Order Cycle TA2.1 of Haq et al. (1987) and the predominantly fine-grained sedimentation of the Lista Formation. The reappearance of DWAF assemblages after their effective elimination during deposition of the Sele and Balder Formations (minor re-colonisations notwithstanding) was during the early Eocene (approximately 52.5 Ma), but again that of the complex lituolids was not until slightly later (approximately 51.5 Ma). The radiation and proliferation of complex lituolids at around the early/middle Eocene boundary (approximately 49 Ma) (e.g., the evolution of Alveolophragmium sp. 1 and the acme of Cyclammina (Reticulophragmium) amplexentis) appears to correlate with Cycles TA2.9 and TA3.1 (Horda Formation). A less significant increase in C. (R.) amplexentis during the late Eocene appears to correlate with Cycles TA4.1-4.3.

The areal distribution of DWAF and complex lituolid assemblages was at its maximum in the North Sea in the Palaeocene, declined in response to shallowing associated with basin-fill from the western margin in the Eocene and Oligocene, and became restricted to the deepest parts of the basin by a continuation of this process by the end of the Miocene. Many DWAF and complex lituolid species exhibit apparent extinctions which are controlled by shallowing and are therefore diachronous (dependent on location with respect to basin margin and bathymetry) not only in the North Sea but also elsewhere.

The purpose of this paper is to study the taxonomic (morphological), stratigraphic and phylogenetic relationships within the complex lituolid group of the North Sea. Inferred phylogenetic relationships are discussed below and graphically depicted on Figure 3. North Sea and global stratigraphic ranges are depicted on Figure 4, the bases for calibration of key events (in the Palaeocene–Eocene) on Figure 5. Selective synonymies, taxonomic notes and detailed documents of North Sea distributions are appended.

DISCUSSION: PHYLOGENETIC RELATIONSHIPS

Previous work

Previous work on taxonomic, stratigraphic and phylogenetic relationships within the complex lituolid group has been undertaken by Banner (1966, 1970), Gradstein (1983), Seiglie and Baker (1983) and Seiglie et al. (1986), Berggren and Kaminiski (1990).

Banner (1970) considered there to be three taxa within the Subfamily Cyclammininae of the Family Spiroycliniidae (Lituolidae), namely Cyclammina and Alveolophragmium s.l. (Alveolophragmium s.s. and Alveolophragmium (Reticulophragmium). He distinguished Alveolophragmium (Reticulophragmium) from Alveolophragmium s.s. on the basis of the interiomarginal as opposed to interio-areal aperture, and Cyclammina from Alveolophragmium s.l. on the basis of the cribrate (multiple areal) aperture and specialised supra-apertural hypodermal zone. These distinctions still hold, though (for reasons outlined in Charnock & Jones (1990) and summarised in the "Systematic Paleontology" of this paper) we regard that between Alveolophragmium and Reticulophragmium as of generic significance, and that between Reticulophragmium and Cyclammina as of subgeneric significance.

Banner (1970) interpreted Alveolophragmium s.l. and
<table>
<thead>
<tr>
<th>TIME (Ma)</th>
<th>AGE</th>
<th>STANDARD BIOSTRATIGRAPHY (Following Haq et al., 1987)</th>
<th>NORTHWEST EUROPE DINO. ZONES</th>
<th>KEY NORTH SEA BIOSTRATIGRAPHIC DATUM LEVELS</th>
<th>SEQUENCE STRATIGRAPHY (Haq et al., 1987)</th>
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<tr>
<td>35</td>
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<td>G. CHROMIOLLA</td>
<td>F16</td>
<td>CAMALEONINA NPF</td>
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</table>

Note 1) * denotes 'base' (evolutionary appearance). Only reliable in cores or sidewall cores.
2) Haq et al. (1987) places the Paleocene/Eocene boundary within calcareous nannofossil zone NP9 rather than more recent schemes where it is taken at the boundary between NP9/NP10 or within NP10.

Fig. 2. Stratigraphic summary of the North Sea Cenozoic. Chronostratigraphy and sequence stratigraphy after Haq et al. (1987); biostratigraphy modified as appropriate after Blow (1979) (planktonic foraminiferal zones), Martini (1971) (nannofossil zones) and Costa et al. (1988) (N.W. Europe dinoflagellate zones); lithostratigraphy after Knox & Holloway (1992).
Cyclammina as having evolved from Haplophragmoides. He further interpreted Cyclammina garciasoi Frizzell, 1943, now known from the Maastrichtian (where it is described as “scarce”) to early Eocene of northern South America, as representing the earliest representative of Alveolophragmium s.l. (A. (Reticulophragmium)), differing from the ancestral Haplophragmoides only in the possession of a coarsely alveolar hypodermis, and C. elegans Cushman & Jarvis, 1932, from the Palaeocene of Trinidad and the Haumurian–Teurian (Maastrichtian–Palaeocene) of New Zealand, as representing the earliest Cyclammina, differing from Alveolophragmium s.l. in the possession of a ciliate aperture and “morphologically primitive” hypodermis. “Advanced” forms did not appear until the Oligo-Miocene.

Gradstein (1983), Seiglie et al. (1986), and Berggren and Kaminski (1990) also interpreted Cyclammina (C. (Cyclammina) and C. (Reticulophragmium)) as having evolved from Haplophragmoides. Gradstein (1983) interpreted C. lamella (?) = C. (R.) sp. 1 from the Late Palaeocene as having evolved from Haplophragmoides walteri, and as having evolved into C. (R.) amplexa, with C. (R.) rotundipars as a separate offshoot, and further interpreted C. (C.) acutidorsata, C. (C.) placenta and C. (C.) cancellata as having evolved from C. (R.) amplexa, while Seiglie et al. (1986) interpreted C. (C.) placenta as a separate offshoot. Berggren and Kaminski (1990) interpreted C. (C.) cancellata to have evolved from C. (C.) placenta.

**Present work**

On the basis of consideration of previous work and of taxonomic (morphological) and stratigraphic relationships, we have provisionally recognised five evolutionary lineages among the North Sea representatives of the complex Alveolina group (i.e., the Subfamilies Cyclammininae and Spiroccammininae of the Family Lituolidae in the sense of Charnock & Jones, 1990). Four (Subfamily Cyclammininae) appear to have originated from Haplophragmoides or Veleroninoides (Subfamily Haplophragmoidinae), one (Subfamily Spiroccammininae) from Ratitidae (Subfamily Ammonomarginulinae), and perhaps ultimately from Sireloctamminina (Subfamily Sireloctamminina, Family Textulariidae). All are essentially Cenozoic.

The lineages are as follows:

1. **Haplophragmoides walteri – Reticulophragmium jarvisi/Cyclammina (Reticulophragmium) amplexa**

Reticulophragmium jarvisi is interpreted as having evolved from Haplophragmoides walteri during the Late Palaeocene (Zone P3B) through the development of an alveolar wall structure (and the invagination of the septa) in the umbilical region. Bolli et al. (1994) suggested that it was "... connected ... through ... intermediate specimens ..." with the “Palaeocene morphotype” of Reticulophragmium cf. garciasoi (Cyclammina (Reticulophragmium) sp. 1 Charnock & Jones, 1990). C. (R.) sp. 1 Charnock & Jones, 1990 is herein interpreted as having evolved from Haplophragmoides walteri (by way of H. sp. 2 Charnock & Jones, 1990 or possibly Reticulophragmium jarvisi (see above)) during the Late Palaeocene (P4) through the development of (a single row of) alveoli along the sutures and periphery. It is further interpreted as having evolved into C. (R.) amplexa, also during the Late Palaeocene (P4). Alveolar development in C. (R.) amplexa is also initially concentrated along the sutures, and only later extends throughout the chambers. Jurkiewicz (1967) and Chruszcz (1984) observed that phylogenetically advanced individuals developed alveoli earlier in ontogeny than primitive individuals (between the 5th and 13th chambers as opposed to between the 10th and 17th chambers).

2. **Haplophragmoides subircularis – Cyclammina (Reticulophragmium) rotundipars**

Cyclammina (Reticulophragmium) rotundipars is interpreted as having probably evolved from Haplophragmoides subircularis during the late Palaeocene (P4) through the development of an alveolar wall structure. Interestingly, while primitive forms of Cyclammina (Reticulophragmium) rotundipars (C. (R.) aff. rotundipars) are known from the late Palaeocene and advanced forms (C. (R.) rotundipars s.s.) from the late middle Eocene onwards, no forms are known from the early or early middle Eocene.

3. **Haplophragmoides sp. 1 – Cyclammina (Cyclammina) placenta – C. (C.) acutidorsata**

Cyclammina (Cyclammina) placenta is interpreted as having evolved from Haplophragmoides sp. 1 Charnock & Jones, 1990 during the Late Palaeocene to middle Eocene through the development of an alveolar wall structure and ciliate aperture (the development of a ciliate aperture took place during the middle Eocene in the North Sea). It is further interpreted as having evolved into C. (C.) acutidorsata (which may in fact represent nothing more than an eco-phenotypic variant) through test compression.

The relationship between Cyclammina (Cyclammina) placenta and C. (C.) cancellata requires further investigation, particularly since, at least in terms of external morphology, one of Brady’’s (1884) figures (reproduced in Jones, 1994) of C. (C.) cancellata (pl. 37, fig. 10) differs from the lectotype designated by Banner (1966) (pl. 37, fig. 9) and approaches C. (C.) placenta in its straight sutures and compact coiling. Berggren and Kaminski (1990) interpreted C. (C.) cancellata as having evolved from C. (C.) placenta through changes in external morphology (increase in size and chamber number, development of straighter sutures etc.); they made no reference to internal morphology. The internal morphology of C. (C.) placenta is poorly known, but it is believed to be characterised by a “primitive” supra-apertural hypodermis in the sense of Banner (1970) (e.g., Charnock & Jones, 1990; pl. 18, fig. 4g). Cyclammina (C.) cancellata is characterised by an “advanced” supra-apertural hypodermis (e.g., Banner, 1970; pl. 3, fig. 10, pl. 12, figs. 1a, 5a, 6).

4. **Veleroninoides scitulus – Alveolophragmium sp. 1**

Charnock & Jones, 1990

Alveolophragmium sp. 1 Charnock & Jones, 1990 is interpreted as having evolved from Veleroninoides scitulus (Labrosira scitula of Charnock & Jones, 1990) during the
early Eocene (P8) through the development of an alveolar wall.

The relationship between *Alveolophragmium* sp. 1 Charnock & Jones, 1990 and *A. orbiculatum* Shchedrina, 1936 requires investigation.

**(5) Eratidis foliaceus – Spirospamina uhligi**

*Spirospamina uhligi* is interpreted as having evolved from *Eratidis foliaceus* during the Early Oligocene through the development of hemisepa. *Eratidis foliaceus* is interpreted as having evolved in turn either directly or indirectly (via an intermediary such as *Duquespamina cubensis*) from *Spiroplectammina* (Spiroplectinella) *spectabilis*.

Morphological and stratigraphic evidence indicates that *Popovia* sp. 1 Charnock & Jones, 1990, which, like *S. uhligi* belongs in the Subfamily Spirospaminiae of the Family Lituolidae, may be ancestral to the essentially Miocene species *Cyclammina* (*Reticuloophragmium*) *venezuelanum* (which unfortunately has not been recorded in the North Sea).

**CONCLUSIONS**

On the basis of consideration of taxonomic (morphological) and stratigraphic relationships, five evolutionary lineages have been recognised among the North Sea lituolid foraminifera with complex structures (i.e., the Subfamilies Cyclammininae and Spirospaminiae of the Family Lituolidae). Four (Subfamily Cyclammininae) appear to have originated from *Haplophragmoides* or *Velerinoides* (Subfamily Haplophragmoidinae), one (Subfamily Spirospaminiae) from *Eratidis* (Subfamily Ammomarginulininae) and perhaps ultimately from *Spiroplectammina* (Subfamily Spiroplectamininae, Family Textulariidae). All are essentially Cenozoic.

The evolution (and extinction) of the various complex lituolid species appears to be related to evolving palaeoenvironmental conditions mediated by tectono-eustasy.

**Recommendations**

In order to further elucidate taxonomic and phylogenetic affinities within the complex lituolid group, it is recommended that the relationships between the following species be investigated:

- *Alveolophragmium* sp. 1 Charnock & Jones and *A. orbiculatum* (Shchedrina);
- *Cyclammina* (*Cyclammina*) *placenta* (Reuss) and *C. (C.) cancellata* Brady (also *C. (?) praeacancella* Voloshinova);
- *Popovia* sp. 1 Charnock & Jones and *Cyclammina* (*Reticuloophragmium*) *venezuelanum* (Mayne).

It is also recommended that evolutionary relationships in areas outside the North Sea be investigated. One area that would readily lend itself to such a study is the Miocene of Central Paratethys, where some work has already been done by Cicha and Zapletova (1966), and Cicha *et al.* (1983).

Studies are also required on the controls on the development of alveolar wall structure and cribrate apertures (i.e., whether evolutionary or environmental). Investigation of variation in these aspects of morphology along coeval transects from the margin to the centre of a basin would be highly instructive in this regard. Variations in other aspects of morphology with depth (cf. Theyer, 1971; Boltovskoy *et al.*, 1991) could also be investigated by this means. Investigation of possible temporal variations in depth distributions (cf. Robinson, 1970) would have to be based around analyses of transects from successive time-slices.

**SYSTEMATIC PALEONTOLOGY**

The following abbreviations are used throughout: FO – first (evolutionary) occurrence (inception); LO – last occurrence (extinction); LCO – last common occurrence; LAO – last abundant occurrence.

Family LITUOLIDAE de Blainville, 1827

Subfamily CYCLAMMININAE Marie, 1941

**Remarks:** Included here are essentially planispiral Lituolidae with alveolar walls. The alveoli are typically numerous and fine; they may bifurcate and then bifurcate again in advanced forms. Their function is unclear but we believe that they might serve to assist in gaseous exchange under dyserotic conditions. They appear neither analogous nor homologous to the canali culi of the advanced ataxophragmiaceans and textulariids, which appear to assist in chamber construction.

**Genus Alveolophragmium** Shchedrina, 1936

Type-species *A. orbiculatum* Shchedrina, 1936; O. D.

**Remarks:** This genus differs from *Cyclammina* (*Reticuloophragmium*) Mayne, 1955 in the intero-areal rather than interiomarginal location of the aperture.

*Alveolophragmium* sp. 1 Charnock & Jones, 1990

Fig. 6 (1a-c), Fig. 7 (1-2)

1990. *Alveolophragmium* sp. 1: Charnock & Jones, 1990, p. 174, pl. 7, figs. 1-2, pl. 18, fig. 1


**North Sea Distribution:** Early-middle Eocene, Zones P8-P11/12 (see below; see also Charnock & Jones, 1990).

The inception of this species postdates the LO of the *Glaciolina* (*Subbotina*) *linaperata* group, predates the LAO of *Cenosphaera* spp. and the LCO of *Eatonicya* *vesculae* and *Hystrichospaeridium* *tubiferum* (e.g., UKCS 9/19-4, 5260'), and is approximately coincident with the LO of *Spiroplectammina navaroana* (e.g., UKCS 16/26-1, 7020'). This enables an indirect calibration against early Eocene Zone P8.

Its extinction postdates the LO of *Diphyes* *fuscoidea* and predates the LO of *Heteralocycta porosa*, and falls within an interval characterised by common *Systematophora* *placacantha*. This enables an indirect calibration against middle Eocene Zone P11 or P12. This is supported by the observation that it falls between the LO of *Spiroplectammina aff. spectabilis* and the LCO of *Cyclammina* (*Reticuloophragmium*) *amplicentis* (e.g., UKCS 22/2-1, 7440').

*Alveolophragmium* sp. 1 occurs consistently, but never commonly, in the uppermost lower and lowermost middle Eocene (particularly in the Central Graben, where it is generally associated with the common to abundant occurrence of *Cyclammina* (*Reticuloophragmium*) *amplicentis*. 
Fig. 6. Camera lucida line drawings; x50 unless otherwise stated: 1 – Alveolophragmium sp. 1: a-b. UKCS 15/20-1, 6000'. c. UKCS 16/21a-B3, 6400'. 2 – Cyclamina (Cyclammina) acutidorsata (von Hantken), NOCS 1/6-2, 8900'. 3 – Cyclamina (Cyclammina) placenta (Reuss); a-b. UKCS 23/11-1, 6750'; c. NOCS 15/12-1, 7160'. 4 – Cyclamina (Reticulophragmium) amplexensis (Grzybowski); a. UKCS 29/5b-2, 9580'; b-d. UKCS 21/14-1, 1910m. 5 – Cyclamina (Reticulophragmium) rotundidorsata (von Hantken); a-b. UKCS 23/21-1ST, 7680'; c. UKCS 21/30-1, 6030'. 6 – Cyclamina (Reticulophragmium) sp. 1: a. UKCS 29/8b-1; b-c. NOCS 16/1-1, 7760'. 7 – Cyclamina (Reticulophragmium) sp. 2. UKCS 21/1-1, 5020'. 8 – ReticulophragmoidesJarvisi (Thalmann), UKCS 22/11-1, 7040b. c. diagrammatic enlargement. 9 – Popovia elegans (Kaminski), UKCS 9/23-1, 5110'. 10 – Popovia sp. 1, NOCS 7/11-1, 7030'. 11 – Spiropsammia ulagi (Schubert), UKCS 30/24-38, 6560'.
Genus *Cyllaemia* Brady, 1879
Type-species *C. cancellata* Brady, 1879; O. D. (M.)

**Remarks:** Two subgenera are recognised within this genus, namely *Cyllaemia* (*Cyllaemia*) Brady, 1879 and *C. (Reticulophragium)* Maync, 1955.

Subgenus *Cyllaemia* (*Cyllaemia*) Brady, 1879
Type-species *C. cancellata* Brady, 1879; O. D. (M.)

**Remarks:** This subgenus differs from *Cyllaemia* (*Reticulophragium*) Maync, 1955 in the development of multiple areal apertures. This might be expected to be a late ontogenetic or phylogenetic feature worthy of recognition at the generic level. However, in our material it is more marked in Eocene than in Oligocene and Miocene populations, implying environmental rather than evolutionary control. Pending further investigations, we have therefore maintained the two as subgenerically distinct only.

*Cyllaemia* (*Cyllaemia*) *acutidorsata* (Hantken, 1868)
Fig. 6 (2a-c), Fig. 7 (3-5)

1990. *Cyllaemia* (*Cyllaemia*) *acutidorsata* (Hantken): Charnock & Jones, p. 175, pl. 7, figs. 3-4; pl. 18, fig. 2.

**Remarks:** One of us (MAC) has, through the good offices of Fred Rogl of the Naturhistorisches Museum, Vienna, examined the autotype of this species (slide labelled: OFEN, Budapest Klein- zeller, Tegel, 1988-24/1/2") and found our North Sea material to be in close conformity. This species only rarely develops areal apertures (Charnock & Jones, 1990, pl. 18, fig. 2b).

**North Sea Distribution:** Early-late Oligocene, Zones P18-P21 (see below; see also King, 1989 (*Reticulophragium*); Charnock & Jones, 1990).

The inception of this species immediately postdates the LO of *Aereospaeridia dictyoplosus* (Eocene) and the log break defining the top of the Horida Formation (e.g., NOCS 1/6-7, 2843m (SWC)), predates the LO of *Globigerina (Subbotina) eocaena*, and falls within an interval characterised by *Rotalina bulimoides*. This enables an indirect calibration against Early Oligocene Zone P18. However, it is rare at this level, and its FCO is typically in the lowermost upper Oligocene, just above the LO of *R. bulimoides* (e.g., UKCS 29a/2a, 5060' (SWC)).

Its extinction in the Central North Sea postdates the LO of *Globorotalia mundae* and predates the FOS of *Globigerina an- guisuturalis* and *Globorotalia opima nova* (e.g., UKCS 29a/2a, 4230'). This enables a calibration against late Oligocene Zone P21. Where planktonic foraminiferal control is lacking, the extinction datum postdates the LOs of *Chorticeridium mepsalum* and Diatom sp. 4 King, 1983, predate the LO of Diatom sp. 3 King, 1983, and is approximately coincident with the LOs of *Spiror- niospinulina compressa* and *Turritella alata* (e.g., UKCS 29a/6, 3860').

**Total Known Stratigraphic Range:** Middle Eocene-early Miocene.

*Cyllaemia* (*Cyllaemia*) *placenta* (Reuss, 1851)
Fig. 6 (3a-c), Fig. 7 (6-8)

1990. *Cyllaemia* (*Cyllaemia*) *placenta* (Reuss): Charnock & Jones, p. 175, pl. 7, figs. 5-12; pl. 18, fig. 4.

**Remarks:** The range of infraspecific variability exhibited by this species probably embraces *Alveolophragium* sp. 1 Gradstein & Berggren, 1981.

**North Sea Distribution:** Eocene-Miocene, Zones P8-N17 (see below; see also Gradstein & Berggren, 1981; Miller et al., 1982; Gradstein et al., 1988, 1992, 1994; King, 1989 (*Reticulophragium*); Charnock & Jones, 1990).

The inception of this species postdates the FOs of *C. (Reticulophragium)* *amplexent* and the Globigerina (*Subbotina*) linaperta group and the LOs of *Dracodinium solidum* and *Spiroplectammina navarroana*, and predates the LOs of *Eocenica utriculata* and *Hystrichosphaeridium tubiferum* and the LCO of *Cenosphaera* spp. (e.g., UKCS 9/18a-18, 4934' (SWC)). This enables a calibration against early Eocene Zone P8. Probable ancestral forms, associated with *C. (Reticulophragium)* sp. 2 Charnock & Jones, 1990, have been identified in significantly (4Ma) older predeltaic muds in the lower part of the Dormoc Formation in the Outer Moray Firth (e.g., UKCS15/12-1, 4450-4810'). These occur immediately above the LO of *Aereoligera gippensgen*; enabling an indirect calibration against late Palaeo- cene Zone P4. The earliest appearance of advanced forms with crinate apertures postdates the LO of *Diphys sisoides* and the LCO of *Cyllaemia* (*Reticulophragium*) *amplexent* and predates the LOs of *Diphys colligera*, *Heterocysta porosa* and *Rotnesia borassica* and falls within an interval characterised by common *Systematophora placanecta* (e.g., UKCS 15/30-1, 5680'; NOCS 15/12-1, 2182m). This is dated as within the middle Eocene.

The extinction of *C. (C.) placenta* is environmentally controlled and diachronous (dependent on location with respect to basin margin and bathymetry). At the basin margin, it falls within the late Oligocene, while at the basin centre (in the deepest parts of the Central Graben), it falls within the middle-late Miocene, within an interval characterised by a remnant low-diversity agglutinated assemblage (Zone NSA12 of King, 1989). In the Central Graben (e.g., UKCS 30/12-1, 4910'), it is approximately coincident with the LOs of *Anmmodicus* spp. and *Usbekistania charoides*, and predates the LO of tubular arborizids; in terms of calcareous benthonic foraminiferal datums, it predates the LO of *Uvigerina pygmaea langeri* and the LCO of *U. venusta saxonica*; in terms of planktonic foraminiferal datums, it postdates the LCO of *Neogloborotalia puncticulata* and the LCO of *Neogloboquadrina atlantica*. This enables a calibration against late Miocene Zone N17.

*C. (C.) placenta* has the longest range of any cyclostomin in the North Sea. It is most common in the Oligocene.

**Total Known Stratigraphic Range:** Eocene-Miocene.

Subgenus *Cyllaemia* (*Reticulophragium*) Maync, 1955
Type-species *Alveolophragium venezuelanum* Maync, 1952; O. D.

**Remarks:** This subgenus differs from *Cyllaemia* (*Cyllaemia*) Brady, 1879 in lacking the development of multiple areal apertures, and from *Alveolophragium* *Shedrini*, 1936 in the interomarginal rather than intero-areal location of the aperture.

*Cyllaemia* (*Reticulophragium*) *amplexent*
Grzybowski, 1898
Fig. 6 (4a-d), Fig. 7 (9-11)

1990. *Cyllaemia* (*Reticulophragium*) *amplexent* Charnock & Jones: p. 176, pl. 8, figs. 1-5, pl. 18, fig. 3.

1993. *Reticulophragium* *amplexent* (Grzybowski): Kamiński & Geroch, pp. 266-267, pl. 11, figs. 5-7.

**Remarks:** We have compared our North Sea specimens against type material, and found them to be in close conformity (Charnock & Jones, 1990). They are undoubtedly conspecific with the lectotype later designated by Kamiński & Geroch (1993).

**North Sea Distribution:** Late Palaeocene, Zone P4 (cf.), Eocene-Oligocene, Zones P8-P21 (see below; see also Berggren & Gradstein, 1980; Gradstein & Berggren, 1981; Miller et al., 1982;

Ancestral forms of this species, herein referred to as “Cyclammina (Reticulophragmium) cf. amplicentis”, have been identified in the upper part of the Lista Formation (e.g., UKCS 15/18-2, 5455° (core)). Their occurrences are approximately coincident with the LO of Areoligera gippingsena, enabling an indirect calibration against late Palaeocene Zone P4.

The inception of C. (R.) amplicentis s.s. is approximately coincident with the LOs of acorinina broedermanni, Muricoglobigerina soldadoensis and the Globigerina (Subbotina) linaperta group (e.g., UKCS 9/19-11, 5400° (SWC)). This enables a calibration against early Eocene Zone P8.

The extinction of C. (R.) amplicentis s.s. is environmentally controlled and diachronous (dependent on location with respect to basin margin and bathymetry). At the basin margin, it falls within the middle Eocene, while at the basin centre (in the deepest parts of the Central Graben) it falls within the late Oligocene. In the Central Graben, it postdates the LOs of Globorotalia munda and Rotaliataea bimoides and the LAO of Globigerina officinalis, and predates the LOs of Globigerina angulisuturalis, Globorotalia opima nana, Spiroplectinilina compressa and Turrilina alsatica (e.g., UKCS 29/3a-7, 4470°). This enables a calibration against late Oligocene Zone P21.

C. (R.) amplicentis s.s. is regarded by many authors as restricted to the Eocene, and is certainly most common at this level. It is commonest of all in the Central Graben and South Viking Graben areas and rarest in the North Viking Graben and Mid-Norway areas.

There are in actuality two C. (R.) amplicentis s.s. acme events within the Eocene. The older, more major, one is at the boundary between the lower and middle Eocene (the boundary between Members H1 (Frigg and Lower Tay Sandstones and Equivalents) and H2 (Upper Tay and Caran Sandstones and Equivalents) of the Horda Formation)(e.g., 22/21-1, 8033° (core), UKCS 30/1-1, 9840°). The younger, more minor, one is at the top of the Eocene (the top of Member H3 (Brodie Sandstone and equivalents) of the Horda Formation)(e.g., UKCS 21/20-1, 7280°). Both acme events appear to be associated with eustatically-maintained lowstands of sea-level and/or subsequent transgressions (within Cycles TA3.1 and TA4.3 of Haq et al. (1987) respectively).

**Total Known Stratigraphic Range:** Latest Palaeocene–Oligocene. The earliest well constrained records are from the lower Eocene (Zones P6b/P7 (based on indirect calibration using palynological data) of the Barents Sea (Nagy et al., in press); Zones P7/P8 (based on calibration using calcareous nannoplankton data) of the Polish Carpathians (Olszewski & Smagowicz, 1977; Kaminski & Geroch, 1993). Older records from the southern hemisphere (Late Cretaceous (?))–Palaeocene, Borneo (Keji, 1965); Palaeocene–Eocene, New Zealand (Hornbrook et al., 1989, and references therein); latest Palaeocene–middle Eocene, Tasman Sea (Webb, 1975)) require verification.

**Cyclammina (Reticulophragmium) rotundidorsata** (Hancken, 1876)

Fig. 6 (5a-c), Fig. 8 (1-2)


**Remarks:** One of us (MAC) has, through the good offices of Fred Rögl of the Naturhistorisches Museum, Vienna, examined one of the autotypes of this species (slide labelled “OFEN, Budapest Kleinzeller, Tegel, 1881 – C1186/2”), and found our North Sea material to be in close conformity. We have both also examined the Recent types of Cyclammina orbicularis Brady, 1879 in the British Museum (Natural History), and regard it as conspecific.

**North Sea Distribution:** Middle Eocene–Oligocene–earliest Miocene, Zones P11, P18-N4 (see below); see also Gradstein & Berggren, 1981; Miller et al., 1982; Gradstein et al., 1988; King, 1989 (Reticulophragmium orbicularis); Charnock & Jones, 1990.

Ancestral forms of this species, herein referred to as Cyclammina (Reticulophragmium) aff. rotundidorsata, characterised by the presence of an inflated test and concentrations of alveoles along the sutures, have been identified in the upper part of the Lista Formation (e.g., UKCS 15/24-W3, 9840°). The inception of C. (R.) rotundidorsata s.s. is poorly dated owing to a lack of reliable planktonic control. There are records in undoubted middle Eocene sections (e.g., UKCS 29/3c-9, 7730°), but these are based on cuttings samples only, and, in view of the possibility of caving, are regarded as questionable. The oldest incontrovertible records (e.g., UKCS 29/2a-6ST, 4453° (SWC)) are from immediately above the FO of Karreriella seigliei and the LO of Areosphaeridium dictypolokus (and the log break defining the top of the Horda Formation), and below the FO of Wertzeilich gochti and the FO of Rotaliataea bimoides, hence (indirectly) Early Oligocene (Zone P18).

The extinction is generally (e.g., UKCS 29/2a-7, 4580° (SWC)) above the LOs of Globorotalia munda and Rotaliataea bimoides, and below the LOs of Chiropteridium mesquilium and Ditom sp. 3 King, 1983 and the LCO of Spiroplectinilina compressa. This enables a calibration against late Oligocene Zone P21. There is, however, a single record (NOCS 1/6-7, 1990m) from between the LOs of Globigerina ciperoensis and Globorotalia opima nana, and below the LCOs of Globigerina woodii and Haplophragmoides spp. This is calibrated against latest Oligocene–earliest Miocene Zone N4.

**Total Known Stratigraphic Range:** Eocene–Recent.

**Cyclammina (Reticulophragmium) sp. 1**

Charnock & Jones, 1990

Fig. 6 (6a-c), Fig. 8 (3-4)

1990. Cyclammina (Reticulophragmium) sp. 1 Charnock & Jones: Charnock & Jones p. 177, pl. 8, figs. 6-7; pl. 19, fig. 2.

**Remarks:** This species differs from Cyclammina garciolasi Friz-
Fig. 8. SEM photographs. 1-2 – Cyclammina (Reticulophragmium) rotundidorsata (Hantken): 1. lateral view, NOCS 1/3-1, 8800'; 2. apertural view, UKCS 16/28-1. 3-4 – Cyclammina (Reticulophragmium) sp. 1: 3. lateral view, UKCS 21/7-1, 6120'; 4. apertural view, UKCS 21/7-1, 6120'. 5-6 – Cyclammina (Reticulophragmium) sp. 2: 5. lateral view, UKCS 15/11-3, 4110'; 6. apertural view, UKCS 21/2-1, 6980'. 7-8 – Reticulophragmoides jarvisi (Thalmann): 7. lateral view, NOCS 7/8-2, 6800'; 8. apertural view, NOCS 7/8-2, 6800'. 9 – Popovia elegans (Kaminski), NOCS 16/1-1, 9080'; lateral view. 10-11 – Popovia sp. 1: 10. lateral view, NOCS 7/11-7, 7030'; 11. apertural view, UKCS 22/27a-3ZST, 5500'. 12 – Spiropsammia uhligi (Schubert), NOCS 1/6-7, 1534m (SWC)
zoll, 1943 and C. pauppera Chapman, 1904 (the latter recently redescribed by Ludbrook, 1977), with which it has been extensively confused (e.g., Gradstein et al., 1988, 1992, 1994 (Reticulophragmium garcilasi) (?) and/or R. pauppera) in that the alveoli are concentrated along the sutures and at the periphery.

**North Sea Distribution:** Late Palaeocene, Zone P4 (see below; see also King, 1989 (R. sp. A); Charnock & Jones, 1990; Neal et al., 1994 (R. cf. garcilasi) (?)).

The inception of this species postdates the LCO of Palaeoeridinium pyrophorum and predate the LCO of Aoreligera gippingensis. This enables an indirect calibration against late Palaeocene Zone P4.

Its extinction immediately postdates the LO of A. gippingensis and is approximately coincident with the LOs of many agglutinated species (including Spiroplectammina spectabilis, Spirosluitolinia naibensis and Trochammina ruthveniurnae) (e.g., UKCS 9/19-11, 6998° (SWC)). This is also (indirectly) calibrated against late Palaeocene Zone P4.

This species has an extremely short stratigraphic range. In terms of geographic distribution, it appears to be restricted to the in the deeper parts of the Central and South Viking Grabens. Its development, and indeed that of the DWAF association of which it forms a component, appears related to the eustatically-mediated high stand of sea-level and the associated predominantly fine-grained sedimentation characteristic of the Lista Formation and its equivalents. The succeeding tectonically-enhanced low stand resulted not only in the locally coarse-grained sedimentation characteristic of the Sel Formation and its equivalents (including the Forties and Cromarty Sandstone Members and their equivalents), but also in the effective elimination of the benthos (through an excess of runoff, water-mass stratification, restricted circulation and development of dysaerobic to anaerobic bottom conditions).

**Total Known Stratigraphic Range:** Palaeocene (Zones P2 (sporadic)-P6A). The earliest record is from upper lower Palaeocene (Zone P2 (sporadic)) of Trinidad (Kaminski et al., 1988).

**Cyclaminia (Reticulophragmium) sp. 2**
Charnock & Jones, 1990
Fig. 6 (7a-b), Fig. 8 (5-6)
1990. Cyclaminia (Reticulophragmium) sp. 2 Charnock & Jones; Charnock & Jones, p. 177, pl. 8, figs. 8-11; pl. 19, fig. 3.

**North Sea Distribution:** Late Palaeocene, Zone P4 (see below; see also Charnock & Jones, 1990).

The inception of this species postdates the LO of Aoreligera gippingensis, and falls within an interval characterised by abundant and diverse agglutinated foraminifera (e.g., UKCS 14/29-1, 4460°). Its typical development and extinction postdate the LOs of Spiroplectammina spectabilis and Spirosluitolinia naibensis and predate the LO of Apectiodinium spp., and fall within an interval characterised by reduced agglutinate abundance and diversity and sporadic occurrences of Cyclaminia (Reticulophragmium) cf. amplexana (e.g., UKCS 9/19-11, 6980°). This enables an indirect calibration against late Palaeocene Zone P4.

This species has an extremely narrow stratigraphic range. In terms of geographic distribution, it appears to be restricted to the western (landward) margins of the Central and South Viking Grabens. Its development appears related to the predominantly fine-grained prodeltaic sediments characteristic of the upper part of the Lista Formation and the lower part of the Dornoch Formation.

**Genus Popovia Suleymanov, 1965**
Type-species Alveolophragmium planum Bykova, 1939; O. D.

**Popovia elegans** (Kaminski, in Kaminski & Geroch, 1987)
Fig. 6 (9), Fig. 8 (9)
1990. Popovia elegans (Kaminski): Charnock & Jones, p. 178, pl. 20, fig. 2.

**Remarks:** M. A. Kaminski has verified our identification of this species.

**North Sea Distribution:** Early Eocene, Zone P8 (see below; see also Charnock & Jones, 1990).

Rare occurrences of this species in the Viking Graben area of the Central North Sea (e.g., UKCS 9/23-1, 5110°) are approximately coincident with those of the Globigerina (Subbotina) inaperta group and Pseudohastigerina wilcoxensis (within an interval dominated by calcareous benthonic and planktonic foraminifera). This enables a calibration against early Eocene Zone P8.
Total Known Stratigraphic Range: Maastrichtian–early Eocene (lapparenti tricarnea Zone-P8).

**Popovia sp. 1** Charnock & Jones, 1990
Fig. 6 (10a-b), Fig. 8 (10-11)

*Popovia sp. 1* Charnock & Jones, 1990, p. 179, pl. 20, fig. 3.

**North Sea Distribution:** Middle Eocene–Early Oligocene, Zones P14-P21 (see below; see also Charnock & Jones, 1990).

In terms of foraminiferal bio-events, the inception of this species is approximately coincident with the L0s of several species of agglutinated foraminifera (including *Annamarginata abertiae* and *Spiropectaminina aff. spectabilis*); in terms of palyno-events, it falls between the L0s of *Arecophoerium dicoryphos* and *Heterovalvula porosa* (e.g., NOCS 6/3-1, 2215m). This enables an indirect calibration against middle Eocene Zone P14.

Its extinction is approximately coincident with the L0 of *Rotaliinana balinoides*. This enables an indirect calibration against late Oligocene Zone P21.

This is a generally rare species, recorded only in the deeper parts of the Central and South Viking Grabens (in both the UK and Norwegian sectors). It is most common in the lower Oligocene.

**Genus Spirosummania Seelig & Baker, 1983**
**Type-species Cyclammina uhligi** Schubert, 1902; O. D.

*Spirosummania uhligi* (Schubert, 1902)
Fig. 6 (11), Fig. 8 (12)


**North Sea Distribution:** Oligocene–Miocene, Zones P18-19/17 (see below; see also Charnock & Jones, 1990).

The inception of this species falls above the log break marking the top of the Horda Formation (Eocene) and below the L0s of *Diatom sp. 3 King*, 1983 and *Glachigerina (Subbotina) eocenii* (e.g., UKCS 30/24-38, 6560'). This enables a calibration against Early Oligocene Zone P18 or P19.

Its extinction falls between the FO of *Globorotalia punctulata* and the LO of *Neogloboquadrina continua*, and immediately above the LCO of *N. acenta* (e.g., NOCS 1/6-7, 1534m (SWC)). This enables a calibration against late Miocene Zone N17. This is in turn supported by its position above the LCO of *Balboaforma metzacheri* and between the L0s of *Uvigerina semiornata* and *U. venusta saxonia*. Interestingly, the extinction of *S. uhligii* is below that of most other deep-water agglutinating foraminifera in the late Miocene.

This is a rare species, recorded only in the deeper parts of the Central North Sea. In the Miocene, it is extremely rare, and recorded only in the deepest parts of the Norwegian sector.

**Acknowledgements**

We were both fortunate enough to have met and worked with Stanislaw Geroch in latter years. We shall miss him not only as a distinguished and respected colleague but also as a man of rare qualities, whose deep knowledge and freely offered help and encouragement (born out of an abiding love of his science and of the spirit of scientific collaboration) were matched by his extraordinary kindness, hospitality and humility.

BP and Robertson Research International Ltd. are thanked for providing word-processing and drafting facilities and permission to publish. The University College of Wales, Aberystwyth is thanked for granting access to their Scanning Electron Microscope. Caroline Maybury for undertaking the SEM photography. The authors thank the reviewers F. M. Gradstein and M. A. Kaminski for discussion and general help.

**REFERENCES**


Streszczenie

OTWORNICE AGLUTYNUJĄCE Z RODZINY LITUOLIDAE Z OSADÓW TRZECIORZĘDOWYCH MORZA PÓŁNOČNEGO; STRUKTURA WewnĘTRZNA SKORUPI, TAKSONOMIA, STRatyGRAFIя I EwolucJA

Michael A. Charnock & Robert W. Jones

Głębokowodne otwornice aglutynujące są charakterystycznym elementem w zespołach mikrofauny w osadach od górnego miocenu w Morzu Północnym oraz w środkowej i południowej części rowu tektonicznego Wikingów (Fig. 1 & 2).
Basen Morza Północnego był w czasie od paleoceneu do środko-
wego miocenu miejscem gwałtownej sedymentacji związanej z częstymi zmianami (obniżeniem) poziomu morza, stymulowanymi przez czynniki eustacyjne i tektoniczne. Towarzyszyło temu szereg innych efektów hydrologicznych jak stratyfikacja wody, jej ograniczona cyrkulacja, obniżona zawartość tlenu, podwyższony udział CO₂ w wodach dennych i porowych. Takie warunki sprzyjały rozwojowi populacji otworów aglutynujących kosztem otworów wapiennych.

Zespoly mikrofauny charakteryzowały w tym czasie obecność głębokowodnych otworów aglutynujących z rodziny Lituolidae (podrodziny: Cyclamininae i Spiropsaminiae), których ewoluacja związana była z procesami tektoniczno-eustacyjnymi (Seiglie, 1987). Pierwsze pojawienie się otworów aglutynujących w centralnej części Morza Północnego odnotowano na najniższą część weńcego paleoceneu, natomiast pierwsze lituolidy znane są z osadów górnego paleoceneu (Fig. 2). Ich rozwój (n.p. Cyclamina (Reticulophragmium) sp. 1) w późnym paleoceneu można skorelować z cyklem transgresywnym (TSTS i HSTS) trzeciego rzędu (TA2.1) według Haq et al. (1987), którego efektem była sedymentacja drobnoziarnistych osadów formacji Lista (fm). Kolejny epizyd pojawienia się zespołu głębokowodnych otworów aglutynujących udokumentowano na wczesny eocen (około 52,5 Ma). Masowa radiacja i wzrost lituolidów (n.p. evolucja Alveolophragmium sp. 1 oraz acme Cyclamina (Reticulophragmium) amplexans) nastąpiła w okresie przełomu wczesnego i środkowego eocenu (około 49 Ma). Można to korelować z cyklami TA2.9 i TA3.1, zapisanymi w osadach formacji Horda (fm). Episód wzrostu tej grupy otworów, nieco mniejszej rangi (dotyczy gatunku C. (R.) amplexans) miał miejsce w czasie późnego eocenu, co odpowiadaloby cyklom TA4.1-4.3.

Maximum radiacji zespołu głębokowodnych otworów aglutynujących w Morzu Północnym nastąpiło w paleocene. Natomiast ograniczenie ewolucji zespółów związane z obniżeniem poziomu wody i wypełnianiem basenu przez osady miało miejsce w czasie od eocenu do końca miocenu. Wymieranie gatunków było diachroniczne i zależało od głębokości zasiedlania dna przez poszczególne zespoły.

W niniejszej pracy przedstawiono badania taksonomicznych lituolidów z obszaru Morza Północnego, przeprowadzając dyskusję na temat ewolucji tej grupy otworów (Fig. 3) i zasięgów stratygraficznych poszczególnych jej taksonów (Fig. 4).

W oparciu o analizę cech taksonomicznych z wykorzystaniem badań innych autorów wyróżniono pięć linii ewolucyjnych wśród reprezentantów tej grupy w Morzu Północnym, dotyczących form należących do podrodzin Cyclamininae i Spiropsaminiae. Cztery linie ewolucyjne (dotyczą podrodziny Cyclamininae) rozpoczyna rodzaj Haplophragmoides lub Veleroninoides (podrodzina Haplophragmoidinae), a przodkiem jednej (dotyczy podrodziny Spiropsaminiae) jest prawdopodobnie rodzaj Eritidis (podrodzina Ammonorotalinae) lub Spiractenammina (podrodzina Spiractenaminia). Są to następujące linie ewolucyjne:

1. Haplophragmoides walteri–Reticulophragmoides jarvisi/Cyclamina (Reticulophragmium) amplexans
2. Haplophragmoides suborbicularis–Cyclamina (Reticulophragmium) rotundidorsa
3. Haplophragmoides sp. 1–Cyclamina (Cyclamina) placent-o-C. (C.) acutidorsa
4. Veleronoides scitulus–Alveolophragmium sp. 1
5. Eritidis foliens–Spiropsaminia ulghi.

Uwzględniając powyższe wyniki autorzy rekomendują pary gatunków do dalszych badań taksonomicznych określających wzajemne relacje filogenetyczne, zarówno w zespołach z Morza Północnego jak i z miocenem centralnej części Paratetydy, które były już wcześniej przedmiotem podobnych studiów (Cicha & Zapletova, 1966; Cicha et al., 1988). Dotyczy to:

– Alveolophragmium sp. 1 Charnock et Jones i A. orbiculatum (Shehdermina);
– Cyclamina (Cyclamina) placent-o (Reuss) i C. (C.) canc-
 cellata Brady (również C. (?C.) praecancellata Voloshinova);
– Popovia sp. 1 Charnock et Jones i Cyclamina (Reticulophragmium) venezuelana (Mayne).

Autorzy proponują zwrócić uwagę na zmiany alveolarnej struktury ścian skorupki oraz na zmiany w kształcie i obecności siatkowatych otworów skorupki, określając czy zmiany te powstały na drodze ewolucyjnej czy związane są ścisłe ze zmianami środowisk. Pomoc temu mogą badania zespołów lituolidów obserwowanych w osadach tego samego wieku ale pochodzących z różnych części basenu. Powinny one być badane w kolejnych sezjoncjach osadów odpowiadających jak najmniejszym jednostkom chronostrograficznym.