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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 Cyclammininae and Spiropsamiinae of the Family Lituolidae) are reviewed. Five essentially Cenozoic evolutionary lineages are recognised, four (Subfamily Cyclammininae) appearing to have originated from *Haplophragmoides* or *Veleroninoides* (Subfamily Haplophragmoidinae), one (Subfamily Spiropsamiinae) from *Eratidus* (Subfamily Ammomarginulininae), and perhaps ultimately from *Spiroplectammina* (Subfamily Spiroplectammininae, Family Textulariidae). Selective synonymies, 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 Cyclamminiae i Spiropsamiinae) biorąc pod uwagę cechy taksonomiczne, zasięgi stratygraficzne oraz określając wzajemne relacje filogenetyczne. Wyróżniono pięć głównych linii ewolucyjnych, z których cztery (dotyczą Cyclamminiae) rozpoczyna rodzaj *Haplophragmoides* lub *Veleroninoides* (podrodzina Haplophragmoidinae), a przodkiem jednej (podrodzina Spiropsamiinae) jest prawdopodobnie rodzaj *Eratidus* (podrodzina Ammomarginulininae) lub *Spiroplectammina* (podrodzina Spiroplectammininae).

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

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

Autorzy proponują zwrócić uwagę na zmiany alweolarnej struktury ścian skorupki oraz na zmiany w kształcie i obecności sitkowatych otworów skorupki, określając czy zmiany te powstały na drodze ewolucyjnej czy związane są ściśle ze zmianami środowiska. Pomóc temu mogą badania zespołów lituolidów z osadów tego samego wieku ale pochodzących z różnych części basenu. Powinny one być badane w kolejnych sekwencjach osadów odpowiadającym jak najmniejszym 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.

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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 tectonoeustatically-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 Spiropsamiinae) whose evolutionary history records their adaptation to palaeoenvironmental conditions mediated by tectonoeustasy (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 high-stand 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 recolonisations 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*) *amplectens*) appears to correlate with Cycles TA2.9 and TA3.1 (Horda Formation). A less significant increase in *C.* (*R.*) *amplectens* 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.

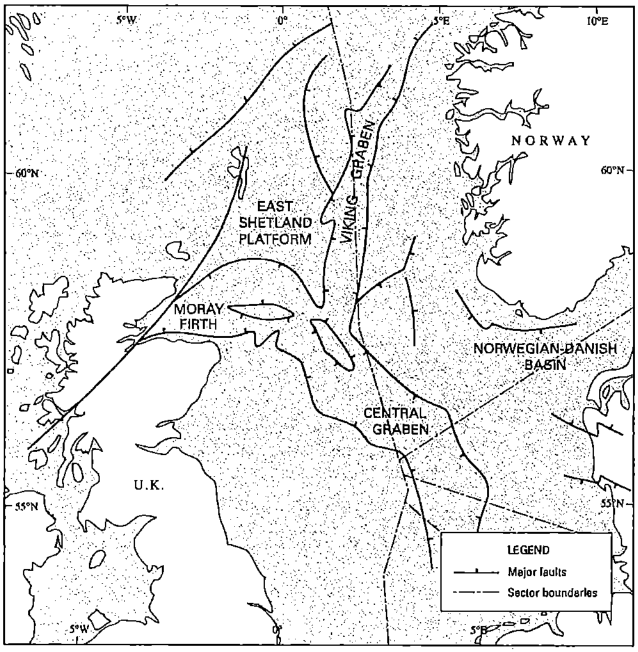


Fig. 1. Location map

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 documentations of North Sea distributions are appended.

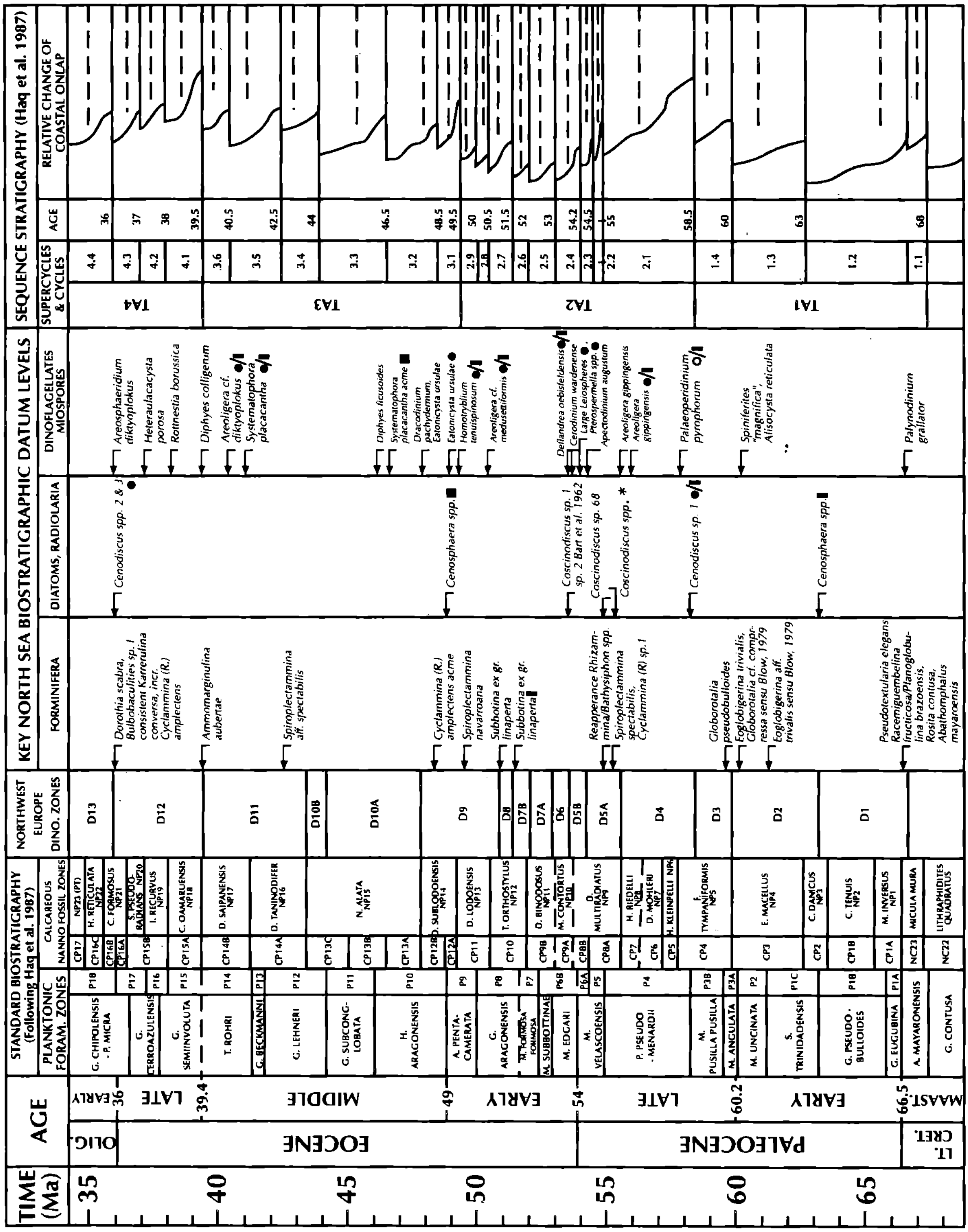
DISCUSSION: PHYLOGENETIC RELATIONSHIPS

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 Kaminski (1990).

Banner (1970) considered there to be three taxa within the Subfamily Cyclammininae of the Family Spirocyclinidae (Lituolidae), namely *Cyclammina* and *Alveolophragmium s.l.* (*Alveolophragmium s.s.* and *Alvelophragmium* (*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



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 garcilasoi* 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 cribrate 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.*) *amplectens*, with *C.* (*R.*) *rotundidorsata* as a separate offshoot, and further interpreted *C.* (*C.*) *acutidorsata*, *C.*(*C.*) *placenta* and *C.* (*C.*) *cancellata* as having evolved from *C.* (*R.*) *amplectens*, 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 lituolid group (i.e., the Subfamilies Cyclammininae and Spiropsamiinae 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 Spiropsamiinae) from *Eratidus* (Subfamily Ammomarginulininae), and perhaps ultimately from *Spiroplectammina* (Subfamily Spiroplectammininae, Family Textulariidae). All are essentially Cenozoic.

The lineages are as follows:

(1) Haplophragmoides walteri – Reticulophragmoides jarvisi/Cyclammina (Reticulophragmium) amplectens

Reticulophragmoides 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. *garcilasoi* (*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 *Reticulophragmoides 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.*) *amplectens* also during the Late Palaeocene (P4). Alveolar development in *C.* (*R.*) *amplectens* 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 suborbicularis – Cyclammina (Reticulophragmium) rotundidorsata

Cyclammina (Reticulophragmium) rotundidorsata is interpreted as having probably evolved from *Haplophragmoides suborbicularis* during the late Palaeocene (P4) through the development of an alveolar wall structure. Interestingly, while primitive forms of *Cyclammina* (*Reticulophragmium*) *rotundidorsata* (*C.* (*R.*) aff. *rotundidorsata*) are known from the late Palaeocene and advanced forms (*C.* (*R.*) *rotundidorsata 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 cribrate aperture (the development of a cribrate 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 ecophenotypic 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, 5, 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* (*Labrospira scitula* of Charnock & Jones, 1990) during the

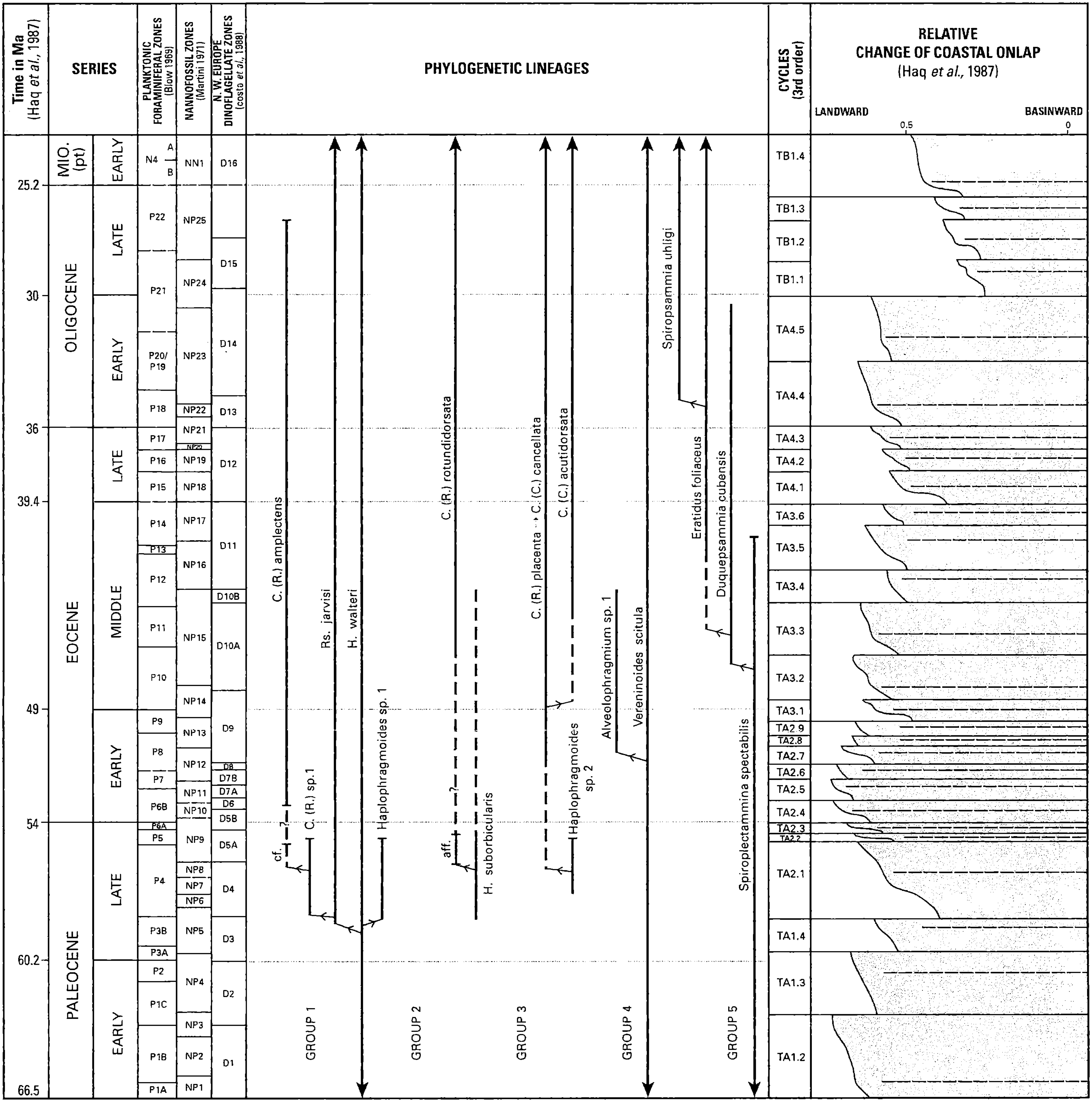


Fig. 3. Stratigraphic ranges and inferred phylogenetic relationships of North Sea Lituolids with complex inner structures

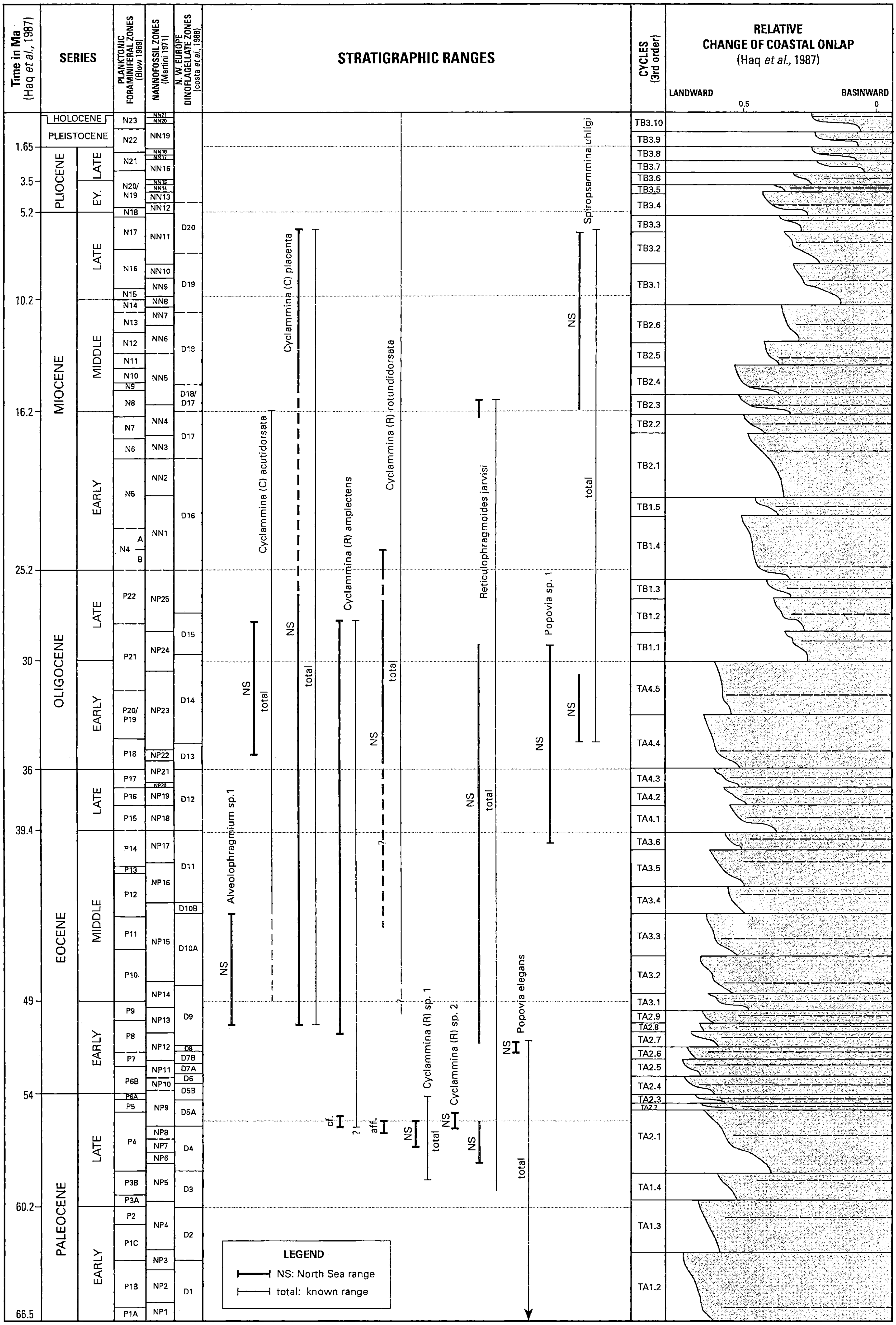


Fig. 4. Global stratigraphic ranges of North Sea Lituolids with complex inner structures. Compiled from various sources

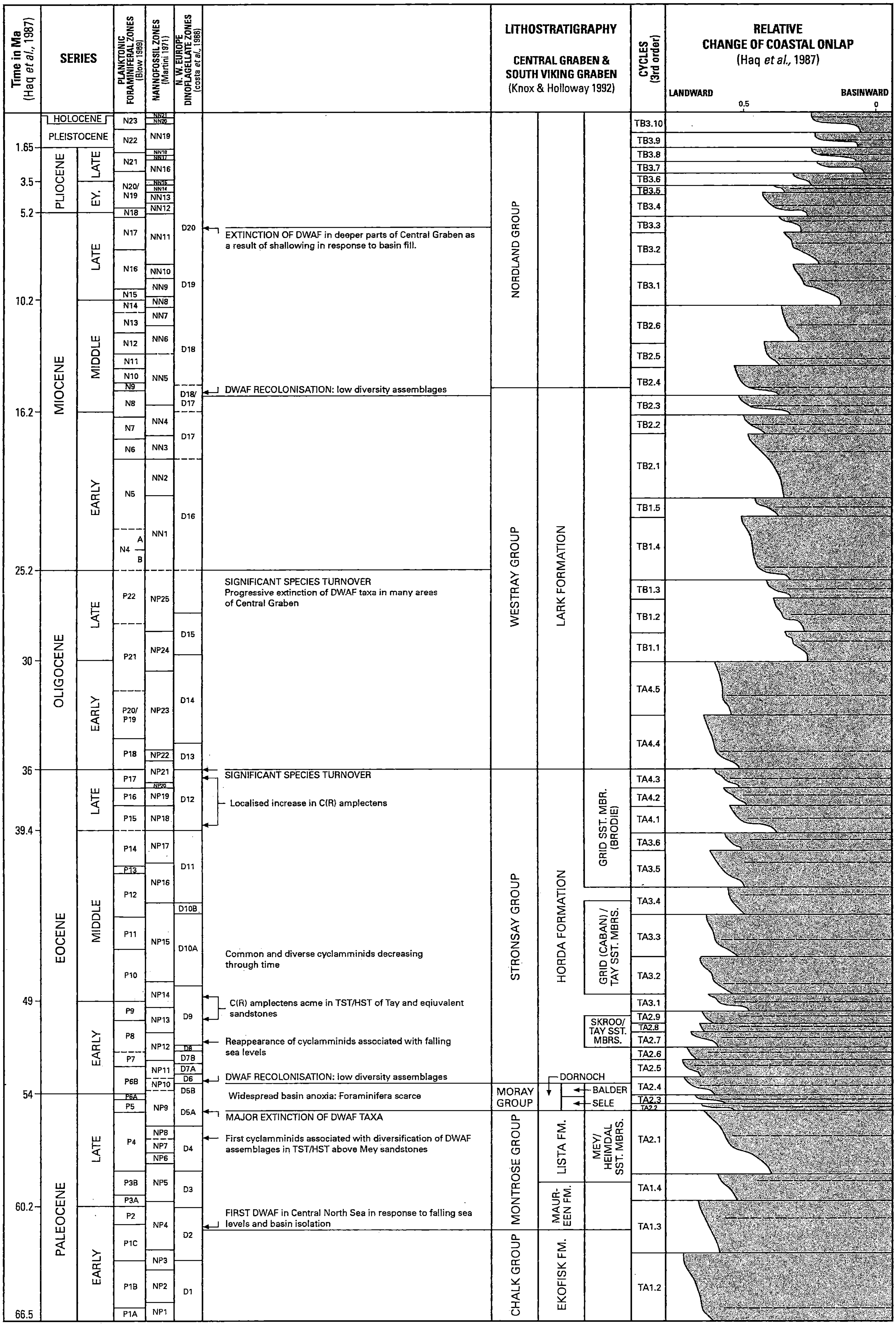


Fig. 5. Summary of biostratigraphic events in the Palaeocene-Eocene of the North Sea

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) Eratidus foliaceus – Spiropsammia uhligi

Spiropsammia uhligi is interpreted as having evolved from *Eratidus foliaceus* during the Early Oligocene through the development of hemisepta. *Eratidus foliaceus* is interpreted as having evolved in turn either directly or indirectly (via an intermediary such as *Duquepsammia 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 Spiropsamiinae of the Family Lituolidae, may be ancestral to the essentially Miocene species *Cyclammina* (*Reticulophragmium*) *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 inner structures (i.e., the Subfamilies Cyclammininae and Spiropsamiinae of the Family Lituolidae). Four (Subfamily Cyclammininae) appear to have originated from *Haplophragmoides* or *Veleroninoides* (Subfamily Haplophragmoidinae), one (Subfamily Spiropsamiinae) from *Eratidus* (Subfamily Ammomarginulininae), and perhaps ultimately from *Spiroplectammina* (Subfamily Spiroplectammininae, 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.* (?*C.*) *praecancellata* Voloshinova);
- *Popovia* sp. 1 Charnock & Jones and *Cyclammina* (*Reticulophragmium*) *venezuelanum* (Maync).

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 dysaerobic conditions. They appear neither analogous nor homologous to the canaliculi 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* (*Reticulophragmium*) Maync, 1955 in the interio-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

not 1981. *Alveolophragmium* sp. 1: Gradstein & Berggren, 1981)

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 *Globigerina* (*Subbotina*) *linaperta* group, predates the LAO of *Cenosphaera* spp. and the LCO of *Eatonicysta ursulae* and *Hystrichosphaeridium tubiferum* (e.g., UKCS 9/19-4, 5260'), and is approximately coincident with the LO of *Spiroplectammina navarroana* (e.g., UKCS 16/26-1, 7020'). This enables an indirect calibration against early Eocene Zone P8.

Its extinction postdates the LO of *Diphyes ficusoides* and predates the LO of *Heteraulacysta 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* (*Reticulophragmium*) *amplectens* (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* (*Reticulophragmium*) *amplectens*.

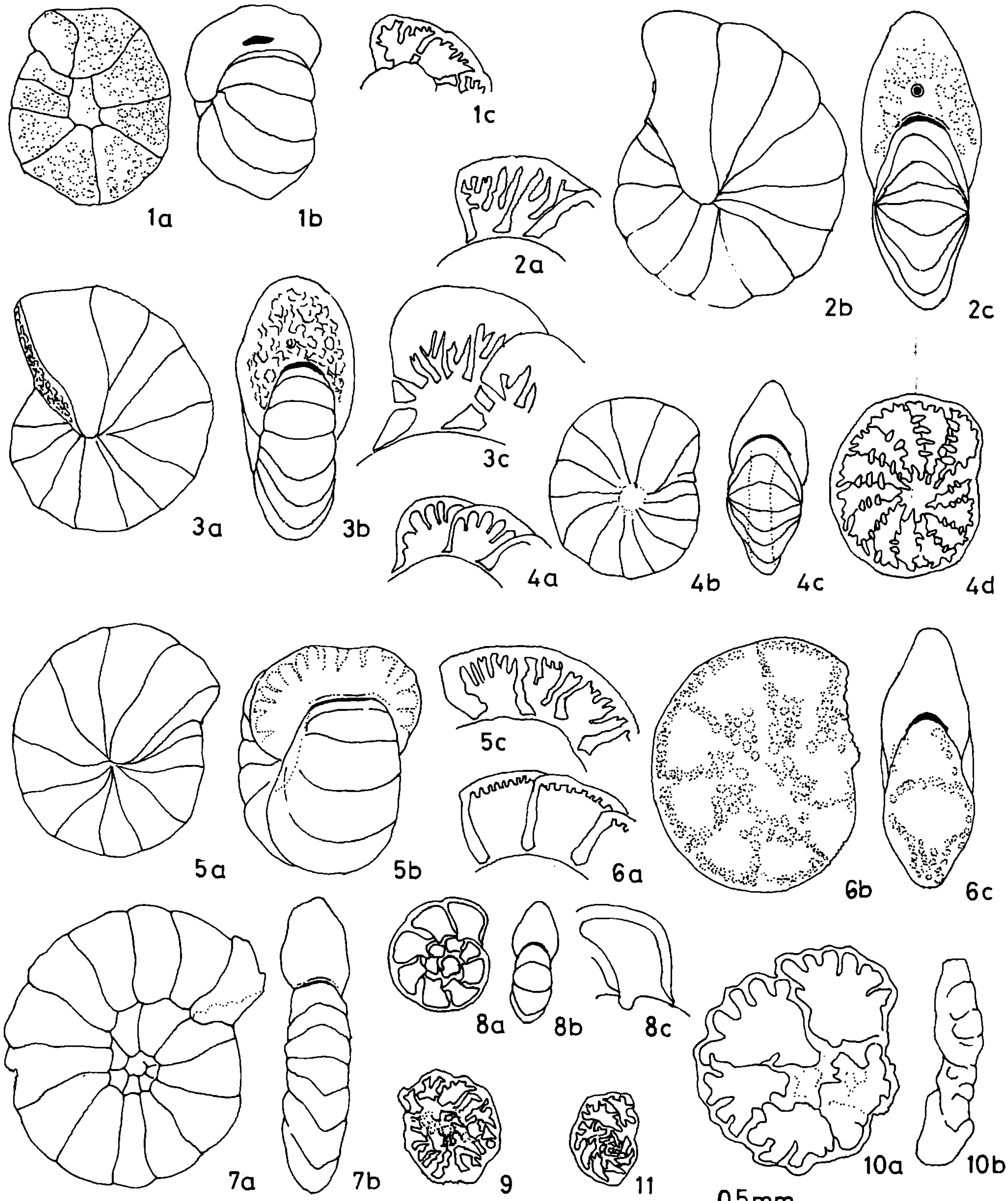


Fig. 6. Camera lucida line drawings; x50 unless otherwise stated: *1 – Alveolophragmium* sp. 1: a-b. UKCS 15/30-1, 6000'; c. UKCS 16/21a-B3, 6400'. *2 – Cyclammina* (*Cyclammina*) *acutidorsata* (von Hantken), NOCS 1/6-4, 8900'. *3 – Cyclammina* (*Cyclammina*) *placenta* (Reuss): a-b. UKCS 23/11-1, 6750'; c. NOCS 15/12-1, 7160'. *4 – Cyclammina* (*Reticulophragmium*) *amplectens* (Grzybowski): a. UKCS 29/5b-2, 9580'; b-d. UKCS 21/14-1, 1910m. *5 – Cyclammina* (*Reticulophragmium*) *rotundidorsata* (von Hantken): a-b. UKCS 23/21-1ST, 7680'; c. UKCS 21/30-1, 6030'. *6 – Cyclammina* (*Reticulophragmium*) sp. 1: a. UKCS 29/8b-1; b-c. NOCS 16/1-1, 7760'. *7 – Cyclammina* (*Reticulophragmium*) sp. 2, UKCS 21/1-1, 5020'. *8 – Reticulophragmoides jarvisi* (Thalmann), UKCS 22/11-1, 7040: c. diagrammatic enlargement. *9 – Popovia elegans* (Kaminski), UKCS 9/23-1, 5110'. *10 – Popovia* sp. 1, NOCS 7/11-7, 7030'. *11 – Spiropsammia uhligi* (Schubert), UKCS 30/24-38, 6560'

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

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

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

Remarks: This subgenus differs from *Cyclammina* (*Reticulophragmium*) 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.

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

1990. *Cyclammina (Cyclammina) 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 autotypes of this species (slide labelled: OFEN, Budapest Kleinzeller, 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 (*Reticulophragmium*); Charnock & Jones, 1990).

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

Its extinction in the Central North Sea postdates the LO of *Globorotalia munda* and predates the FOs of *Globigerina angulisuturalis* and *Globorotalia opima nana* (e.g., UKCS 29/2a-7, 4230'). This enables a calibration against late Oligocene Zone P21. Where planktonic foraminiferal control is lacking, the extinction datum postdates the LOs of *Chiropteridium mespilanum* and Diatom sp. 4 King, 1983, predates the LO of Diatom sp. 3 King, 1983, and is approximately coincident with the LOs of *Spirosigmoilinella compressa* and *Turrilina alsatica* (e.g., UKCS 29/2a-6, 3860').

Total Known Stratigraphic Range: Middle Eocene-early Miocene.

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

1990. *Cyclammina* (*Cyclammina*) *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 *Alveolophragmium* 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 (*Reticulophragmium*); Charnock & Jones, 1990).

The inception of this species postdates the FOs of *C.* (*Reticulophragmium*) *amplectens* and the *Globigerina* (*Subbotina*) *linaperta* group and the LOs of *Dracodinium solidum* and *Spiroplectammina navarroana*, and predates the LCOs of *Eatonicysta ursulae* and *Hystrichosphaeridium tubiferum* and the LAO 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.* (*Reticulophragmium*) sp. 2 Charnock & Jones, 1990, have been identified in significantly (4Ma) older prodeltaic muds in the lower part of the Dornoch Formation in the Outer Moray Firth (e.g., UKCS15/12-1, 4450-4810'). These occur immediately above the LO of *Areoligera gippingensis*, enabling an indirect calibration against late Palaeocene Zone P4. The earliest appearance of advanced forms with cribrate apertures postdates the LO of *Diphyes ficusoides* and the LCO of *Cyclammina* (*Reticulophragmium*) *amplectens* and predates the LOs of *Diphyes colligerum*, *Heteraulacysta porosa* and *Rottnestia borussica* and falls within an interval characterised by common *Systematophora placacantha* (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 *Ammodiscus* spp. and *Usbekistania charoides*, and predates the LO of tubular astrorhizids; 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 *Neogloboquadrina continuosa*, and predates the FO of *Globorotalia puncticulata* and the LAO of *Neogloboquadrina atlantica*. This enables a calibration against late Miocene Zone N17.

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

Total Known Stratigraphic Range: Eocene–Miocene.

Subgenus *Cyclammina* (*Reticulophragmium*) Maync, 1955
Type-species *Alveolophragmium venezuelanum* Maync, 1952; O. D.

Remarks: This subgenus differs from *Cyclammina (Cyclammina)* Brady, 1879 in lacking the development of multiple areal apertures, and from *Alveolophragmium* Shchedrina, 1936 in the interiomarginal rather than interio-areal location of the aperture.

Cyclammina* (*Reticulophragmium*) *amplectens
Grzybowski, 1898
Fig. 6 (4a-d), Fig. 7 (9-11)

1990. Cyclammina (*Reticulophragmium*) *amplectens* Charnock & Jones: p. 176, pl. 8, figs. 1-5, pl. 18, fig. 3.

1993. *Reticulophragmium amplectens* (Grzybowski): Kaminski & 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 Kaminski & 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;

King, 1983, 1989 (*Reticulophragmium*); Moe, 1983; Gradstein *et al.*, 1988, 1992, 1994 (*Reticulophragmium*); Vinken, 1988; Charnock & Jones, 1990).

Ancestral forms of this species, herein referred to as "*Cyclammina* (*Reticulophragmium*) cf. *amplectens*", 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 gippingensis*, enabling an indirect calibration against late Palaeocene Zone P4.

The inception of *C.* (*R.*) *amplectens s.s.* is approximately coincident with the LOs of *Acarinina 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.*) *amplectens 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 *Rotaliatina bulimoides* and the LAO of *Globigerina officinalis*, and predates the LOs of *Globigerina angulisuturalis, Globorotalia opima nana, Spirosigmoilinella compressa* and *Turrilina alsatica* (e.g., UKCS 29/2a-7, 4470'). This enables a calibration against late Oligocene Zone P21.

C. (*R.*) *amplectens 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.*) *amplectens 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-mediated low-stands 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 (Olszewska & Smagowicz, 1977; Kaminski & Geroch, 1993). Older records from the southern hemisphere (Late Cretaceous (?)–Palaeogene, Borneo (Keij, 1965); Palaeocene–Eocene, New Zealand (Hornibrook *et al.*, 1989, and references therein); latest Palaeocene–middle Eocene, Tasman Sea (Webb, 1975)) require verification.

Cyclammina* (*Reticulophragmium*) *rotundidorsata

(Hantken, 1876)

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

1990. *Cyclammina* (*Reticulophragmium*) *rotundidorsata* (Hantken): Charnock & Jones, pp. 176-177, pl. 7, figs. 13-15; pl. 19, fig. 1.

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 orbiculare*); 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 29/2c-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 dictyoplokus* (and the log break defining the top of the Horda Formation), and below the LO of *Wetzeliella gochtii* and the FO of *Rotaliatina bulimoides*, 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 *Rotaliatina bulimoides*, and below the LOs of *Chiropteridium mespilanum* and Diatom sp. 3 King, 1983 and the LCO of *Spirosigmoilinella 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 woodi* and *Haplophragmoides* spp. This is calibrated against latest Oligocene–earliest Miocene Zone N4.

Total Known Stratigraphic Range: Eocene–Recent.

***Cyclammina* (*Reticulophragmium*) sp. 1**

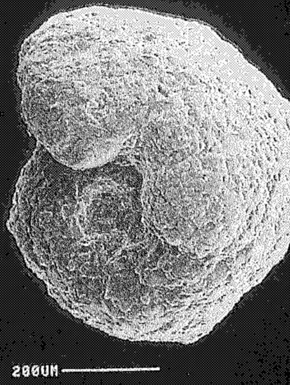
Charnock & Jones, 1990

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 garcilasoi* Friz-

Fig. 7. SEM photographs. *1-2 – Alveolophragmium* sp. 1: *1.* lateral view, UKCS 22/27a-3ZST, 6580'; *2.* apertural view, UKCS 21/24-1, 5660'. *3-5 – Cyclammina* (*Cyclammina*) *acutidorsata* (von Hantken): *3.* lateral view, UKCS 21/24-1, 4830'; *4.* apertural view, NOCS 1/3-2, 9600'; *5.* detail of above, showing arrangement of supplementary areal openings, NOCS 1/3-2, 9600'. *6-8 – Cyclammina* (*Cyclammina*) *placenta* (Reuss): *6.* lateral view, UKCS 15/23-2, 4210'; *7.* apertural view, UKCS 15/23-2, 4120'; *8.* apertural view of laterally inflated specimen, UKCS 15/30-1, 5680'. *9-10 – Cyclammina* (*Reticulophragmium*) *amplectens* (Grzybowski): *9.* lateral view, UKCS 21/14-1, 2035m; *10.* apertural view, UKCS 21/14-1, 2035m. *11. Cyclammina* (*Reticulophragmium*) *cf. amplectens* (Grzybowski), UKCS9/23-1; lateral view of ancestral form from Late Palaeocene *Apectodinium augustum* Zone



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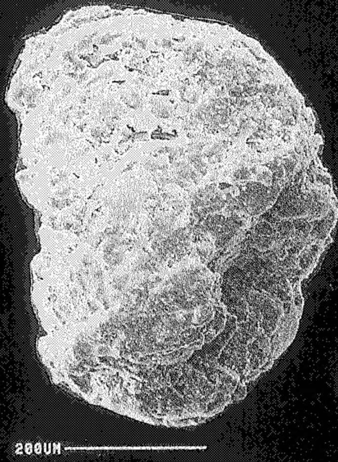

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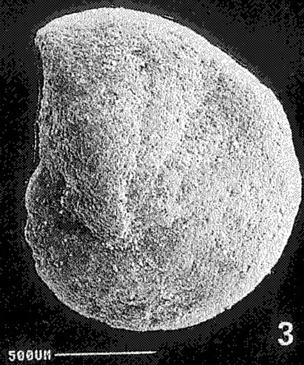

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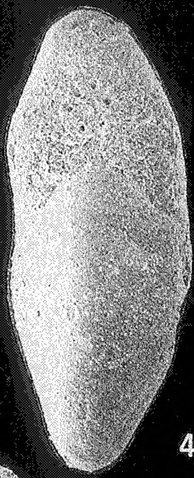

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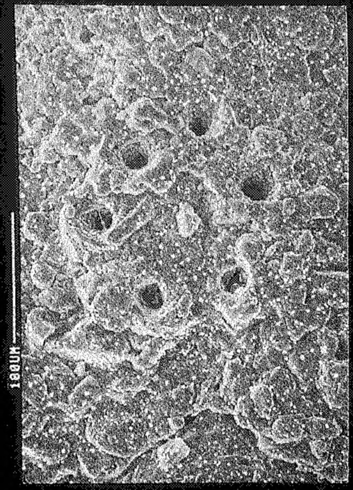

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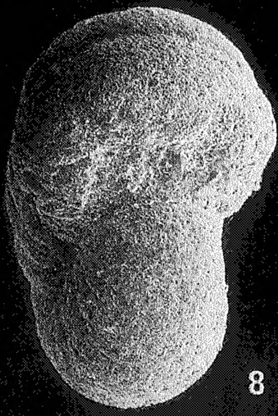

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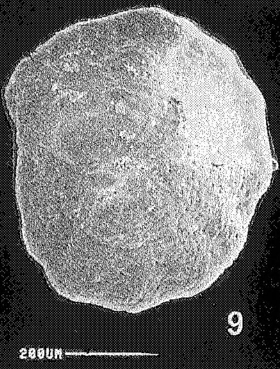

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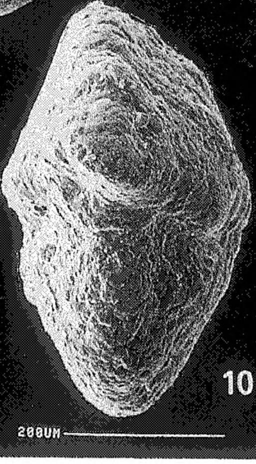

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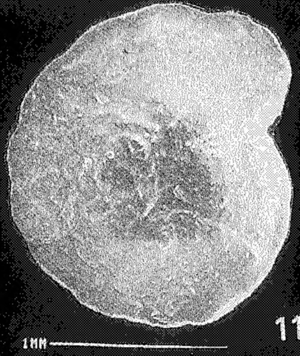

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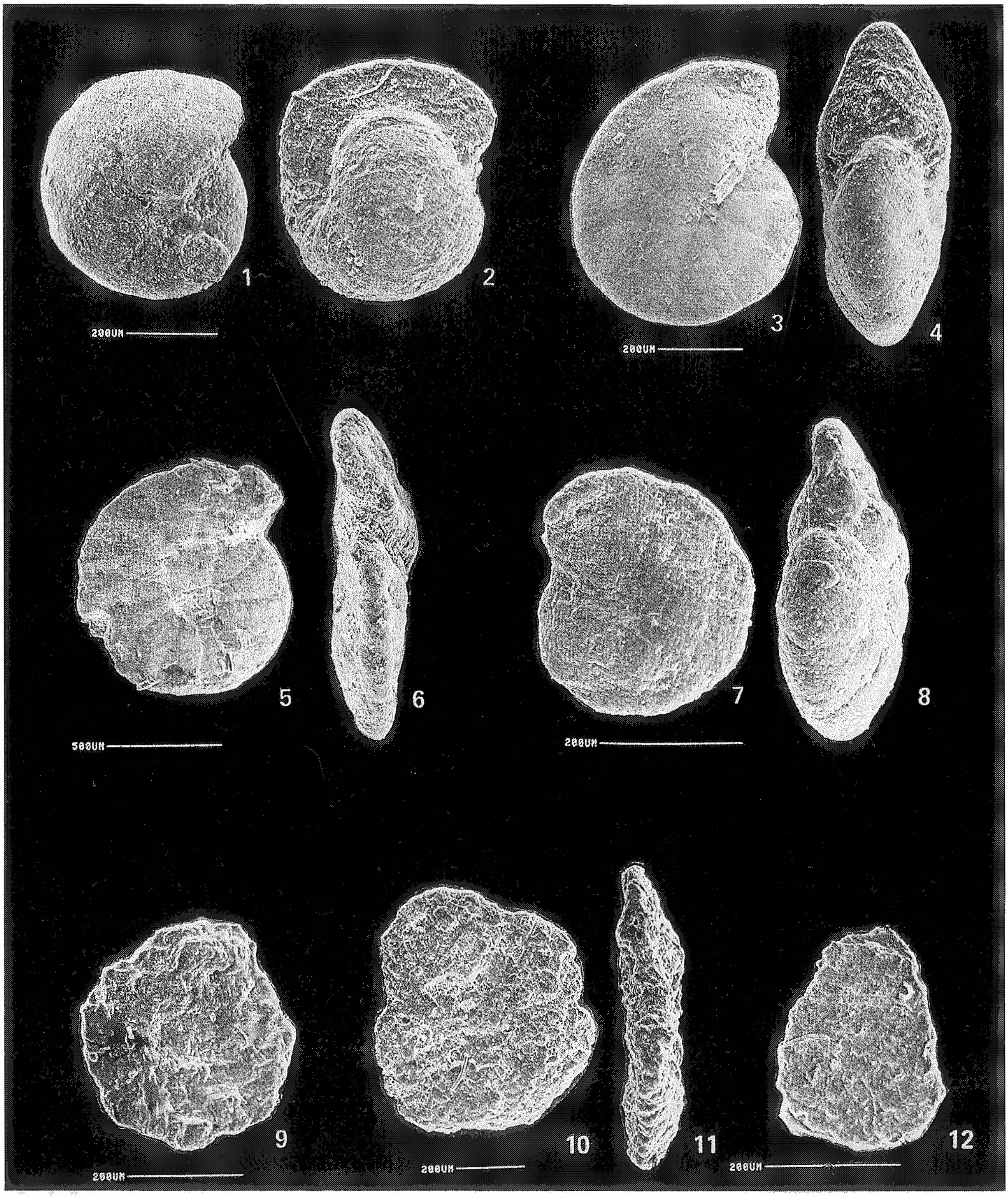

Fig. 8. SEM photographs. *1-2 – Cyclammina* (*Reticulophragmium*) *rotundidorsata (*Hantken): *1.* lateral view, NOCS 1/3-1, 8800'; *2.* apertural view, UKCS 16/28-1. *3-4 – Cyclammina* (*Reticulophragmium*) sp. 1: *3.* lateral view, UKCS 21/7-1, 6120'; *4.* apertural view, UKCS 21/7-1, 6120'. *5-6 – 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)

zell, 1943 and *C. paupera* 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 garcilasoi* (?) and/or *R. paupera*) 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. *garcilasoi*) (?)).

The inception of this species postdates the LCO of *Palaeoperidinium pyrophorum* and predates the LCO of *Areoligera 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*, *Spirosigmoilinella naibensis* and *Trochammina ruthvenmurrayi*) (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 a ?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 Sele 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).

Cyclammina (*Reticulophragmium*) sp. 2
Charnock & Jones, 1990
Fig. 6 (7a-b), Fig. 8 (5-6)

1990. *Cyclammina* (*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 *Areoligera 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 *Spirosigmoilinella naibensis* and predate the LO of *Apectodinium* spp., and fall within an interval characterised by reduced agglutinate abundance and diversity and sporadic occurrences of *Cyclammina* (*Reticulophragmium*) cf. *amplectens* (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 sedimentation characteristic of the upper part of the Lista Formation and the lower part of the Dornoch Formation.

Genus *Reticulophragmoides* Gradstein & Kaminski, 1989
Type-species *Nonion jarvisi* Thalmann, 1932, emend. Gradstein & Kaminski, 1989; O. D.

Remarks: This genus differs from *Haplophragmoides* Cushman, 1910 principally in the incipient alveolar development in late growth stages of advanced individuals.

Reticulophragmoides jarvisi (Thalmann, 1932), emend. Gradstein & Kaminski, 1989
Figs. 6–8

1990. *Reticulophragmoides jarvisi* (Thalmann): Charnock & Jones, p. 177, pl. 8, figs. 12-13; pl. 19, fig. 4.

North Sea Distribution: Late Palaeocene–early/middle Miocene, Zones P4-N8 (see below; see also Gradstein & Kaminski, 1989; Charnock & Jones, 1990; Gradstein *et al.*, 1994).

R. jarvisi is the earliest "cyclamminoid" in the Central North Sea. In terms of foraminiferal bio-events, its inception postdates the LO of *Cenodiscus lenticularis* and predates the development of diverse agglutinated foraminiferal assemblages characterised by abundant *Spiroplectammina spectabilis;* in terms of palyno-events, it falls between the LO of *Areoligera gippingensis* and the LCO of *Palaeoperidinium pyrophorum* (e.g., UKCS 9/19-10Z, 8550' (Heimdal Formation)). This enables an intra-late Palaeocene age assignment.

Its extinction is environmentally controlled and diachronous (dependent on location with respect to basin margin and bathymetry). At the basin margin (e.g., UKCS 16/26-1, 5980'), it falls within the Eocene, while in intermediate locations (e.g., UKCS 29/2a-7, 4980') it falls within the upper Oligocene (above the LO of *Rotaliatina bulimoides*), and at the basin centre (e.g., NOCS 1/6-7, 1795m (SWC)) it falls within the lower or middle Miocene (depending on where the boundary is drawn) (immediately above the LOs of *Asterigerina guerichi staeschei* and *Globorotalia zealandica*, and approximately coincident with the LO of *Sphaeroidinellopsis disjuncta* (enabling a calibration against Zone N8)).

In the Central Graben area, *R. jarvisi* peaks in abundance (with *Cyclammina* (*Reticulophragmium*) *amplectens*) at the top of the Eocene (the top of the Horda Formation)(e.g., NOCS 6/3-1, 2190m).

Total Known Stratigraphic Range: Late Palaeocene–middle Miocene (Zones P3B-N8). The earliest record is from the lower Upper Palaeocene (Zone P3B of the Zumaya Flysch, Northern Spain (Gradstein & Kaminski, 1989).

Subfamily SPIROPSAMIINAE Seiglie & Baker, 1983

Remarks: Included here are planispiral to uniserial Lituolidae with internally partitioned chambers.

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*) *linaperta* 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 tricarinata* 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 LOs of several species of agglutinated foraminifera (including *Ammomarginulina aubertae* and *Spiroplectammina* aff. *spectabilis*); in terms of palyno-events, it falls between the LOs of *Areosphaeridium dictyoplokus* and *Heteraulacysta 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 LO of *Rotaliatina bulimoides*. 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 *Spiropsammia* Seiglie & Baker, 1983
Type-species *Cyclammina uhligi* Schubert, 1902; O. D.

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

1990. *Spiropsammia uhligi* (Schubert): Charnock & Jones, p. 179, pl. 20, fig. 4.

North Sea Distribution: Oligocene–Miocene, Zones P18/19-N17 (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 LOs of Diatom sp. 3 King, 1983 and *Globigerina* (*Subbotina*) *eocaena* (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 puncticulata* and the LO of *Neogloboquadrina continuosa*, and immediately above the LCO of *N. acostaensis* (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 *Bolboforma metzmacheri* and between the LOs of *Uvigerina semiornata* and *U. venusta saxonica*. Interestingly, the extinction of *S. uhligi* 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.

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Streszczenie

OTWORNICE AGLUTYNUJĄCE Z RODZINY LITUOLIDAE Z OSADÓW TRZECIORZĘDOWYCH MORZA PÓŁNOCNEGO; STRUKTURA WEWNĘTRZNA SKORUPKI, TAKSONOMIA, STRATYGRAFIA I EWOLUCJA

Michael A. Charnock & Robert W. Jones

Głębokowodne otwornice aglutynujące są charakterystycznym elementem w zespołach mikrofauny w osadach od paleocenu do górnego miocenu w Morzu Północnym oraz w środkowej i południowej części rowu tektonicznego Wikingów (Fig. 1 & 2).

Basen Morza Północnego był w czasie od paleocenu do środkowego miocenu miejscem gwałtownej sedymentacji związanej z częstymi zmianami (obniżaniem) poziomu morza, stymulowanymi przez czynniki eustatyczne i tektoniczne. Towarzyszyło temu szereg innych efektów hydrologicznych jak stratyfikacja wody, jej ograniczona cyrkulacja, obniżona zawartość tlenu, podwyższony udział CO_2 w wodach dennych i porowych. Takie warunki sprzyjały rozwojowi populacji otwornic aglutynujących kosztem otwornic wapiennych.

Zespoły mikrofauny charakteryzowała w tym czasie obecność głębokowodnych otwornic aglutynujących z rodziny Lituolidae (podrodziny: Cyclammininae i Spiropsamiinae), których ewolucja związana była z procesami tektononiczno-eustatycznymi (Seiglie, 1987). Pierwsze pojawienie się otwornic aglutynujących w centralnej części Morza Północnego odnotowano na najmłodszą część wczesnego paleocenu, natomiast pierwsze lituolidy znane są z osadów górnego paleocenu (Fig. 2). Ich rozwój (n.p. *Cyclammina* (*Reticulophragmium*) sp. 1) w późnym paleocenie można skorelować z cyklem transgresywnym (TSTs i HSTS) trzeciego rzędu (TA2.1) według Haq *et al.* (1987), którego efektem była sedymantacja drobnoziarnistych osadów formacji Lista (fm). Kolejny epizod pojawienia się zespołu głębokowodnych otwornic aglutynujących udokumentowano na wczesny eocen (około 52,5 Ma). Masowa radiacja i wzrost lituolidów (n.p. ewolucja *Alveolophragmium* sp. 1 oraz *acme Cyclammina* (*Reticulophragmium*) *amplectens*) 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). Epizod wzrostu tej grupy otwornic, nieco mniejszej rangi (dotyczy gatunku *C.* (*R.*) *amplectens*) miał miejsce w czasie późnego eocenu, co odpowiadałoby cyklom TA4.1-4.3.

Maximum radiacji zespołu głębokowodnych otwornic aglutynujących w Morzu Północnym nastąpiło w paleocenie. Natomiast ograniczenie ewolucji zespołów związane z obniżaniem 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 taksonomiczne lituolidów z obszaru Morza Północnego, przeprowadzając dyskusję na temat ewolucji tej grupy otwornic (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 Cyclammininae i Spiropsamiinae. Cztery linie ewolucyjne (dotyczą podrodziny Cyclammininae) rozpoczyna rodzaj *Haplophragmoides* lub *Veleroninoides* (podrodzina Haplophragmoidinae), a przodkiem jednej (dotyczy podrodziny Spiropsamiinae) jest prawdopodobnie rodzaj *Eratidus* (podrodzina Ammomarginulininae) lub *Spiroplectammina* (podrodzina Spiroplectammininae). Są to następujące linie ewolucyjne:

(1) *Haplophragmoides walteri–Reticulophragmoides jarvisi/ Cyclammina* (*Reticulophragmium*) *amplectens*

(2) *Haplophragmoides suborbicularis–Cyclammina (Reticulophragmium) rotundidorsata*

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

(4) *Veleroninoides scitulus–Alveolophragmium* sp. 1 Charnock & Jones, 1990

(5) *Eratidus foliaceus–Spiropsammia uhligi.*

Uwzględniając powyższe wyniki autorzy rekomendują pary gatunków do dalszych badań taksonomicznych określających wzajemne relacje filogenetyczne, zarówno w zespołach z Morza Północnego jak i z miocenu centralnej części Paratetydy, które były już wcześniej przedmiotem podobnych studiów (Cicha & Zapletova, 1966; Cicha *et al.*, 1983). Dotyczy to:

– *Alveolophragmium* sp. 1 Charnock et Jones i *A. orbiculatum* (Shchedrina);

– *Cyclammina* (*Cyclammina*) *placenta* (Reuss) i *C.*(*C.*) *cancellata* Brady (również *C.* (*?C.*) *praecancellata* Voloshinova);

– *Popovia* sp. 1 Charnock et Jones i *Cyclammina* (*Reticulophragmium*) *venezuelanum* (Maync).

Autorzy proponują zwrócić uwagę na zmiany alweolarnej struktury ścian skorupki oraz na zmiany w kształcie i obecności sitkowatych otworów skorupki, określając czy zmiany te powstały na drodze ewolucyjnej czy związane są ściśle ze zmianami środowiska. Pomóc temu mogą badania zespołów lituolidów obserwowanych w osadach tego samego wieku ale pochodzących z różnych części basenu. Powinny one być badane w kolejnych sekwencjach osadów odpowiadającym jak najmniejszym jednostkom chronostratygraficznym.