Middle to Late Eocene paleoenvironmental changes in a marine transgressive sequence from the northern Tethyan margin (Adelholzen, Germany)

Holger GEBHARDT[1)*)], Stjepan ĆORIĆ[1)], Robert DARGA[2)], Antonino BRIGUGLIO[3)], Bettina SCHENK[1)],
Winfried WERNER[4)], Nils ANDERSEN[5)] & Benjamin SAMES[1)3)]

[1)] Geologische Bundesanstalt, Neulinggasse 38, A-1030 Wien, Austria;

[2)] Naturkundemuseum Siegsdorf, Auenstr. 2, D-83313 Siegsdorf, Germany;

[3)] Universität Wien, Institut für Paläontologie, Althanstraße 14, A-1090 Wien, Austria;

[4)] Bayerische Staatssammlung für Paläontologie und Geologie und GeoBioCenterLMU, Richard-Wagner-Str. 10,
D-80333 München, Germany;

[5)] Leibniz Laboratory for Radiometric Dating and Stable Isotope Research, Christian-Albrechts-Universität Kiel,
Max-Eyth-Str. 11, D-24118 Kiel, Germany;

[*)] Corresponding author, holger.gebhardt@geologie.ac.at

Abstract

The northern Tethyan margin is a key region for determining environmental changes associated with the collision of continental and oceanic tectonic plates and Alpine orogeny. Herein we investigated Middle to Late Eocene neritic to bathyal sediments deposited during an interval of unstable climatic conditions. In order to quantify paleoenvironmental changes, we developed a detailed age model based on biozonations of planktic foraminifera, calcareous nannoplankton, and larger benthic foraminifera. The section at Adelholzen covers the almost complete Lutetian Stage (calcareous nannoplankton zones NP15a-16, planktic foraminifera zones E8-11, shallow benthic (foraminifera) zones SBZ13-15) and large parts of the Priabonian Stage (NP18-20, E14/15), while the intermediate Bartonian Stage (NP17) is completely missing. Foraminiferal, calcareous nannoplankton, and macrofossil assemblages were analyzed for changes in paleo-water depth, mixing and stratification, paleo-primary productivity (pPP), food supply, and bottom water oxygenation. Paleo-water depth estimates range from 50 m (middle neritic, early Lutetian) to nearly 500 m (upper bathyal, late Priabonian). The combination of assemblage composition, planktic and benthic foraminiferal accumulation rates, and derived parameters (carbon-flux to sea floor, pPP) enabled us to identify a series of distinct paleoceanographic events of at least regional significance. Such events are characterized by considerable changes in primary productivity or reduced bottom water ventilation. Calculated pPP-values indicate oligotrophic conditions throughout.

Der nördliche Tethysrand ist von besonderer Bedeutung für die Ermittlung von Umweltveränderungen verbunden mit der Kollision kontinentaler und ozeanischer Platten, sowie der alpinen Orogenese. In diesem Beitrag untersuchen wir neritische bis bathyale Ablagerungen des mittleren bis späten Eozäns, einer Periode instabiler Klimabedingungen. Um die Umweltveränderungen quantifizieren zu können, wurde auf der Basis von Biozonen planktischer Foraminiferen, kalkigem Nannoplankton, und Großforaminiferen ein genaues Altersmodell entwickelt. Das Profil von Adelholzen umfasst fast das gesamte Lutetium (kalkige Nannoplankton Zonen NP15a-16, planktische Foraminiferen Zonen E8-11, "shallow benthic (foraminifera) zones" SBZ13-15) und weite Teile des Priaboniums (NP18-20, E14/15). Das dazwischenliegende Bartonium (NP 17) fehlt vollständig. Foraminiferen, kalkiges Nannoplankton und Makrofossilassoziationen wurden auf Veränderungen der Paläowassertiefe, Durchmischung und Schichtung, Paläoprimärproduktivität (pPP), Nahrungszufluß und Bodenwasserbelüftung hin analysiert. Die Paläowassertiefen reichen von 50 m (mittleres Neritikum, frühes Lutetium) bis nahezu 500 m (oberes Bathyal, spätes Priabonium). Die Verbindung aller Fossilassoziationen mit planktischen und benthischen Foraminiferenakkumulationsraten sowie abgeleiteten Parametern (Kohlenstoff-Fluß zum Meeresboden, pPP) erlaubte die Identifizierung mehrerer unterschiedlicher paläoozeanographischer Ereignisse von mindestens regionaler Bedeutung. Diese Ereignisse zeichnen sich durch deutliche Änderungen der Primärproduktivität und Sauerstoffversorgung im Bodenwasser aus. Die errechneten pPP-Werte deuten auf durchgehend oligotrophe Bedingungen hin.

1. Introduction

The Middle to Late Eocene period is characterized by a long term cooling and therefore of special interest for the understanding of the development towards the modern ice house climate system. This process is punctuated by a number of short-lived climatic events, e.g., the Middle Eocene Climatic Optimum (MECO, c. 41.5 Ma; Bohaty and Zachos, 2003; Bowen et al., 2006; Luciani et al., 2007; Bijl et al., 2009; Edgar et al., 2010; Stap et al., 2010; Spofforth et al., 2010; Sexton et al., 2011). The foci of most of these studies are the paleoceanographic developments of major ocean basins and their importance for global climatic change during or across these crucial time periods. The progressive climatic deterioration and instability after the Early Eocene Climatic Optimum (c. 52-49 Ma) until a permanent ice sheet developed on Antarctica close to the Eocene/Oligocene boundary (e.g., Zachos et al., 2001; Coxall et al., 2005) influenced the depositional sys-

tems worldwide. Evidence for Eocene glacial ice in Greenland (Eldrett et al., 2007) clearly shows the climatic effects also for the northern hemisphere.

Paleoenvironmental data from Middle to Late Eocene marginal basins and in tectonically deforming regions are few. Moreover, modern approaches for the interpretation of Eocene fossil assemblages have almost only been applied to records from ocean drilling programs but barely to records from 'classical' outcrops and shallow water settings, particularly of Central Europe. We therefore took the unique opportunity to study the response of Middle to Late Eocene faunal and floral assemblages to environmental changes from an exceptional fossil-rich and comparatively complete record from the Penninic Basin situated at the northern margin of the Tethys Ocean system. In order to bridge the gap between shallow and deep-sea sites, we analyzed the transgressive sequence of Adelholzen in southeastern Bavaria. We analyzed planktic (foraminifera, calcareous nannofossils) and benthic (foraminifera, macrofossils) assemblages from a key section with progressively increasing paleo-water depths. The succession provides valuable information on related environmental parameters, in particular on surface water nutrient availability, food supply to the sea floor, water column stratification, oxygenation, and paleo-primary productivity of surface and bottom waters for the investigated periods.

1.1 Geological background

The Adelholzener Schichten (Adelholzen Beds) are part of the Helvetic (tectonic) Unit and record the sedimentary processes that took place on the southern margin of the European platform at that time. Mesozoic to Paleogene Helvetic units crop out continuously at the northern margin of the Alpine Chain between Switzerland and the area around Salzburg and in tectonic windows also east of Salzburg (e.g., Hagn et al., 1981; Prey, 1983; Rasser and Piller, 1999, 2001; see Fig. 1). Results of field mapping in the region suggests highly differentiated depositional systems with various lithologies due to the existence of structural highs and lows that were caused by antithetic fracturing and an echeloned subsiding European continental margin (pers. comm. Ulrich Blaha).

The nummulitic marls and sands around Siegsdorf in SE Bavaria (Fig. 1) are famous for their high contents of very large sized *Nummulites* and *Assilina*, as in the Adelholzen Section (Heyng, 2012). These highly fossiliferous units are probably lateral equivalents of the Weitwies Member, which is part of the Kressenberg Formation (Rasser and Piller, 1999). However, we retain the less formal name Adelholzener Schichten because of distinct differences in lithofacies to the type localities of the Kressenberg Formation and the Weitwies Member (see Rasser and Piller, 1999 for detailed lithological descriptions). For Lutetian rocks of southeastern Bavaria and Austria, Hagn et al. (1981) distinguish between a "shallower" marine Northern Helvetic Unit (Adelholzener Schichten) and a "deeper" marine Southern Helvetic Unit (Kressenberg Formation). The latter unit is characterized by more continuous sedimen-

tation since the Late Cretaceous, and typical iron ore deposits. Both units are divided by a postulated swell of igneous rocks. Coeval deposits in Switzerland with similar lithology are called Bürgen Formation (Herb, 1988). Facies differences disappeared and a uniform sedimentation ("Globigerina-Marls", Stockletten) prevailed in Austria and Bavaria during the Priabonian. Moreover, the studied record at Adelholzen probably represents one of the northernmost mass occurrences of symbiont-bearing larger benthic foraminifera, still characterizing tropical climates (compare e.g., Racey, 2001).

1.2 Location and lithology

The section at Adelholzen is situated at the southwestern tip of the "Adelholzener Mineralwasser" bottling plant (Fig. 1, 47° 48'37,31 N, 12°36'41,02 E) and became accessible in 1996 after excavations for a new building. The total thickness of all units exposed is about 18 m from which 142 samples were obtained in regular intervals. Six lithologic units occur within the Adelholzen Section (Fig. 2). These lithologic units are, from base to top, 1) marly, glauconitic sands with predominantly *Assilina* (thickness exposed c. 4 m), 2) marly bioclastic sands with predominantly *Nummulites* (c. 4.5 m), 3) glauconitic sands (c. 0.6 m), 4) marls with *Discocyclina* (c. 4.2 m), and 5) marly brown sand (c. 1.1 m). The brown color of the latter unit results from its high content of sub-mm sized glauconitic grains coated with iron-hydroxides. These units were combined as "Adelholzener Schichten" (Hagn et al., 1981) with unit 1 as "Untere Adelholzener Schichten" (lower Adelholzen Beds), unit 2 as "Mittlere Adelholzener Schichten" (middle Adelholzen Beds), and units
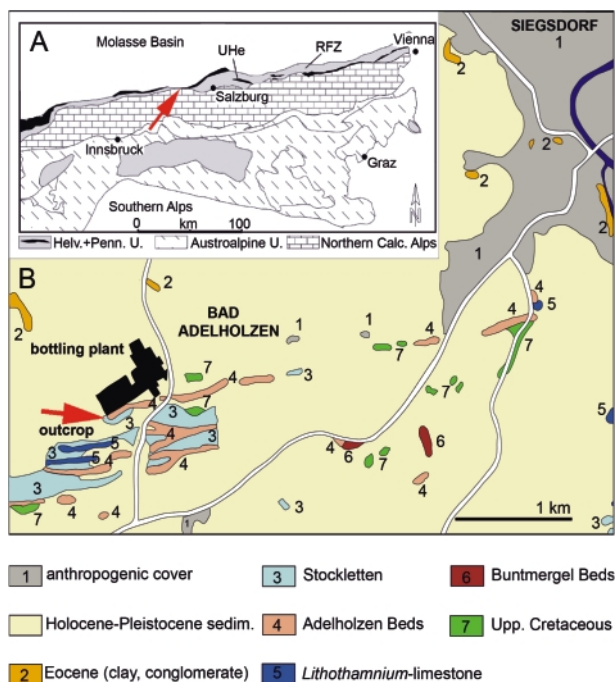

Figure 1: Location of the Adelholzen Section and geological-tectonical background. A. Tectonic map of the Eastern Alps (UHe - Ultrahelvetic units, RFZ - Rhenodanubian Flysch Zone, Helv.+ Penn.U. - Helvetic and Penninic Units). B. Geologic map of the Adelholzen area (according to BIS, Bayerisches Landesamt für Umwelt).

3 to 5 as "Obere Adelholzener Schichten" (upper Adelholzen Beds). For the sixth unit, Stockletten, no formal name has been established so far and the traditional name is still in use. Lateral equivalents in the west are called "*Globigerina*-Marls" (Hagn et al., 1981; Rasser and Piller, 1999). The local name Stockletten refers to the sticky character of this marls (Letten = claystones, marls).

2. Material and methods

To collect and study smaller benthic and planktic foramini

fera, 200 g of dry sediment were disintegrated with hydrogen peroxide and washed over a 0.063-mm sieve. Residues were dried and larger foraminifera bearing samples were dry sieved into 0.063 to 0.125 and 0.125 to 2 mm fractions in order to prevent coverage by large tests during scanning under light microscope. A representative series of 31 samples was selected for quantitative analyses on foraminifera. The samples (or fractions) were split into manageable subsamples (aliquots) and completely picked for foraminifera. The number of specimens picked per subsample varies between 40 and 538, with an average of 206 individuals. However, according to Fatela and Taborda (2002) 100 specimens are sufficient to obtain reliable results if only the dominant taxa (>5%) are interpreted. Our interpretations on foraminifera are based on taxa or groups of taxa with much higher proportions and are therefore considered to be reliable even if the number of specimens picked is lower. Foraminiferal specimens were identified and counted, numbers for individual fractions were recombined according to the split, and the number of specimens per gram dry sediment was calculated (abundance). Accumulation rates (AR, specimens x cm^{-2} x ky^{-1}) were calculated for planktic and benthic foraminiferal assemblages. Additional samples were prepared to collect the larger benthic foraminifera. Up to 500 g of sediment were disintegrated with hydrogen peroxide and washed over a 0.125-mm sieve for this purpose. In order to concentrate the stratigraphically important planktic foraminiferal index species, we dry sieved the total washed residue of 53 standard samples from selected levels over a 0.250 mm sieve.

Due to the inadequate preservation state of microfossils from the studied section (diagenetic overprint), carbon and oxygen stable isotope analyses were obtained from bulk rock samples (see electronic supplements). Consequently, we rely on the interpretation of assemblage counts for paleoceanographic reconstructions and stable isotope analyses are used for complementary stratigraphic purposes only.

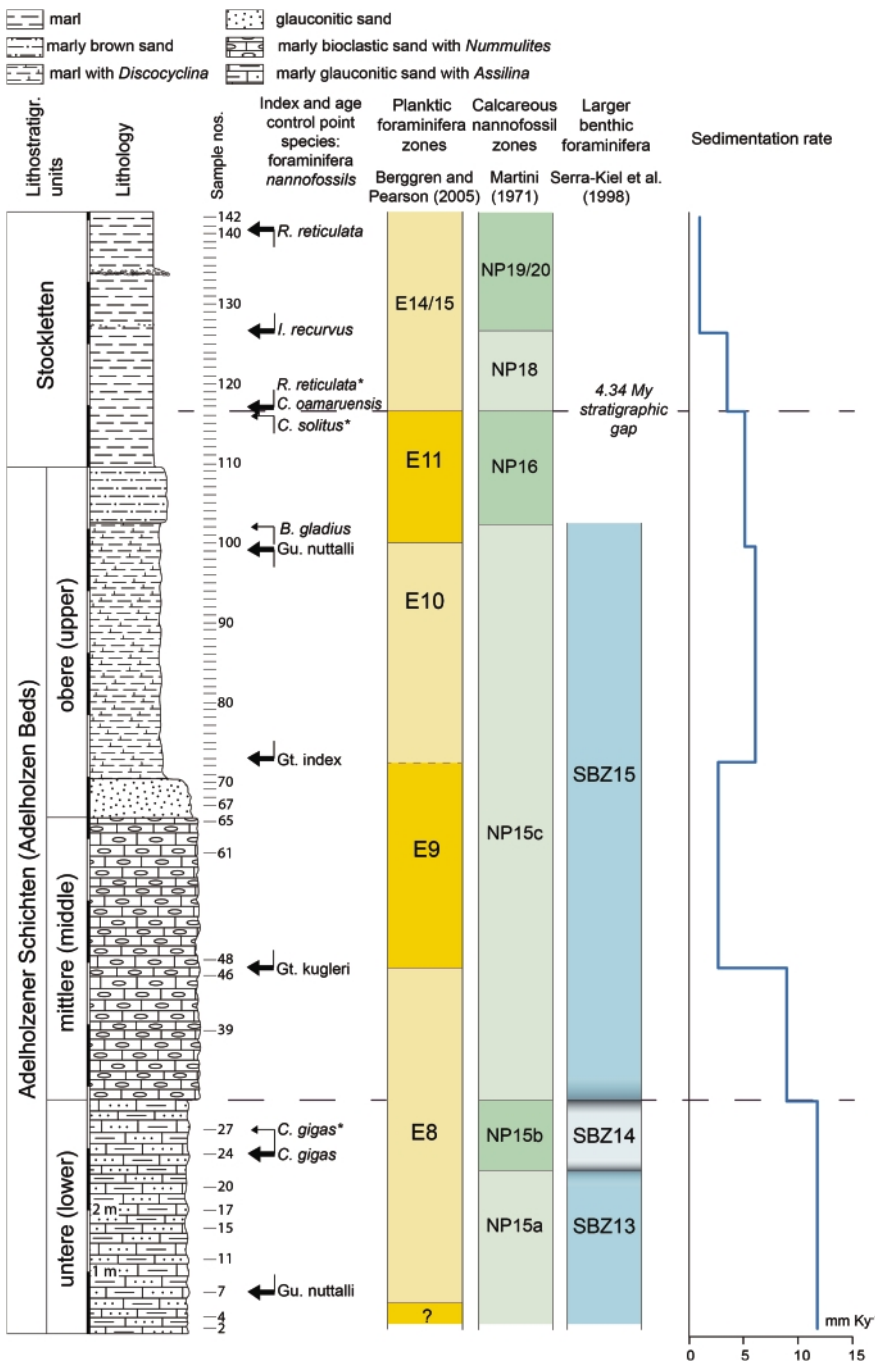Despite the poor preservation in many samples, at least an allocation

Figure 2: Lithology of the Adelholzen Section with biostratigraphic zonations (planktic foraminifera, calcareous nannoplankton, larger benthic foraminifera), calculated sedimentation rates, * indicate first or last findings of index species. Horizontal dashed lines indicate identified stratigraphic gaps. Bold arrows indicate age control points.

of foraminiferal remains to planktic or benthic modes of life was possible in all samples. In a few samples, a high number of foraminifera could not be classified at genus or species level (up to 60% in planktic, 30% in benthic foraminifera) and are consequently ignored for further calculations and interpretations. Nevertheless, planktic to benthic foraminifera ratios remain very similar if undeterminable specimens are included.

We applied the taxonomic and stratigraphic concepts published in Berggren et al. (2006a, b), Coxall and Pearson (2006), Huber et al. (2006), Olsson and Hemleben (2006), Olsson et al. (2006a, b, c), Pearson and Berggren (2006), Pearson et al. (2006a, b), and Premoli Silva et al. (2006) for planktic foraminifera. For benthic foraminifera, the taxonomic concepts of Hagn (1954), Gohrbandt (1962), Hillebrandt (1962b), Schaub (1981), Petters (1982), Tjalsma and Lohmann (1983), van Morkhoven et al. (1986), Hagn and Kuhn (1989), Kuhn (1992), Revets (1996), Speijer et al. (1996), and Cicha et al. (1998) were used. We assume potentially continuous stratigraphic occurrence for all found benthic taxa, except for larger foraminifera (Nummulitids, Orthophragminids), which are biostratigraphically relevant. A complete list of all identified taxa is provided in the electronic supplements (Tabs. S1-S4).

According to the Benthic Foraminiferal Accumulation Rate (BFAR; explained in Gooday, 2003, with further references therein) we calculated accumulation rates for planktic and benthic foraminifera in order to account for different sedimentation rates during the investigated time intervals. In this contribution, the accumulation rates are the number of foraminiferal tests > 0.063 mm per cm^2 per ky (individuals per g of dry sediment x sedimentation rate (cm/ky) x dry bulk density (g/cm^3)). BFAR is used to estimate primary productivity, or delivery of food to the sea floor. Gooday (2003) and Jorissen et al. (2007) explained in detail the limitations and possible problems (e.g., effect of oxygen depletion, taphonomic processes etc.) of the method. We applied the transfer functions of Herguera (2000) to calculate the flux of organic carbon to the sea-floor (*Jsf*) and paleo-primary productivity (pPP): *Jsf* = 6.5 BFAR$^{0.64}$; pPP = 0.4 Z$_{km}$ BFAR$^{0.5}$, with Z = water depth in km.

For absolute paleo-water depth estimates, we applied the transfer function of van der Zwaan et al. (1990; water depth = e$^{(3.58718+(0.03534 \ x\%P))}$), which is based on the percentage of planktic foraminifera (%P or P/B-ratio) of the entire foraminiferal assemblage, although we are aware of the limitations of this method with respect to eutrophication, anoxia, salinity fluctuations, or other processes that can alter the original assemblages. Occurrences of macrofossils were used to confine the paleoecological parameter derived from microfossils. For the upper part of the section (above sample AH-089) we used Jsf for the estimation of the paleo-water depth (i.e., the progressive deterioration of organic matter during sinking) because of strong ecologic disturbances during the deposition of the foraminiferal assemblages ruling out the application of the formula given above ('disturbed' samples;see Chapter 6 for details).

For investigations on calcareous nannoplankton, smear slides were prepared for 44 samples using standard proce-

dures described by Perch-Nielsen (1985). All samples were examined under light microscope with 1000x magnification. Quantitative data were obtained by counting at least 300 specimens from each slide. A further 100 view fields per slide were checked for biostratigraphically and paleoecologically important species. Due to the limited amount of ecological information on Eocene taxa, statistical investigations were performed on percentages of the most important and predominating species (or genera), using the PAST 2.15-software package (Hammer et al., 2001). Clustering of samples was performed by Ward's method based on standardized Euclidean distances with a subsequent determination of species that are indicative for the obtained cluster. We also performed a SIMPER (Similarity Percentage) -analysis in order to evaluate the contributions of the different nannoplankton taxa. Nonmetrical Multidimensional Scaling (nMDS) is based on standardized Euclidean distance too.

Total Organic Carbon (TOC) was measured with a LECO CS 200 Carbon-Sulfur analyser, following standard procedures (analytical error <10% of carbon content, ±0.01 to 0.04%). All sample material is stored in the repository of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (collection number BSPG 2003 XXXI).

All occurrences as well as other raw and derived data are available as supplementary tables (electronic supplements) from the AJES website (Tables S1: planktic foraminifera, S2: benthic foraminifera, S3: stratigraphically important planktic foraminifera, S4: calcareous nannofossils, S5: C- and O-isotopes, S6: Dry bulk density, sedimentation rates, percentage of planktic foraminifera, estimated paleo-water depths, organic

Figure 3: Planktic foraminiferal species identified in the Adelholzen Section. 1. *Acarinina boudreauxi*, sample AH-95. 2. *Acarinina bullbrooki*, sample AH-101. 3. *Acarinina collactea*, sample AH-97. 4. *Acarinina praetopilensis*, sample AH-101. 5. *Acarinina pseudosubsphaerica*, sample AH-77.6. *Acarinina punctocarinata*, sample AH-116. 7. *Acarinina rohri*, sample AH-117. 8. *Acarinina topilensis*, sample AH-116. 9. *Catapsydrax unicavus*, sample AH-75. 10. *Chiloguembelina ototara*, sample AH-77 11. *Globigerinatheka euganea*, sample AH-133. 12. *Globigerinatheka index*, sample AH-129 13. *Globigerinatheka korotkovi*, sample AH-129. 14. *Globigerinatheka kugleri*, sample AH-127 15. *Globigerinatheka luterbacheri*, sample 133. 16. *Globigerinatheka subconglobata*, sample AH-129. 17. *Globorotaloides quadrocameratus*, sample AH-7 18. *Guembelitroides nuttalli*, sample AH-77. 19. *Hantkenina* cf. *compressa*, sample AH-129. 20. *Hantkenina liebusi*, sample AH-93. 21. *Igorina broedermanni*, sample AH-95. 22. *Jenkinsina columbiana*, sample AH-85. 23. *Jenkinsina triseriata*, sample AH-105. 24. *Morozovelloides coronatus*, sample AH-77. 25. Morozovelloides lehneri, sample AH-89. 26. *Parasubbotina pseudowilsoni*, sample AH-7. 27. *Planorotalites capdevilensis*, sample AH-133. 28. *Pseudohastigerina micra*, sample AH-105. 29. *Pseudohastigerina wilcoxensis*, sample AH-101. 30. *Streptochilus martini*, sample AH-129. 31. *Subbotina angiporoides*, sample AH-139. 32. *Subbotina corpulenta*, sample AH-101. 33. *Subbotina crociapertura*, sample AH-97. 34. *Subbotina eocaena* , sample AH-115. 35. *Subbotina gortanii*, sample AH-142. 36. *Subbotina hagni*, sample AH-115. 37. *Subbotina jacksonensis*, sample AH-141. 38. *Subbotina linaperta*, sample AH-139. 39. *Subbotina senni*, sample AH-2. 40. *Turborotalia cerroazulensis*, sample AH-135. 41. *Turborotalia frontosa*, sample AH-97. 42. *Turborotalia increbescens*, sample AH-139. 43. *Turborotalia pomeroli*, sample AH-116. 44. *Turborotalia possagnoensis*, sample AH-113. Length of scale bars: 0.1 mm.
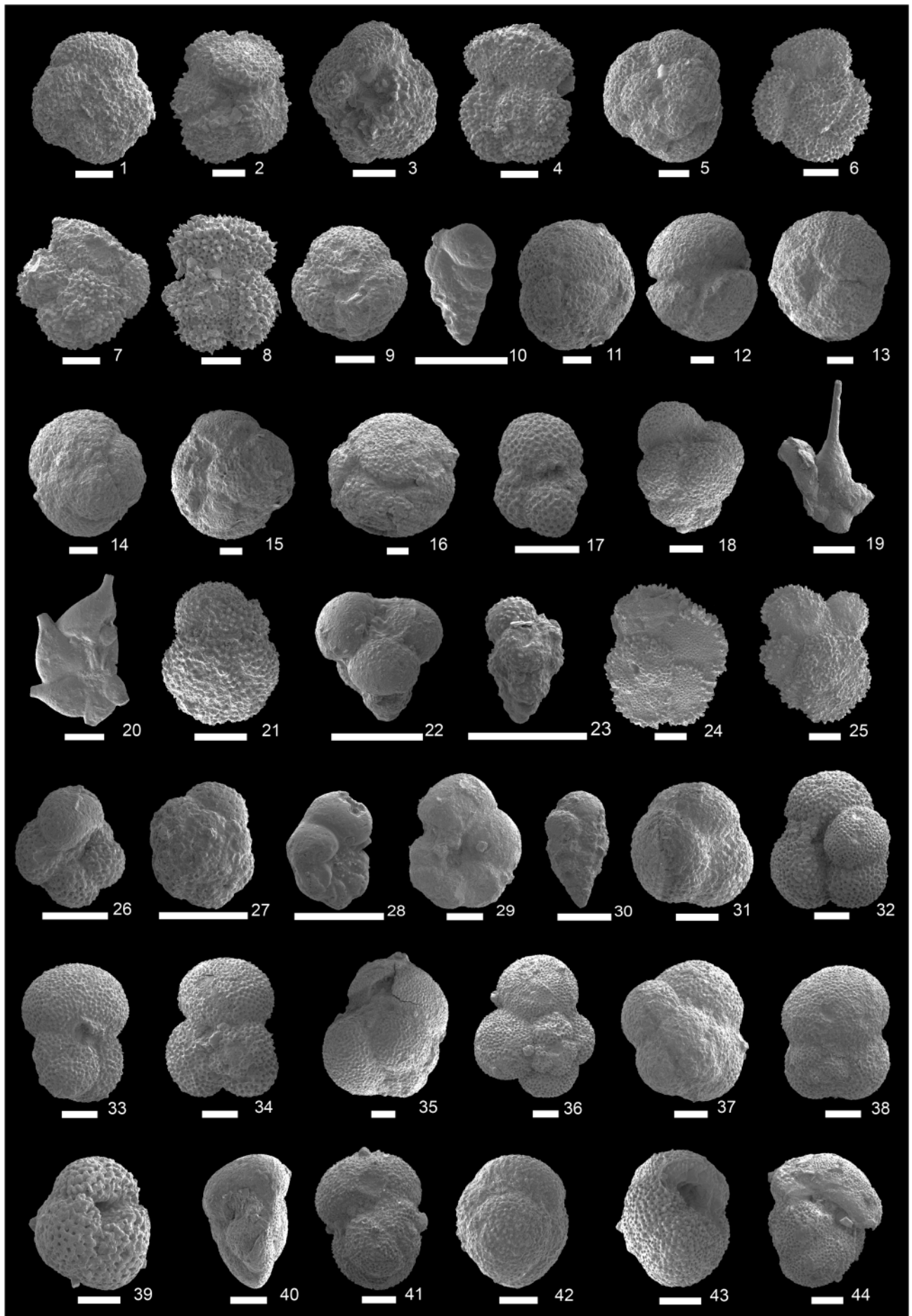
carbon flux to sea-floor, and paleo- primary productivity).

3. Biostratigraphy and age model

We adopted the biostratigraphic zonation proposed by Gebhardt et al. (2011) with some minor modifications for the subdivision of the Adelholzen Section. Figure 2 shows the first (FO) and last occurrences (LO) of index species and the resulting zonations for planktic foraminifera (E-zones), calcareous nannoplankton (NP-zones), and the Shallow Benthic Zones (SBZ, sensu Serra-Kiel et al., 1998) for larger benthic foraminifera. However, Shallow Benthic Zones are based on full lineages of benthic foraminifera and represent Oppelzones. For this reason, they have not been considered as age control points. Nevertheless, the concurrent presences of large benthic foraminiferal index species confirm the zonations based on planktic foraminifera (cf. Fig. 3) and calcareous nannoplankton (cf. Fig. 4). For the estimation of sedimentation rates and for the calculation of foraminifera accumulation rates we applied ages recently published in Gradstein et al. (2012, Geological Time Scale 2012; FAD = First Appearance Datum, LAD = Last Appearance Datum).

The following biostratigraphic events were used to erect the age model:

| Event	Age (Ma)
1. FAD *Guembelitroides nuttalli*, base E8	45.72
2. FAD *Chiasmolithus gigas*, base NP15b	45.49
3. LAD *Chiasmolithus gigas*, top NP15b	44.12
4. FAD *Globigerinatheka kugleri*, base E9	43.88
5. FAD *Globigerinatheka index*	42.64
6. LAD *Guembelitroides nuttalli*, top E10	42.07
7. FAD *Reticulofenestra reticulata*	41.66
8. LAD *Chiasmolithus solitus*, top NP16	40.40
9. FAD *Chiasmolithus oamaruensis*, base NP18	37.32
10. FAD *Isthmolithus recurvus*, base NP19-20	36.97
11. LAD *Reticulofenestra reticulata*	35.40

The age of the FAD of *Gt. kugleri* is not well constrained (44.4 to 42.6 Ma, Wade et al., 2011). The E9/E10-boundary (LAD of *M. aragonensis*) is at 43.26 Ma (Gradstein et al., 2012) but this index species was not recorded from the Adelholzen Section. Instead, we used the FAD of *Gt. index* shortly after the base of E10 as an age control point. The last occurrence of the nannofossil *Blackites gladius* (top NP15) at Adelholzen is after the FO of *Gt. index* and the LO of *Gu. nuttalli*. We therefore assume a diachronous LAD of *B. gladius* and do not use its LAD (43.09 Ma according to Gradstein et al., 2012) as an age control point. The last finding of *C. solitus* indicates the beginning of a stratigraphic gap of at least 4.34 My duration that encompasses parts of NP 16 and the entire NP17. The gap ends with the FO of *C. oamaruensis* (base NP 18). It therefore also includes the planktic foraminiferal zones E12, E13, and large parts of E11 and E14. Consequently, the Middle Eocene Climatic Optimum (MECO, at 39.35 Ma, Bijl et al. 2009) is not documented in the Adelholzen Section. *R. reticulata* (FAD 41.66 Ma) is a common species in the samples above the 4.34 My-stratigraphic gap and no indication exists

to assume ecologic causes for its non-occurrence before 40.40 Ma (top NP16). We consequently used its FAD as minimum age for the beginning of the stratigraphic gap (see supplementary Fig. S1). The LO of *R. reticulata* is used to determine the temporal end of the exposed record at Adelholzen. Although its LAD is probably diachronous (Gradstein et al., 2012), the datum is the last within NP19/20 and is therefore used for the calculation of sedimentation rates.

In addition to the biostratigraphic age indicators, we compared peaks and trends in bulk rock stable oxygen and carbon isotope records with global composite records (Zachos et al., 2008; Bijl et al., 2009) in order to narrow down the duration of the stratigraphic gap around NP17 and to help to identify other potential stratigraphic gaps in the Adelholzen record. Supplementary Figure S1 shows the stable isotope trends of the Adelholzen record. Furthermore, the isotope curves suggest a restart of deposition approximately coeval with the beginning of NP18 (sample AH-118). However, the resolution of the isotope record is too low to identify characteristic patterns suitable as age contol points. Since the data are new, we publish them in the supplements for potential further interpretations. The LAD of *C. solitus* (boundary NP16/17) falls within the stratigraphic gap. This datum has therefore not been considered for further calculations.

Larger benthic foraminifera (LBF, Fig. 4) in the lower part of the section are represented by the genera *Assilina*, *Nummulites* and *Discocyclina*. Taxa belonging to the younger part of the *Assilina exponens* phylum (*sensu* Schaub, 1981) (i.e., *A. cuvillieri*, *A. tenuimarginata*, *A. exponens*) are the most abundant within the sediment. They allow the biostratigraphic determination of the shallow benthic zones SBZ 13 to SBZ 15 along the section (Fig. 2). The limits between these Oppelzones at Adelholzen have been defined by biometric determination of the investigated taxa (e.g., Schaub, 1981). Specimens of *Assilina tenuimarginata*, abundant in both A and B

Figure 4: Selected ecologically (1-9) and stratigraphically important (10-14) calcareous nannoplankton species and examples of larger benthic foraminifera and macrofossils. Calcareous nannoplankton: 1. *Coccolithus cachaoi*, sample AH-27. 2. *Coccolithus mutatus*, sample AH-27. 3. *Coccolithus pelagicus*, sample AH-2. 4. *Reticulofenestra bisecta*, sample AH-135. 5. *Reticulofenestra dictyoda*, sample AH-140. 6. *Reticulofenestra minuta* (b, with *Coronocyclus bramlettei* (a)), sample AH-115. 7. *Reticulofenestra scripsae*, sample AH-135. 8. *Reticulofenestra umbilica*, sample AH-108. 9. *Cyclicargolithus floridanus*, sample AH-80. 10. *Chiasmolithus gigas*, sample AH-27. 11. *Blackites gladius*, sample AH-7. 12. *Chiasmolithus solitus*, sample AH-117. 13. *Chiasmolithus oamaruensis*, sample AH-140. 14. *Isthmolithus recurvus*, sample AH-130. Length of scale bar for all nannoplankton species: 10 μm. Larger foraminifera: 15. *Assilina tenuimarginata* B-form, scale bar: 1 mm, sample AH-7, 16. *Assilina cuvillieri*, A-form, scale bar: 1 mm, sample AH-2. 17. *Nummulites millecaput*, A-form, scale bar: 1 mm, sample AH-61. 18. *Assilina exponens* larger specimen, A-form, scale bar: 1 mm, sample AH-24. 19. *Nummulites millecaput*, B-form, scale bar: 5 mm, sample AH-65. 20. *Assilina exponens*, B-form, scale bar: 5 mm, sample AH-65. Macrofossils: 21. *Spondylus* sp, Upper Adelholzen beds, marly brown sand, scale bar: 1 cm. 22. *Conoclypus* cf. *subcylindricus*; Upper Adelholzen bed, marl with *Discocyclina*, scale bar: 1 cm. 23. *Harpactocarcinus quadrilobatus*, Upper Adelholzen beds, marl with *Discocyclina*, scale bar: 1 cm. 24. *Pycnodonte gigantica*, Lower Adelholzen Beds, scale bar: 1 cm.
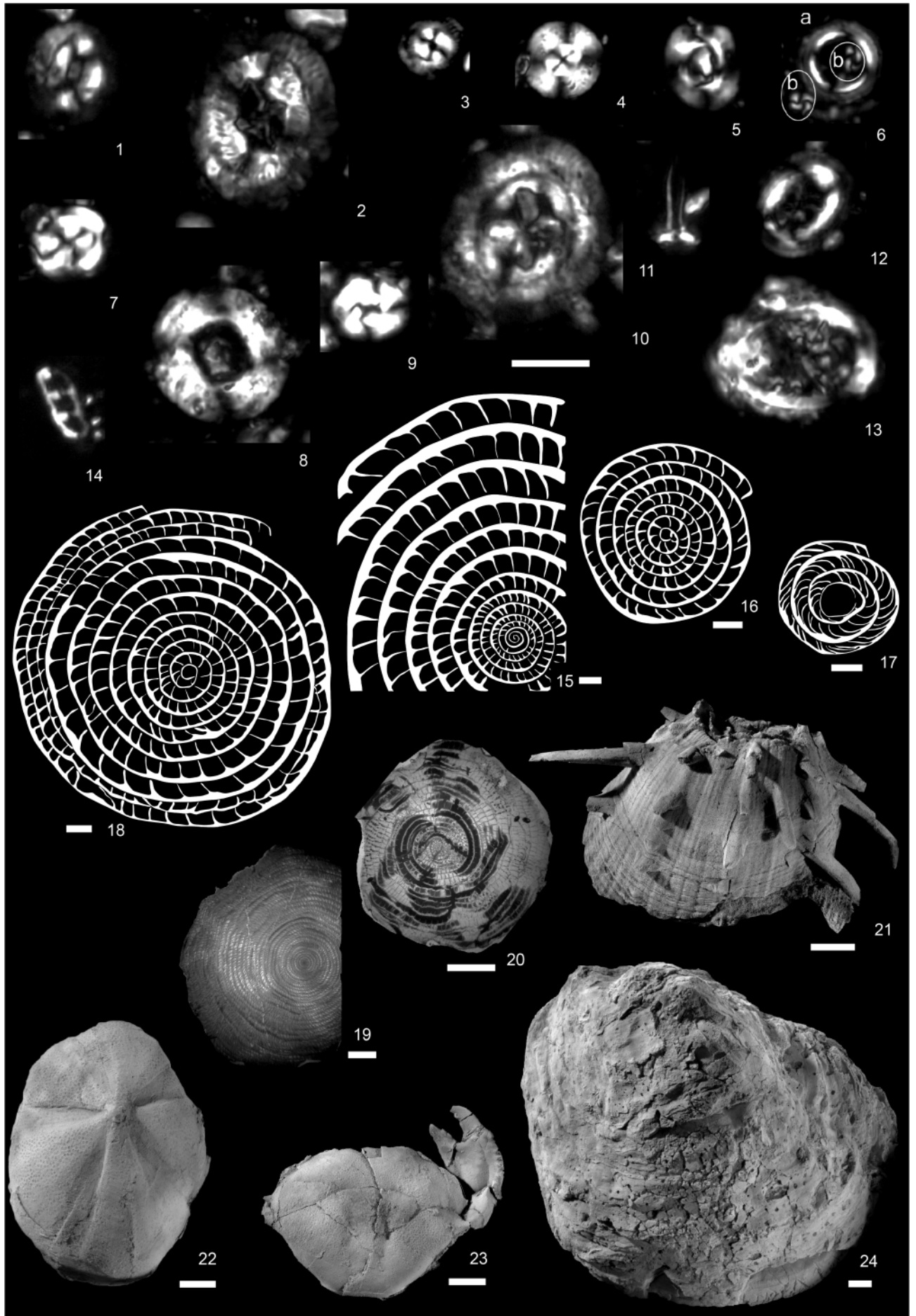
forms in the lowest part of the section, indicate lowermost Lutetian. *A. tenuimarginata* is replaced by *A. exponens* further above and indicates middle to late Lutetian and Bartonian ages (SBZ 14-17). *All Nummulites* specimens belong to the phylum of *N. distans - millecaput*. In the lower part of the section (samples AH-4 - 17), *N.* cf. *kaufmanni* and *N. alponensis* are present. The very small proloculus is the clear indication for the species preceding *N. millecaput* and later on *N. maximus*. In fact, *N. millecaput* starts to be present from sample AH-24 and later became abundant, indicating SBZ 15 (upper, but not uppermost, Lutetian). *N. millecaput* is present as A and B forms up to sample AH-61, which is the last sample where LBF have been collected and identified.

4. Sedimentation rates, stratigraphic gaps, and reworked microfossils

Sedimentation rates were calculated from the FAD of *Gu. nuttalli* (base E8, 45.72 Ma), to the LO of *R. reticulata* within NP19-20 at 35.40 Ma with the stratigraphic gap ranging from 41.66 to 37.32 Ma. For the few samples deposited before and after these age control points, sedimentation rates of the adjacent intervals are used. Calculated rates vary between 12 mm ky^{-1} in the lower Adelholzen Beds and 1 mm ky^{-1} in the upper portion of the Stockletten (Fig. 2). Our approach bears some uncertainties that limit the accuracy of our calculated sedimentation rates. Shorter unconformities in between age control points may be undetected, leading to underestimations of these rates. Distinct lithologic units are combined in one interval with average values that are too low for coarse grained units, and too high for fine grained units (e.g., upper portion of middle Adelholzen Beds or the E11/NP16-part of the Stockletten). Such problems are not unusual. For example, Beavington-Penney et al. (2006) also reported very low sediment accumulation rates from a nummulitic limestone succession of Oman. They concluded that the comparison with "unrepresentative, localized high rates of modern sediment production" leads to the recognition of accumulation rates of fossil deposits as anomalously low.

Other uncertainties may be related to the accuracy of the biostratigraphically based age model (preservation, reworking, relatively high paleolatitude and correlation with standard subtropical-tropical zonations, or partly marginal marine environments). In general, the calculated rates are possibly underestimates (merely sediment accumulation rates) and the derived paleoecological parameters might have higher values than calculated (e.g., paleo-primary productivity, pPP). However, our age model did not produce extreme high or low sedimentation rates and the resulting foraminiferal accumulation rates are within the range of other studies (e.g., Alegret and Thomas, 2007; Jorissen et al., 2007; Smart et al., 2007) and we therefore consider our results to be reliable (see also Chapter 8 Discussion).

We attribute the stratigraphic gap to either tectonic causes (uplift of blocks of the Northern Helvetic Unit *sensu* Hagn et al., 1981, coupled with the Alpine Orogeny) or a major regression during NP 17 (e.g., Hardenbol et al., 1998), or a combination of both processes. Results of field mapping point to rotating blocks (pers. comm. U. Blaha, see Introduction) and temporarily exposed areas without deposition during the Eocene.

The relatively long interval of NP15b is only represented by a few centimeters in the lithologic log (Fig. 2, samples AH-24, AH-27). Consequently, we assume an erosive surface and, therefore, another stratigraphic gap between the lower and the middle Adelholzen Beds. Since lithology does not change, we assume the same sedimentation rate for the underlying part of the section. For all other intervals, we assume constant sedimentation rates between the age control points.

4.1 The problem of reworking

In the lower and middle Adelholzen Beds, high numbers of reworked planktic foraminifera of Early Eocene age do occur (Fig. 5), which were washed into open spaces between the LBF. Possible sources for these tests are Lower Eocene marls in the surrounding of Salzburg. Hillebrandt (1962a, b) and Gohrbandt et al. (1963) reported "very frequent" to "extremely frequent" abundances of planktic species from the nearby Reichenhall-Salzburg Basin and Mattsee area (see also Rögl and Egger, 2012), pointing to high planktic to benthic ratios. Many of these species were found reworked at Adelholzen (e.g., *Morozovella aequa*, *Acarinina pentacamerata*, *A. soldadoensis*; Tables S1, 3). Consequently, the proportion of reworked smaller benthic foraminifera in the Adelholzen Beds is probably similarly low as in the sediments of the basins given above. Also among larger benthic foraminifera, small quantities of reworked specimens were observed in the lowermost part of the section (*A. cuvillieri* from the uppermost Ypresian). The contamination of the smaller benthic assemblages is thought to be very low (corresponding to given low numbers of benthic specimens in the potential source rocks, Hillebrandt, 1962a, b; Gohrbandt et al., 1963) and was therefore neglected for the ecological interpretation. Reworked planktic taxa could be easily identified and excluded from further interpretations. Contrary to planktic foraminifera, the proportion of reworked calcareous nannofossils is very low (Table S4). We do not have a satisfying explanation for this phenomenon yet, since usually high proportions of reworked calcareous nannofossils are coupled with low proportions of reworked foraminifera.

5. Results

5.1 Planktic foraminifera

We noticed a general trend of increasing numbers of planktic foraminifera and their ARs within the investigated section. Four genera became extinct within the investigated time interval (Fig. 5). Most prominent is the disappearance of *Acarinina* shortly after the 4.34 My stratigraphic gap (early Priabonian, Wade et al., 2011). This corresponds to observations from Tethyan sections further south (e.g., Luciani et al., 2010). *Jenkinsina* became extinct shortly after the MECO in zone E13 (Huber et al., 2006; Luciani et al., 2010), that is within the stratigraphic gap at Adelholzen. *Igorina* (with *I. broedermanni* as

the only occurring species) and *Guembelitroides nuttalli* became extinct within the upper Adelholzen Beds.

Planktic foraminifera (Fig. 3) comprise up to 80% of the total foraminiferal assemblages in the Stockletten, but also the basal nummulitic marls contain about 20% of planktic species. The relative abundance patterns (percentages) of the planktic foraminiferal assemblages (Fig. 5) not only coincide with the lithostratigraphic changes but also indicate extinction events and changes in the water column. Assemblages from the lower and middle Adelholzen Beds are dominated by *Acarinina* with various proportions of *Igorina*, *Subbotina*, *Guembelitroides*, *Turborotalia*, and *Jenkinsina*. The strength of the fluctuations of these proportions is partly a result of the relative small sample sizes in this part of the section, or due to shallow water depths (high proportion of shallow water dweller *Jenkinsina* in sample AH-61). The upper Adelholzen Beds are characterized by a decreasing content of *Acarinina* and increasing contents of *Pseu-*

dohastigerina, *Parasubbotina* and *Globorotaloides*. *Subbotina* and *Turborotalia* occur continuously and *Planorotalites* and *Globigerinatheka* contribute with higher percentages to the assemblages. Prominent in the Stockletten are the disappearance of *Acarinina*, the higher abundance of *Subbotina*, and strongly increased abundances of *Chiloguembelina* and *Streptochilus*. Furthermore, *Globigerinatheka* occurs with generally higher contents as well as *Hantkenina* and *Morozovelloides* which have their sporadic occurrences in this part of the section. After the 4.34 My stratigraphic gap, the increases of *Subbotina* and of *Turborotalia* are prominent phenomena.

5.2 Smaller benthic foraminifera

We applied a mofified morphogroup concept based on Bernhard (1986) and Kaiho (1994, 1999) for the deduction of bottom water conditions. In order to simplify the ecological interpretation and due to difficulties in species recognition caused
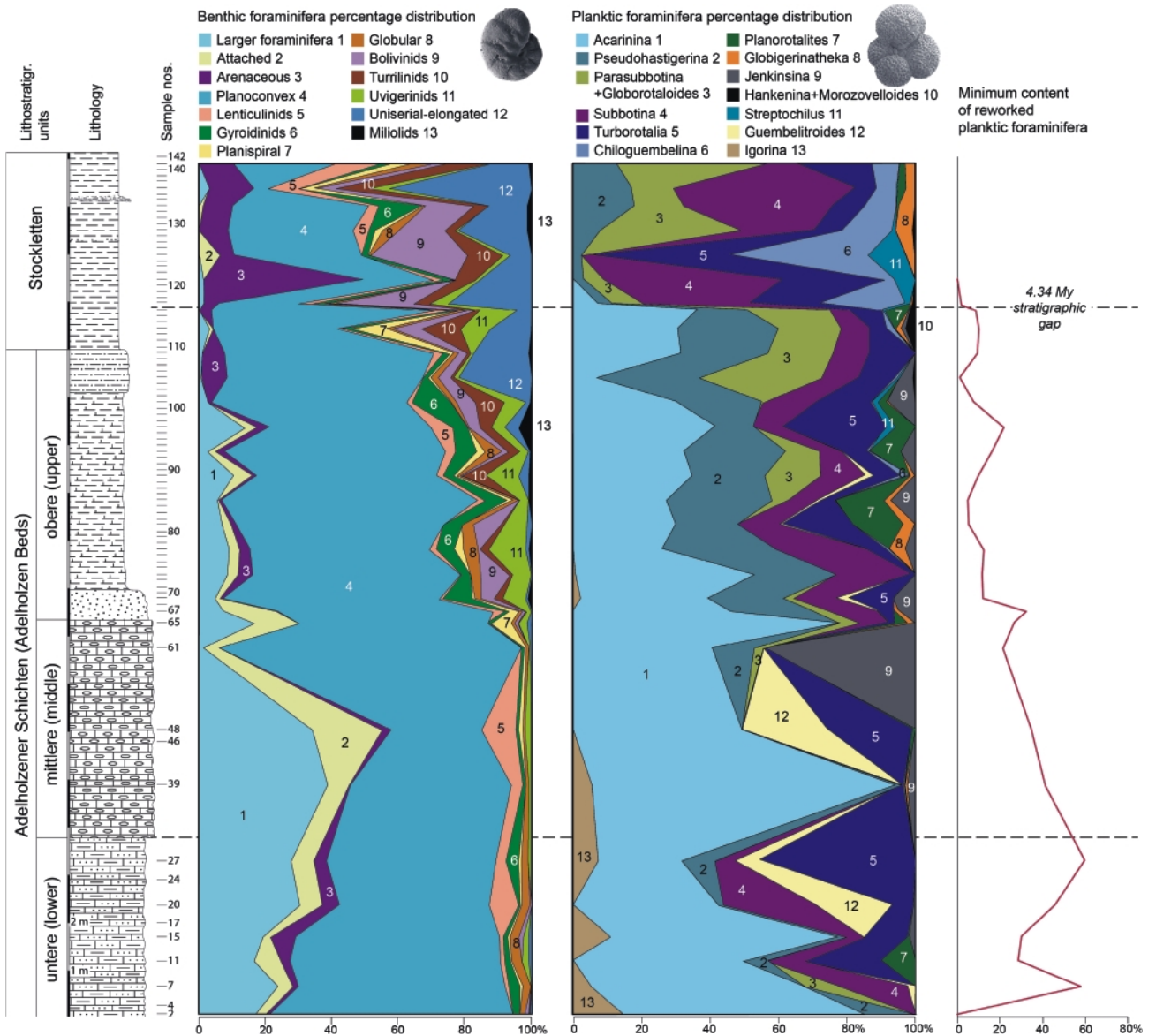

Figure 5: Relative abundance of planktic and benthic foraminifera in the Adelholzen Section. Lithology as in Fig.2. Horizontal dashed lines indicate identified stratigraphic gaps.

by partially poor preservation (cf. Figs 6 and 7), we combined several genera of the same or very similar morphotypes or test material to groups of taxa with common ecological preferences (Fig. 5, left column). Miliolids are extremely rare at Adelholzen and are not further interpreted here.

As in planktic foraminifera, relative abundances of benthic foraminifera at Adelholzen show a correlation to the lithologic change. However, the proportional changes of ecologic groups are more gradually (Fig. 5) and rather correspond to the increasing paleo-water depth. Thus, the lithologic boundaries are hardly displayed in the relative distribution patterns of benthic foraminifera. The Planoconvex group dominates the entire section but becomes less important in the Stockletten. Percentages of LBF and Attached group develop in parallel. Their content is highest in the lower part of the middle Adelholzen Beds (55%). They become less important in the upper Adelholzen Beds (c. 10%) and almost disappear in the Stockletten. Besides these two groups, only the Planoconvex group occurs with considerable proportions in the lower and middle Adelholzen Beds. All other groups share less than 15%. Within the upper Adelholzen Beds, Uvigerinids and Gyroidinids became more important and reached their highest contents (10 and 9 % respectively). The content of Bolivinids and Turrilinids also increases. Most prominent is the gradual increase of the Uniserial-elongated group. These taxa rise from 1 to 22%. In the Stockletten, the Uniserial-elongated group further increases its content to a maximum of 42%. Also Turrilinids (13%) and in particular Bolivinids (30%) have their maximum contents in the Stockletten. Contrary to this, the content of Uvigerinids decreases and the Planoconvex group reaches a minimum of 5%. Arenaceous taxa show their maximum content shortly after the 4.34 My stratigraphic gap and continue with relatively high percentages until the end of the section.

5.3 Accumulation rates of planktic and benthic foraminifera

Four major phases of increased total PFAR are conspicuous: elevated values at the base of the section, a bulge shaped increase with a peak in the middle part of the upper Adelholzen Beds, a very prominent peak at the base of the Stockletten and a less prominent increase in its upper part (Fig. 8). Benthic foraminiferal taxa show their highest accumulation rates in the lower part of the upper Adelholzen Beds (*Discocyclina* marls, Fig. 8). The accumulation rates of benthic foraminifera are about three times higher than those of planktic foraminifera in this part of the section. Prominent foraminiferal AR-peaks are most likely not an effect of concentration since the relative composition of the corresponding planktic and benthic foraminiferal assemblage show distinct shifts in their assemblages before and after the events.

5.4 Calcareous nannoplankton

All investigated samples contain very well preserved and relatively abundant autochthonous calcareous nannoplankton

assemblages (supplementary Table S4) and only very low percentages of reworked nannoplankton (<1%). Most common among these are Upper Cretaceous taxa (*Arkhangelskiella*, *Retecapsa*, and *Kamptnerius*), less common are lower Eocene taxa (*Discoaster*). *Coccolithus pelagicus* has its highest relative abundance in the middle Adelholzen Beds (19%, Fig. 8). Lowest relative abundances are in the middle part of the upper Adelholzen Beds (1%) whereas the values increase again towards the top of the section (up to 12%). In contrast, *Reticulofenestra minuta* has its highest relative abundances in the upper Adelholzen Beds (up to 71%) and reduced values in the Stockletten (down to 12%). *Cyclocargolithus floridanus* is the most frequent species in many samples with prominent negative peaks in the middle and upper part of the section (Fig. 8).

5.5 Results of multivariate statistical analysis

Cluster analyses of calcareous nannofossil assemblages identified four main clusters (groups of samples, correlation coefficient = 0.7049, Fig. 9a). Cluster 1 contains the highest percentages of the *Coccolithus* group (max. 18.9%), very high amounts of *Cy. floridanus* (max. 47.8%), followed by high numbers of the *R. bisecta* group and very low percentages of small reticulofenestrids. The separation of subclusters 1a and 1b is based on different numbers of species lumped in the *R. bisecta* group. Cluster 2 differs from the others by the highest values of the species *Cr. reticulatum* (max. 18.8%), and of species of the *Lanternithus* group (max. 19.9%). This cluster is also characterized by high percentages of the *Coccolithus* group and lowest contents of small reticulofenestrids. Samples grouped in cluster 3 are characterized by low contents of the *Coccolithus* group and middle sized reticulofenestrids,

Figure 6: Benthic foraminiferal species identified in the Adelholzen Section. 1. *Alabamina dissonata*, sample AH-27. 2. *Ammobaculites* sp., sample AH-141. 3. *Ammodiscus cretaceus*, sample AH-129. 4. *Amphistegina* sp., sample AH-65. 5. *Anomalinoides capitatus*, sample AH-141. 6. *Anomalinoides darwini*, sample AH-141. 7. *Anomalinoides nobilis*, sample AH-07. 8. *Astacolus crepidulus*, sample AH-101. 9. *Asterigerinata(?) pustulosa*, sample AH-69. 10. *Asterocyclina* sp., sample AH-20. 11. *Bolivina vaceki* subsp. glabra, sample AH-97. 12. *Bolivina* sp. 1, sample AH-77 13. *Bolivina* sp. 2, sample AH-77. 14. *Bolivinoides oedumi*, sample AH-129. 15. *Bulimina coprolithoides*, sample AH-77. 16. *Bulimina subtruncana*, sample AH-141. 17. *Bulimina tuxpamensis*, sample AH-85. 18. *?Cassidella* sp., sample AH-77. 19. *Cibicides lobatulus*, sample AH-93. 20. *Cibicides ribbingi*, sample AH-65. 21. *Cibicides simplex*, Brotzen, sample AH-85. 22. *Cibicides subspirata*, sample AH-07. 23. *Cibicidoides grimsdalei*, sample AH-15. 24. *Cibicidoides incrassatus*, sample AH-101. 25. *Cibicidoides pachyderma*, sample AH-69. 26. *Citarinella* cf. *watersi*, sample AH-101. 27. *Dentalina consobrina*, sample AH-77. 28. *Discocyclina* sp., sample AH-89. 29. *Ellipsoglandulina labiata*, sample AH-137. 30. *Entosolenia crebra*, sample AH-141. 31. *Epistominella minuta*, sample AH-077. 32. *Epistominella vitrea*, sample AH-109. 33. *Fissurina* cf. *formosa*, sample AH-101. 34. *Gaudryina mcleani*, sample AH-27. 35. *Gavelinella* sp., sample AH-07. 36. *?Globocassidulina* cf. *subglobosa*, sample AH-137. 37. *Gyroidinoides* sp., sample AH-07. 38. *?Haplophragmoides* sp., sample AH-141. 39. *Heterostegina costata*, sample AH-85. 40. *Karreriella subglabra*, sample AH-137. 41. *Lagena clavata*, sample AH-141. 42. *Lagena gracilicosta*, sample AH-101. Lengths of scale bars 0.1 mm, unless stated otherwise.
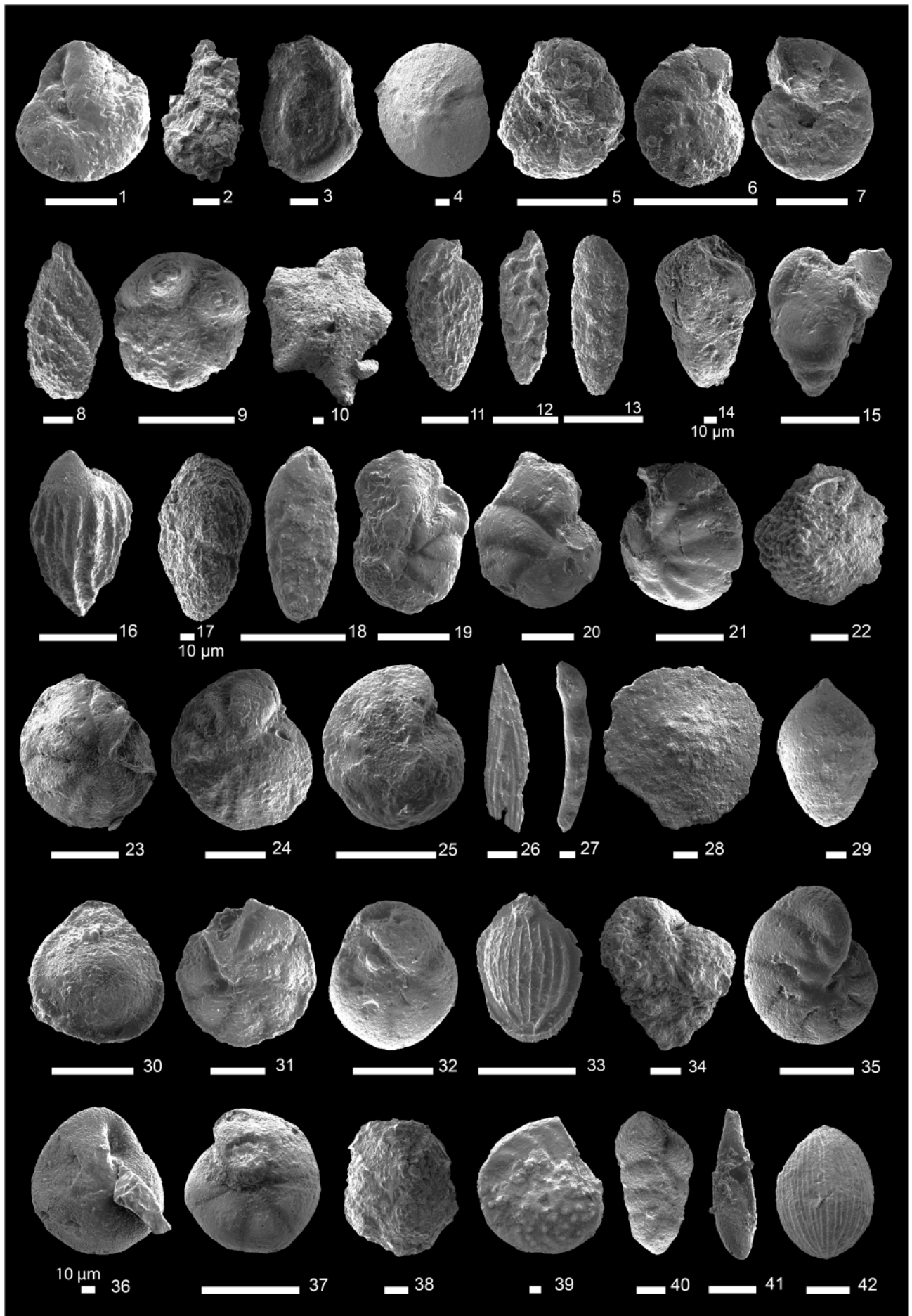
whereas *Cy. floridanus* and *R. minuta* occur with relatively high percentages. The subdivision of cluster 3 into three sub-groups (3a, 3b and 3c) was based on different amounts of *Cy. floridanus* and small reticulofenestrids. Cluster 4 contains samples dominated by high amounts of small reticulofenestrids and mid-sized resticulofenestrids *R. dictyoda* and *R. wadae*, and very low amounts of *Cy. floridanus* and specimens of the *Coccolithus* group. In nMDS, samples plots follow a rough clockwise circle in the co-ordinate system if seen biostratigraphically. Starting and ending points plot close to each other and are situated at the positive end of co-ordinate 1 with slightly negative values of co-ordinate 2 (Fig. 9b). A Shepard-Plot gave a "stress value" of 0.0667, indicating a very good quality of the nMDS result. The performed SIMPER-analysis showed that the content of *R. minuta* contributed most to the result of the cluster analysis (33%), followed by combined *R. dityoda* and *R. wadeae* (26%), and *Cy. floridanus* (13%).

5.6 Larger benthic foraminifera

Larger benthic foraminifera (*Assilina*, *Nummulites*, and *Discocyclina*, Fig. 4) are rock-forming elements of the lower and middle Adelholzen Beds (cf. Fig. 2). Within the samples AH-24 and 27, some larger specimens belonging to *A. exponens* have been found. They are up to 15 mm in diameter with 8 or 9 whorls in A forms; no B forms have been found. Multispiral growth is evident as well as opposite growth direction. Specimens belonging to the genus *Nummulites* are lower in abundance along the section (*N. distans - millecaput* phylum *sensu* Schaub, 1981). The species *N. millecaput* has been identified with A and B forms until sample AH-61. The largest B forms belonging to *N. millecaput* are 6 cm in diameter with more than 45 whorls. Other specimens have a radius of 20 - 24 mm for 34 - 42 whorls. LBFs also occur in the upper Adelholzen Beds but could not be classified at species level. Bioturbated tests (microborings?) occurred abundantly and mainly on discocyclinids. More than 50 specimens have been sectioned on the equatorial plane, always revealing completely bioturbated embryonic apparatuses. Therefore a consistent taxonomy on such forms cannot be provided yet.

5.7 Macrofossil occurrences

A number of macrofaunal elements were found at Adelholzen too (Fig. 4). The lower Adelholzen Beds contain articulated large oysters (*Pycnodonte gigantica*), spondylids with preserved spines, sea urchin remains, and occasionally internal molds of bivalves. The middle Adelholzen beds yielded only a few serpulids grown on *Nummulites* and some sea urchin remains. Various macrofossils were found in the upper Adelholzen Beds. The glauconitic sands contain free serpulids, oysters (*Pycnodonte* sp.), and large but rare crabs. In the *Discocyclina* marl, sea urchins (*Conoclypus* sp.), spines of *Spondylus* sp., crabs with preserved limbs (*Harpactocarcinus quadrilobatus*), free serpulids, and nodular bryozoan colonies were found. The marly brown sand yielded crabs (*H. quadrilobatus*), partly with limb preservation, spondylids, shark teeth,

rare amber, and lumachelles at the very bottom of this unit. The Stockletten is almost free of macrofossils, only a few tiny bivalves have been found at its base.

## 5.8 Ratio of planktic to benthic foraminifera (percent planktic foraminifera)

The percentage of planktic foraminifera (Fig. 8) is relatively low in the Lower Adelholzen Beds (max. 26%) and decreases to 8% in the Middle Adelholzen Beds. From the bottom of the Upper Adelholzen Beds, it constantly increases with highest values at their top (49%). This trend continues in the Stockletten but with strong fluctuations (35 to 83%).

6. Derived parameters

6.1 Paleo-water depth

The ratio of planktic to benthic foraminifera (P/B-ratio or percent planktic foraminifera, Table S6) is proportional to water depth in modern oligotrophic open marine settings (e.g., van der Zwaan et al., 1990, Szarek, 2001). It is considered to be a good estimator for paleo-water depth at least during the Cenozoic. The percentages of planktic foraminifera in the assemblages are displayed in Figure 8. Absolute paleo-water depth estimates for the lower two thirds of the Adelholzen section (Fig. 10) are based on the formula of van der Zwaan et al., (1990). Oceanographic perturbations of hitherto unknown causes in the upper third made it necessary to apply a different approach (see below). In order to demonstrate the possible range of paleo-water depths estimated from P/B-ratios, we added an envelope of uncertainty to the curve in Fig. 10. Besides the general increase in paleo-water depth in the up-

Figure 7: Benthic foraminiferal species identified in the Adelholzen Section (continuation). 1. *Lagena gracilicosta* var., sample AH-101. 2. *Lagena sulcata*, sample AH-101. 3. *Lenticulina inornata*, sample AH-69. 4. *Lenticulina limbosa*, sample AH-141. 5. *Lenticulina* sp. 1, sample AH-137. 6. *Lenticulina* sp. 2, sample AH-85. 7. *Loxostoma plummerae*, sample AH-93. 8. *Loxostomoides applinae*, sample AH-129. 9. *Marginulina hirsuta*, sample AH-109. 10. *Marginulina similis*, sample AH-141. 11. *Marsonella floridana*, sample AH-141. 12. *Melonis affinis*, sample AH-27. 13. *Melonis pompilioides*, sample AH-141. 14a,b. *Neoconorbina ystadiensis*, sample AH-48. 15. *Nodosaria* sp., sample AH-137. 16. *Nonionella robusta*, sample AH-85. 17. *Nummulites* sp., sample AH-137. 18. *Operculina* sp., sample AH-109. 19. *Planulina austriaca*, sample AH-69. 20. *Pleurostomella incrassata*, sample AH-137. 21. *Porosononion* sp., sample AH-77. 22. *Pullenia bulloides*, sample AH-137. 23. *Quinqueloculina brevidentata*, sample AH-101. 24. *Rectuvigerina multicostata*, sample AH-11. 25. *Rectuvigerina* sp., sample AH-116. 26. *Reophax nodulosa* var. *brevior*, sample AH-129. 27. *Rhabdammina* sp., sample AH-141. 28. *Rhizammina* sp., sample AH-141. 29. *Saccammina globosa*, sample AH-109. 30. *Spiroloculina canaliculata,* sample AH-129. 31. *Spiroplectammina dentata*, sample AH-93. 32. *Spiroplectammina* sp., sample AH-48. 33. *Stilostomella adolphina*, sample AH-129. 34. *Stilostomella paleocenica*, sample AH-137. 35. *Stilostomella plummerae*, sample AH-141. 36. *Trifarina bradyi*, sample AH-69. 37. *Tristrix excavatus*, sample AH-105. 38. *Trochammina* sp., sample AH-105. 39. *Turrilina brevispira*, sample AH-137. 40. *Turrilina robertsi*, sample AH-77. 41. *Uvigerina hispida* Schwager, sample AH-77. 42. *Uvigerina moravia*, a: sample AH-93, b: sample AH-85. 43. *Uvigerina* cf. *semiornata*, sample AH-069. Lengths of scale bars 0.1 mm.
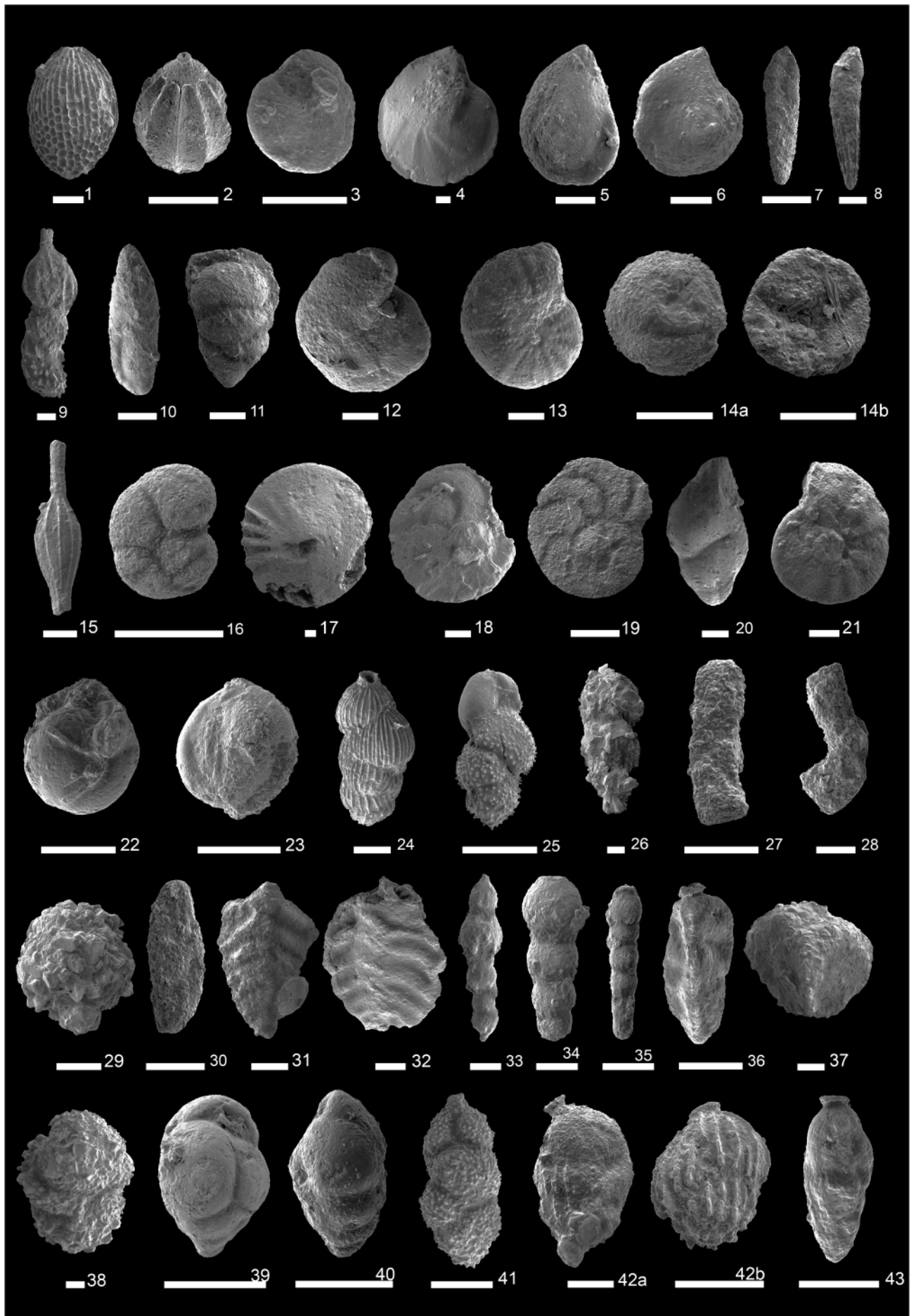
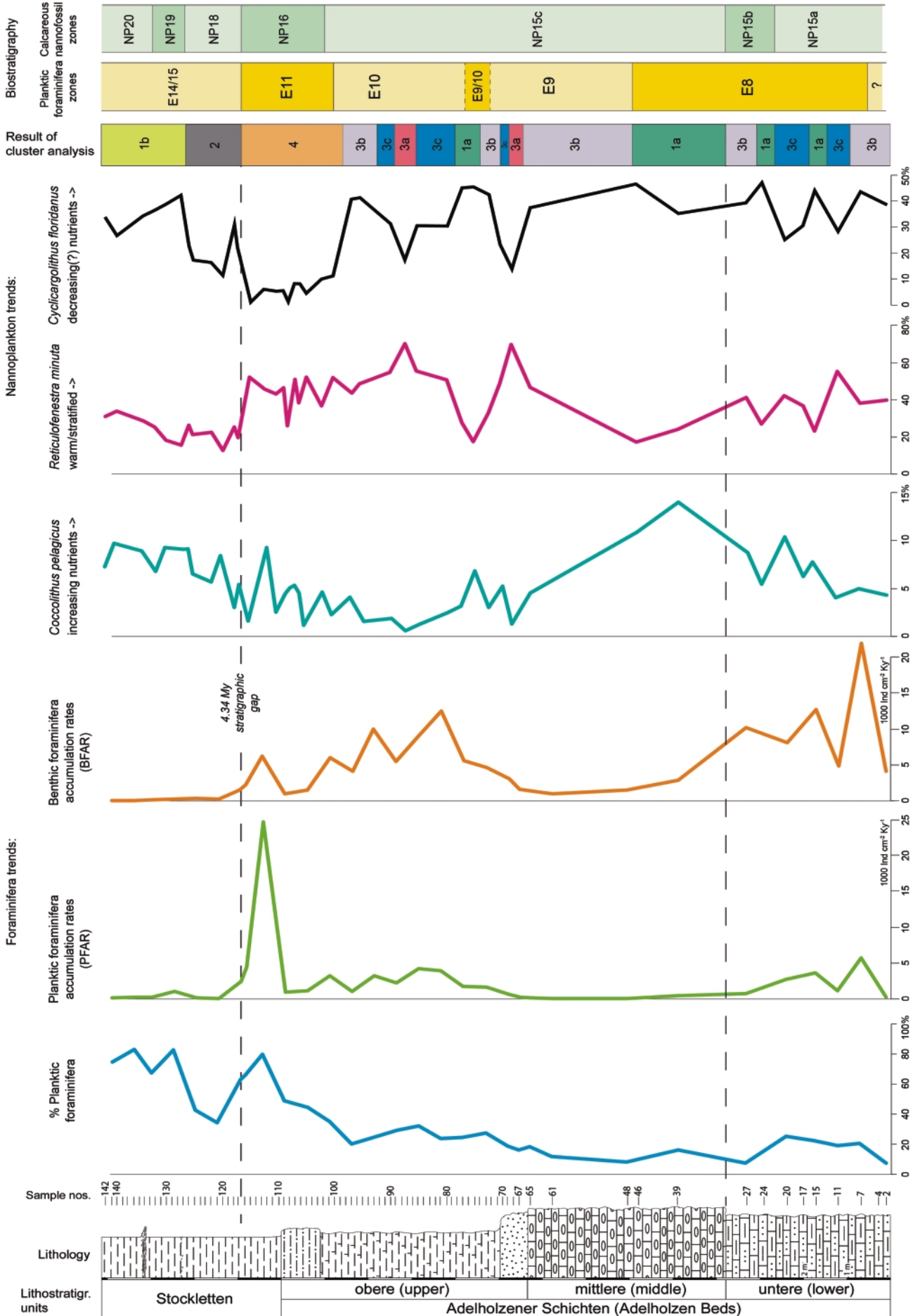| Genus	Depth habitat	Nutrient status of habitat and live strategy
Morozovelloides (+)	surface mixed layer	oligotrophic
Igorina (+)	surface mixed layer	oligotrophic
Acarinina (+)	lower mixed layer	oligotrophic
Globigerinatheka (+)	lower mixed layer	oligotrophic
Jenkinsina	(shallow water)*	highly eutrophic, opportunistic
Chiloguembelina	intermediate (thermocline to surface mixed layer)	low oxic tolerant, opportunistic
Streptochilus	intermediate (thermocline to surface mixed layer)	low oxic tolerant, opportunistic
Pseudohastigerina	intermediate (thermocline to close to surface)	low oxic tolerant, opportunistic
Guembelitroides	intermediate	
Hantkenina	intermediate (cold deep-water to surface mixed layer)	
Planorotalites	intermediate	
Turborotalia	intermediate (mixed layer to sub-thermocline)	
Subbotina	below thermocline	
Parasubbotina	below thermocline	(eutrophic)
Globorotaloides	below thermocline	(eutrophic)

TABLE 1: Depth ranking and life strategies of middle to late Eocene planktic foraminifera derived from stable isotope data, biogeographic distribution, and morphology. Genera in the order of depth habitat and food availability. (+) indicates symbiont bearing genera. Ecologic information according to Pearson et al. (1993), Berggren et al. (2006a, b), Coxall and Pearson (2006), Olsson and Hemleben (2006), Olson et al. (2006a, b), Pearson and Berggren (2006), Pearson et al. (2006a, b), Premoli Silva et al. (2006), Wade et al. (2006), Luciani et al. (2007), Wade and Pearson (2008), Luciani et al. (2010) with further references therein, and this paper. * in analogy to triserial Late Cretaceous Guembelitria (e.g., Leckie et al. 1998).

per Upper Adelholzen beds and the Stockletten, indications for strong paleoceanographic disturbances were recorded above the 4.34 My stratigraphic gap. Here, the P/B-ratio decreases drastically, pointing to low paleo-water depths. However, planktic foraminiferal assemblages that contain high proportions of deep-dwelling *Subbotina* and *Turborotalia*, still indicate bathyal depths and, thus, a continuing increase of paleo-water depth. In addition, co-occurring benthic assemblages point to stressful conditions on the seafloor (very low AR with dominance of agglutinating taxa or bolivinids, compare Table 2). In the context of the semi-enclosed paleogeographic situation of the Penninic Basin, the recorded changes in the benthic assemblages may reflect temporary dysoxic conditions at the seafloor (possibly caused by sluggish circulation?) for the period shortly after the stratigraphic gap.

Consequently, we did not consider the 'disturbed' samples (AH-121, 125) for paleo-water depth estimates. Because of these disturbances of the P/B-ratio, we included the depth-depending flux of organic matter to the sea-floor (*Jsf*) for the paleo-water depth estimation for this portion of the section. A "partial correlation" (statistics) showed a highly significant negative correlation between *Jsf* and paleo-water depth (r = -0.6770; p = 1.4*10^{-5}) if the abundance of planktic foraminiferal is partialized. We therefore used a correlation between P/B-derived water depths and *Jsf* excluding the 'disturbed' samples to finally estimate the paleo-water depths above sample AH-089 by paleo-water depth = $511.38e^{-0.0008 Jsf}$ (r^2 = 0.51; Fig. 10, Table S6). From this part of the section, we assume the paleo-water depth to be high enough to influence the flux of organic matter to the sea-floor crucially, i.e., a paleo-water depth below the productive surface waters.

Minimum values of paleo-water depths (c. 50 m) are indicated at the base of the section, the transition from lower to middle Adelholzen Beds, and in the middle part of the middle Adelholzen Beds. Slight increases in planktic foraminifera percentage point to increased paleo-water depths for the middle parts of the lower Adelholzen Beds and the lower part of the middle Adelholzen Beds. A nearly continuous increase in paleo-water depth is indicated from the minimum in the middle part of the middle Adelholzen Beds to the top of the upper Adelholzen Beds (max. c. 360 m) and beyond. Directly before the 4.34 My stratigraphic gap, a very distinct depth increase took place in the area that ended with (upper) bathyal depths (c. 480 m) at the top of the exposed Stockletten. Among benthic foraminifera, *Bulimina tuxpamensis* is an indicator of bathyal depths (van Morkhoven et al., 1986) and its occurrence in the upper Adelholzen Beds confirms the depth grading during deposition of these strata and the Stockletten. The commonly used bathyal indicator *Nuttallides truempyi* does not occur at Adelholzen. This species is already rare to very rare in the Middle Eocene of the Betic Cordillera (Ortiz and Thomas, 2006). It disappeared from upper bathyal sites since the late Middle Eocene (Tjalsma and Lohmann, 1983) and can therefore not be used as bathyal indicator for upper bathyal sites such as Adelholzen in general.

FIGURE 8: Summary of ecologic parameters in the Adelholzen Section: percentage planktic foraminifera, planktic foraminifera accumulation rates, benthic foraminifera accumulation rates, and percentages of calcareous nannoplankton indicators (nutrients, temperature/stratification) and results of cluster analysis of nannoplankton assemblages. Lithology as in Fig. 2. Horizontal dashed lines indicate identified stratigraphic gaps. Color scheme for results of cluster analysis corresponds to Fig. 9.

Holger GEBHARDT, Stjepan ĆORIĆ, Robert DARGA, Antonino BRIGUGLIO, Bettina SCHENK, Winfried WERNER, Nils ANDERSEN & Benjamin SAMES

Morphogroup	Depth	Oxygenation	Food availability	Habitat	Stress tolerance
Larger benthic foraminifera: *Amphistegina, Assilina, Discocyclina, Heterostegina, Nummulites, Operculina*	photic zone	oxic	low	epifaunal	low
Attached: *Neocorbina, Asterigerinata(?), Cibicides lobatulus*	photic zone	oxic	low	epifaunal	low(?)
Arenaceous: *Ammobaculites, Ammodiscus, Gaudryina, ?Haplophragmoides, Karreriella, Marsonella, Reophax, Rhabdammina, Rhizammina, Saccammina, Spiroplectammina, Tristrix, Trochammina*	all depths	mostly low oxic	low to high	in- to epifaunal	high
Planoconvex: *Alabamina, Anomalinoides, Cibicides* (without *C. lobatulus*), *Cibicidoides, Epistominella, Gavelinella, Planulina*	all depths	oxic	moderate	epifaunal	moderate
Lenticulinids: *Astacolus, Lenticulina, Marginulina*	all depths	oxic	moderate	epifaunal	moderate
Gyroidinoids: *Gyroidinoides*	all depths	oxic	moderate	epifaunal	moderate
Planispiral: *Melonis, Nonionella, Porosononion, Pullenia*	all depths	low oxic	moderate	mostly infaunal	moderate
Globular: *Ellipsoglandulina, Entosolenia, Fissurina, Globocassidulina, Lagena*	all depths	low oxic	moderate	in- to epifaunal	moderate
Bolivinids (flattened, tapered): *Bolivina, Loxostoma, Loxostomoides*	all depths	dysoxic to low oxic	high, opportunistic	mostly infaunal	high
Turrilinids (tapered): *Bulimina, Cassidella, Turrilina*	all depths	dysoxic to low oxic	high, opportunistic	infaunal	high
Uvigerinids (tapered): *Rectuvigerina, Trifarina, Uvigerina*	all depths	dysoxic to low oxic	high, opportunistic	mostly infaunal	high
Uniserial elongate: *Cytharina, Dentalina, Nodosaria, Stilostomella, Pleurostomella*	below wave base	dysoxic to low oxic	moderate	probably infaunal	moderate

TABLE 2: Ecologic classification of benthic foraminiferal morphogroups (with their genera) occurring at Adelholzen. Ecologic information according to Bernhard (1986), Kaiho (1994), Leckie et al. (1998), Kaiho (1999), Murray (1991b), Speijer et al. (1996), Gebhardt et al. (2004, 2010) with further references therein, and this paper.

6.2 Flux of organic carbon to the seafloor and paleo-primary productivity (pPP)

Because of the strong dependence of benthic foraminifera abundances on food availability (e.g., van der Zwaan et al., 1990, 1999; Gooday, 2003), BFAR may be directly related to organic matter flux to the seafloor if the loss of organic matter during the passage through the water column is known (Herguera and Berger, 1991). Herguera (2000) developed a transfer function based on empirical results from glacial paleo-productivity patterns of the eastern equatorial Pacific. The function for the calculation of paleo-primary productivity (pPP) accounts for the depth of the seafloor and therefore for the decay of the organic matter during sinking. Additional TOC measurements may support the interpretations of carbon flux to the sea floor.

We applied the transfer functions of Herguera (2000) and assume similar (tropical) climatic conditions, constant decay of organic matter during sinking, and a largely unchanged (despite increased paleo-water depth) structure of the water column for the study interval. However, the resulting changes in organic matter flux and pPP (Table S6), as well as those for PFAR and BFAR, appear to be too strong to exclude changes of the water column structure (e.g., depth of mixed layer, intensity of vertical mixing). Therefore, such changes have to be considered for the interpretation. The BFAR approach in general appears to work adequately in well oxygenated sediments (Gooday, 2003), as is the case at Adelholzen (see below).

The calculation of organic matter flux to the seafloor and of pPP based on the transfer functions of Herguera (2000) requires a number of constant preconditions (see above and also Jorissen et al., 2007) that are normally not fulfilled in geological records, which applies to the Adelholzen succession as well. Here, the record covers several million years of depositional history including changes in transport mechanisms of organic matter and of benthic foraminiferal tests. We therefore consider the organic flux and pPP records (Fig. 10) only as estimates for surface primary productivity or food availability and consequently only interpret the relative changes in detail.

Estimated organic flux rates vary between 100 and 3900 mgC/cm^2 ky (Fig. 10). They generally decrease with paleo-water depth but show distinct maxima in the middle part of the upper Adelholzen Beds and at the base of the Stockletten.

The calculated pPP increases up-section with minimum values in the middle Adelholzen Beds (0.8 mgC/cm^2 ky) and reach maximum values at the base of the Stockletten (7.0 mgC/cm^2 ky). The values decrease significantly in the Priabonian part of the Stockletten (2.7 to 1.6 mgC/cm^2 ky; Fig. 10). It is intriguing that the pPP values calculated for the Adelholzen Section are very low and similar to those of the centers of modern tropical-

subtropical anticyclonic gyres (e.g., Goddard Space Flight Center, 2003). Consequently, we interpret the entire section at Adelholzen as a highly oligotrophic succession, although the basal Stockletten were deposited with a seven times higher pPP if compared with the middle Adelholzen beds. TOC values (Fig. 10) vary between 0.1 and 0.5 % and show several maxima. The TOC-values largely reflect the accumulation of foraminiferal tests as well as the derived pPP and calcareous nannoplankton assemblages (nMDS co-ordinate 1 values). The deduction of oligotrophic conditions during deposition is supported by the relatively low contents of *Coccolithus pelagicus* and relatively high proportions of *Cyclocargolithus floridanus*.

Note: In order to check the reliability of our results, we calculated pPP with extremely increased sedimentation rates (factor 10) and minimum paleo-water depths (cf. Fig. 10, left margin of 'envelope of uncertainty'). The results are still in the same range of values and are in accordance with our interpretations.
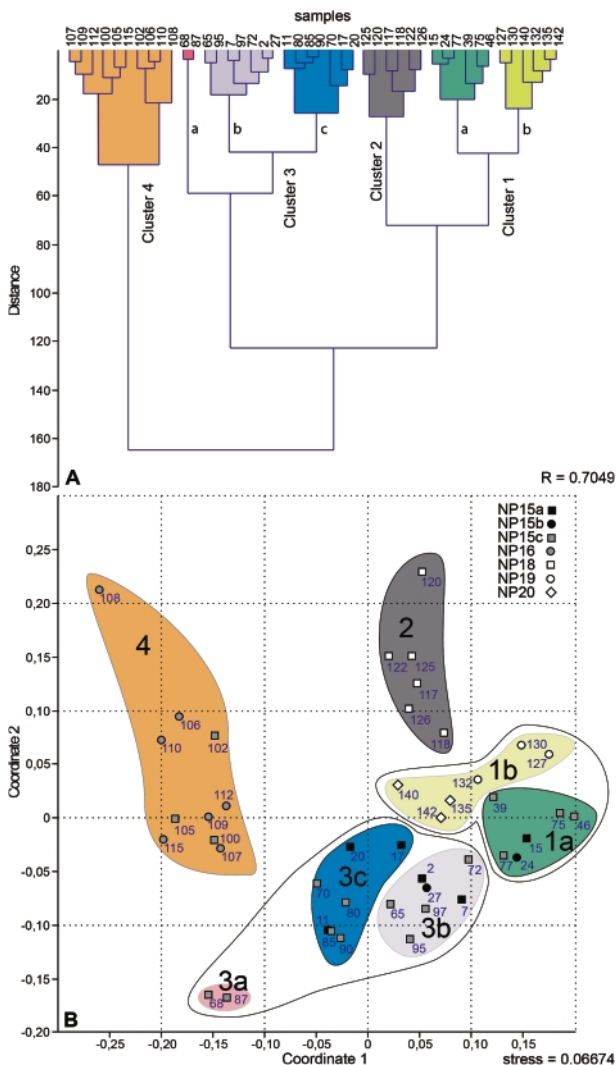

Figure 9: Multivariate statistical analysis of calcareous nannofossil assemblages, sample numbers without prefix. A: Result of cluster analysis (Ward's method, standardized Euclidian distance). B: Result of nonmetrical Multidimensional Scaling (nMDS, standardized Euclidean distance), stratigraphic development is shown by symbols for nannoplankton zones (NP15a - NP20).

7. Interpretation

7.1 Planktic foraminifera

We interpreted the structure of the water column based on the ecological preferences, habitats, or reproduction depths of the occurring species. The necessary information is based on stable C and O isotope analysis of the calcareous tests (e.g., Wade and Pearson, 2008, among many others), Mg/Ca-ratios (paleo-temperatures, e.g., Hollis et al., 2009) or biogeographic distribution of genera and species. We summarized life strategies, depth rankings, and further ecologic preferences for occurring genera at Adelholzen in Table 1. Furthermore, availability of food is essential, particularly for non-symbiont bearing taxa, and largely governs the abundance of planktic and benthic foraminifera standing stocks (e.g., van der Zwaan et al. 1990, 1999). As well, symbiont bearing planktic foraminifera are more abundant in regions with increased food supply (or export production, e.g., Žarić et al., 2005). These taxa also feed on prey such as copepods, diatoms, coccolithophores or other algae (e.g., Hemleben et al., 1989; Murray, 1991a) and therefore we applied planktic foraminifera accumulation rates (PFAR) as a reflection of food availability, as well as relative abundance patterns to interpret the planktic foraminifera assemblages in order to describe the changes within the water column.

The general trend of increasing numbers of planktic foraminifera and their ARs within the investigated section is certainly a function of increasing water depth. Changes in paleo-water depths are not only indicated by the increase in the P/B-ratio and reduced flux to the sea floor (Figs. 8, 10) but also by changes in the planktic foraminiferal assemblage composition. The percentage of surface mixed layer taxa decreases gradually along the entire section. Contrary to this, intermediate (thermocline) and deep dwellers (sub-thermocline) became more abundant with time.

The bulge shaped elevated PFAR values within the upper Adelholzen Beds are paralleled by even more pronounced BFARs (Fig. 8). Within the PFAR bulge, all taxa contribute to the increase but with different shares. Mainly non-opportunistic taxa account for the last positive excursion of the PFAR bulge, but also *Pseudohastigerina* plays an important role. The positive phases within the PFAR bulge show increased ARs for the highly opportunistic *Jenkinsina*. In Summary, the PFAR bulge reflects both, increasing paleo-water depth and pPP.

The most prominent PFAR event (sample AH-113) at the base of the Stockletten was shortly after the assumed climatic optimum. Here, ARs are about four times higher than during time intervals represented by the other peaks (Fig. 8). This event is characterized by AR increases of all planktic taxa (except *Planorotalites*), but most prominent are those of *Acarinina* and, in particular of meso to eutrophic indicators such as *Pseudohastigerina*, *Parasubbotina*, and *Globorotaloides* (Fig. S2), pointing to increased primary surface productivity. Thermocline and sub-thermocline dwellers also thrived well during this phase and high stress indicators such as *Chiloguembelina*, *Streptochilus*, or *Jenkinsina* remained low in numbers (and ARs). Such

productive paleoceanographic conditions were apparently disturbed during a distinct period after the 4.34 My stratigraphic gap when the P/B-ratios decreased strongly and the relative abundances show first a shift towards *Subbotina*, later towards *Turborotalia* and *Chiloguembelina*. Similar conditions are assumed for other positive PFAR peaks in the Stockletten.

7.2 Smaller benthic foraminifera

An analysis of occurring genera or species (Figs. 6, 7) can give detailed information on the changing conditions at the seafloor during the time of deposition. An overview on the ecologic requirements of the relevant groups (including occurring genera) is given in Table 2.

The benthic assemblages are dominated by planoconvex or lenticular taxa (*Cibicidoides*, *Planulina*, *Lenticulina* etc.) and indicate general oxic conditions at the seafloor (Kaiho, 1994, 1999). Contrary to the dominating Planoconvex group, arenaceous genera are always rare and occur with higher percentages only in samples of the Stockletten above the 4.34 My stratigraphic gap (Fig. 5). Some samples above the gap are further characterized by the lowest recorded BFAR and organic carbon fluxes. This points to extremely low food availability, and resembles paleoenvironmental conditions similar to contemporary flysch-sediments deposited further south below the carbonate compensation depth (CCD, compare e.g., Kaminski et al., 1999). This coincides with changes in the planktic foraminiferal patterns (see previous chapter). The levels around samples AH-89, 101, 113, 125, and 129 are characterized by high ARs and percentages of Bolivinids, Turrilinids, and Uvigerinids. These peaks point to reduced oxygen levels caused by either increased food supply (organic matter flux) or decreased ventilation of the bottom waters (see below). The high surface to volume ratio of the tests supports effective oxygen uptake for respiration (e.g., Bernhard, 1986; Kaiho, 1994). Lenticulinids and Gyroidinoids, together with the Globular group show opposite abundance patterns to the dysoxic indicators at Adelholzen. This may be due to their high volume to surface ratio that reduces potential oxygen uptake from ambient water. Accumulation rates and relative abundance of the Uniserial-elongated group start to increase in the upper Adelholzen Beds and are highest in the Stockletten. Intensity of turbulence and therefore water depth appears to be the most important factor that governs the distribution of this group with fragile tests. Consequently, they are frequent only in sediments deposited below a certain threshold, possibly the storm wave base (i.e., at c. 100 m paleo-water depth at Adelholzen, see chapter on changing paleo-water depths below). Todd (1979) report their characteristic occurrence in modern middle shelf and deeper environments.

The general relative abundance picture shows a gradual change with increasing paleo-water depth from typical shallow water assemblages with nummulitids towards deep water assemblages with uniserial and other infaunal taxa (Fig. 5). Relative peaks of low-oxygen tolerant opportunistic taxa indicate periods of reduced oxygen supply. In combination with increased ARs, periods of elevated food supply and therefore increased pPP may be identified.

7.3 Calcareous nannoplankton

The ecological requirements of calcareous nannoplankton taxa are poorly known and knowledge is mostly restricted to modern species. However, some common taxa can be utilised for the interpretation of the changing paleo-environments. Table 3 gives an overview on ecological indications of calcareous nannofossils relevant at Adelholzen. The succession of assemblages reflect the transition from relatively stable shallow water conditions with low nutrient availability (high relative abundances of *Cy. floridanus*) during the deposition of the lower and middle Adelholzen Beds (cluster 1a, 3b,c) to the highly variable conditions of the upper Adelholzen Beds (cluster 1a, 3a,b,c, 4; Fig. 8). This was followed by a period of relatively stable conditions that shows a development from high paleo-temperatures with probably increased nutrient availability and subsequent increased paleo-primary productivity (pPP) in the uppermost Adelholzen Beds (cluster 4) towards open oceanic (cooler?) conditions and reduced pPP in the Stockletten (cluster 1b, 2). These changes correspond to nMDS co-ordinate 1 values as displayed in Fig. 9. Higher values of eutrophic favoring *C. pelagicus* in the middle Adelholzen Beds and stepwise increase in the Stockletten point to increases in surface water nutrient availability, whereas low contents of *C. pelagicus* in the upper Adelholzen Beds point to warming during this intervals and even more oligotrophic conditions. Generally low percentages of discoasters, an open ocean taxon with highest values in cluster 1a (1.4%), i.e., in the lower part of the section, confirm the shallow paleo-water depths inferred from foraminifera data. According to the relative abundance pattern at Adelholzen, Cy. floridanus might be interpreted as a species that avoids inferred elevated temperatures.

7.4 Larger benthic foraminifera

Modern Nummulitidae host diatoms as photosynthetic sym-

Taxon	(Paleo-) Ecological indications
Coccolithus pelagicus	high nutrients, eutrophication, increased vertical mixing, subarctic (modern) to subtropical (past)
small *Reticulofenestra*	non-deep sea, continental margins
Reticulofenestra minuta	increased paleotemperatures, stratification
Cyclocargolithus floridanus	low nutrients
Discoaster spp.	warm, open oceanic (blooms and diversity maxima)

Table 3: Paleoecological indications of calcareous nannoplankton taxa. Ecologic information according to Okada and McIntire (1979), Haq (1980), Aubry (1984), Winter et al. (1994), Monechi et al. (2000), Ćorič and Roegl (2004), Villa et al. (2008) with further references therein, and this paper.

bionts and inhabit the photic zone of oligotrophic environments (Hallock-Müller, 1985; Hallock, 1999; Hohenegger et al., 1999; Holzmann et al., 2006). Light penetration into the water column is limited by turbidity, which depends on fluvial influx of organic material and plankton density in shallow water environments (Hallock-Müller 1986, Renema and Troelstra, 2001). The depth distribution limits of single species of fossil LBF are mostly unknown, but an actuo-paleontological approach reduces such ranges significantly. The shallowest depth for a test to survive is given by a relation between test shape and hydrodynamics (Briguglio and Hohenegger, 2011), while the deepest depth for an individual to survive is influenced by the light dependency of the hosted symbionts which vary among species (Holzman et al., 2006). Normally, nummulitids prefer quiet environments where they can increase the surface/volume ratio and host the highest number of symbionts within their test. The high abundance of nummulitids in the lower part of the section indicates optimal conditions for LBF and most probably a quiet and restricted environment that let such "opportunistic" K-strategists flourish. This hypothesis is supported by relatively low species diversities and by the presence of tests with signs of extremely fast growth rate (multi-spiral growth, Ferràndez-Cañadell, 2012). Such biological behaviour, quite common in very large nummulitids (Schaub, 1981), fits with oligotrophic environments characterized by adequate light availability to permit very high photosynthetic rates of the symbionts. As no particular abundance of B-forms (Aigner, 1982, 1983) among the collected specimens has been noted, the outcrop probably does not represents a so called "nummulite bank". The succession of dominating genera fits well with existing schemes along depth gradients (e.g., Hottinger, 1983; Menkfeld-Gfeller, 1995; Hohenegger, 2004) and the estimated paleo-water depths derived from P/B-ratios. Dominance of *Assilina* in the lower Adelholzen Beds correlates with slightly increased depths (50-90 m). The assumed shallowing (50-60 m) during the middle Adelholzen Beds corresponds to the dominance of *Nummulites*. During deposition of the upper Adelholzen Beds, *Discocyclina* and *Asterocyclina* became more and more frequent, corresponding to successively increasing water depths (70-200 m).

7.5 Macrofossils

Paleo-water depth estimations of foraminiferal assemblages fit reasonable well with the inferred paleoecology of the identified macrofossils. Vogeltanz (1968, 1972) estimated the depth habitat for the crab species found at Adelholzen (*Harpactocarcinus quadrilobatus*) from beach to outer shelf environments and addressed the problem of postmortem transport. The depth ranges of modern *Spondylus* (bivalvia) reach from shallower than 50 to 100 m (e.g., Lamprell, 1987; Huber, 2010) or 350 m, respectively (Rützen-Kositzkau, 1999; Grill and Zuschin, 2001). No larger accumulations of *Spondylus* were found at Adelholzen and we therefore assume that single larvae settled on larger sediment particles or mollusc shells and grow up subsequently. Many *Spondylus* specimens of the brown marls at Adelholzen

exhibit thick, broadly flattened spines up to 40 mm long, pointing to warm paleo-water temperatures (> 20 °C) if compared with recent bivalves (e.g., Nicol, 1967). Extremely thick shells of articulated *Pycnodonte gigantica* and *Pycnodonte* sp. in the lower part of the section are typical features in shallow tropical water environments. This is supported by the depth range of the echinoid *Conoclypus* that lived in shallow water up to about 50 m (Mitrović-Petrović, 2002). The numerous shark and ray teeth (*Iago*, *Megacyliorhinus*, deep water cat sharks) of the brown marls point to a warm tropical sea and paleo-water depths deeper than 80 m (F. Pfeil, pers. comm. 2012).

8. Discussion

We applied some mathematical calculations for paleo-water depth, flux of organic carbon to the sea floor, or pPP that give exact numerical values. However, it must be noted that such values result from a mathematical model but each certain value does not necessarily represent the actual value as it was in the past. It only represents an approximation expressed as a number, which can be used for further calculations. For example, the underlying method for the paleo-water depth estimation (van der Zwaan et al., 1990) is not exact in that the correlation of paleo-water depth to certain P/B-ratios has certain intervals of confidence that define possible respective ranges of variation. That is to say that the plausibility for each single value must be corroborated by additional evidence.

8.1 Application of planktic to benthic foraminifera-ratio to a Middle to Late Eocene record

The application of the P/B-ratios has widely been used for the calculation of paleo-water depths of normal marine, oligotrophic Neogene settings. At the same time, the applicability of the modern planktic to benthic relation to pre-Neogene records is considered problematic for various reasons (e.g., limited bentho-pelagic coupling, see e.g., van der Zwaan et al., 1999). There are different lines of evidence for a fundamental change as early as at the Early to Middle Eocene transition: 1) beginning of divergence of average test size between low (temperate-subpolar) and high latitude (subtropical-tropical) planktic foraminiferal assemblages (Schmidt et al., 2004), 2) end of the Paleocene-Early Eocene super-greenhouse period with frequent hyperthermals (compare Zachos et al., 2001; Bijl et al., 2009), or 3) successive occurrence of planktic foraminiferal morphogroups similar to those dominating today's oceans (e.g., *Cassigerinella*, *Catapsydrax*, *Dentoglobigerina*, *Turborotalia*) combined with extinction of characteristic Paleocene to Early Eocene taxa during the Middle Eocene (e.g., *Igorina*, *Morozovella*, most *Acarinina* species; Pearson et al., 2006b). Based on these developments, we argue that the Middle to Late Eocene oceanic system and its foraminiferal faunas were closer to today's system than during the Early Eocene. We further argue that the P/B-ratio depth reconstructions can be applied to at least Late Eocene records with a similar reliability as they are applied to Neogene records.
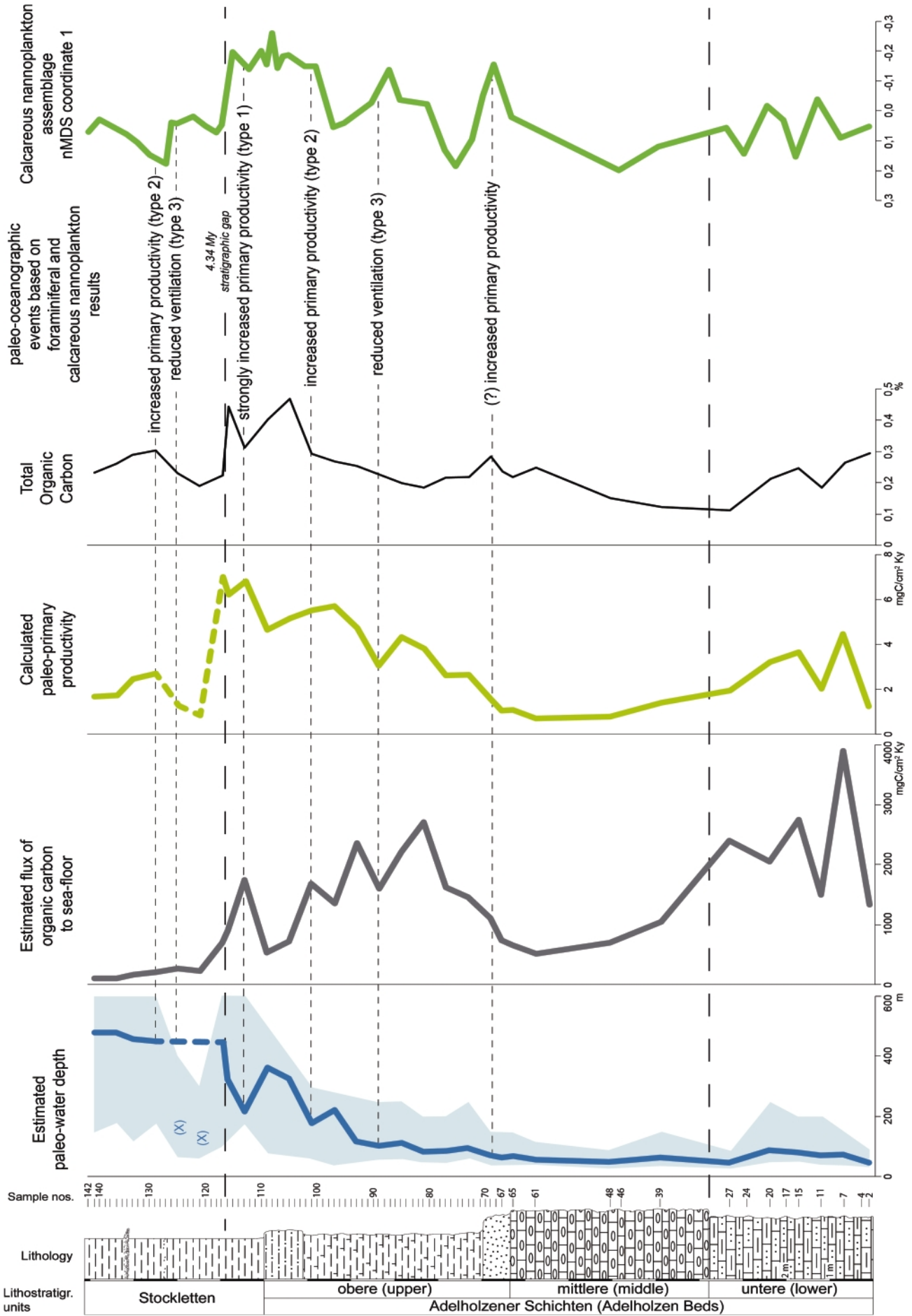
8.2 Changing paleo-water depths

Reconstructed paleo-water depths from percentages of planktic foraminifera and flux of organic carbon to the sea floor range from 50 m (middle neritic according to van Morkhoven et al., 1986) at the base of the section to 480 m in the Stockletten (upper bathyal; Fig. 10). The general transgressive trend is interrupted several times but only on a low magnitude. Maxima in paleo-water depth may reflect also planktic productivity peaks in some cases (see below) but minima are in good agreement with the stratigraphic positions of sequence boundaries (Lu3, Lu4; sea level lowstands) as indicated in Gradstein et al. (2004). However, the overall increase in paleo-water depth was driven by regional tectonics as the Helvetic Unit became influenced by the northward movement of the Alpine Chain (for a visualization see Darga, 1992).

The minimum percentage of planktic foraminifera, i.e., shallowest water depth in the middle Adelholzen Beds corresponds with maximum contents and accumulation rates of larger benthic foraminifera and attached taxa. This points to the highest light availability during this period and represents an advantage for symbiont-bearing taxa such as *Nummulites* or *Assilina*. The potential presence of sea-grasses is indicated by the high amount of attached dwelling (or clinging) genera such as *Neoconorbina*, *Asterigerinata*(?), and *C. lobatulus*. Macrofossil occurrences (oysters, spondylids, sea urchins) are largely in agreement with the depth interpretation of the Adelholzen Beds. The Stockletten occassionally yielded some specimens of the LBF and Attached group which seem to have been transported into the deep-water depositional environment.

In order to get an idea of the reliability of the estimated (calculated) paleo-water depths, we present the minimum and maximum water depths for each respective given P/B-ratio as published in van der Zwaan et al. (1990) for modern environments. This results in a quasi 'envelope of uncertainty' that confines the possible minimum and maximum paleo-water depths (Fig. 10). Our paleo-water depth estimations fall within this 'envelope' and therefore appear to be plausible within the limits of the applied method.

8.3 Stable isotope record

The values of stable O- and C-isotopes of bulk rock samples are considered to be altered by diagenetic processes with intensities of which we are unable to assess accurately. However,

Figure 10: Development of paleo-water depth, BFAR based organic matter flux to the sea-floor, BFAR based paleo primary productivity (pPP), relative distribution of Total Organic Carbon (TOC), foraminifera based paleoceanographic (bottom water oxygenation and productivity) events, and coordinate 1 of calcareous nannoplankton nMDS at Adelholzen. Lithology as in Fig.2. Bright blue area around the estimated paleo-water depth curve ('Envelope of uncertainty', see discussion for details) is based on modern minimum and maximum P/B-ratios for given water depths as published by van der Zwaan et al. (1990). X indicates calculated paleo-water depth values of ecologically 'disturbed' samples not considered for paleo-water depth estimates. Horizontal dashed lines indicate identified stratigraphic gaps.

we see some potential information in the dataset as outlined below. Consequently, we provide the data in the electronic supplements to facilitate evaluation and further discussion.

For the Middle to Late Eocene interval, a general cooling trend would be expected (successively heavier δ^{18}O-values, see supplementary Fig. S1). This trend is only apparent in the Stockletten and an opposite trend is indicated for all other periods, pointing to diagenetic alteration of these rocks.

The cold water indicator *C. pelagicus* exhibits low relative abundances at the transition from the marly brown sands (uppermost Adelholzen Beds) to the Stockletten. The measured lightest δ18O-values occur in the same interval of the section. Although these measured values may not represent those in equilibrium with the ambient sea water, this phase can nevertheless represent the warmest phase of the Adelholzen record. Thus, we assume a, probably regional, climatic optimum for the respective time interval (i.e., at the transition from the Upper Adelholzen Beds to the Stockletten). This interpretation also fits well with the increased pPP directly after the assumed temperature maximum as outlined below. Speculatively, the δ^{18}O-values of the transition from marly brown sands of the Upper Adelholzen Beds to the Stockletten may indeed be more reliable than apparent from direct comparison with the global composite record (Fig. S1).

8.4 Changing paleo-productivity, stratification, and oxygenation

The interconnections between interpreted stratification or mixing of the water body and oxygenation at the sea-floor, as well as calculated paleo-primary productivity at the ocean surface derive from a number of proxies. This includes PFARs, BFARs, calcareous nannofossil assemblages and statistic parameters, TOC as well as organic matter flux to the seafloor and pPP. All these parameters show strong fluctuations along the Adelholzen Section.

Figure 8 shows similar curves for planktic and benthic foraminiferal accumulation rates, emphasizing the bentho-pelagic coupling. The highest planktic foraminiferal accumulation rate was reached shortly after an assumed climatic optimum (lightest δ^{18}O-values) at the base of the Stockletten (zones E11, NP16). We conclude that the planktonic system benefitted from increased vertical mixing and subsequent nutrient supply caused by the cooling after the assumed climatic optimum. Different to planktic foraminifera, the benthic foraminifera show their highest accumulation rates in the lower part of the marls with *Discocyclina* (middle upper Adelholzen Beds). Food supply to the seafloor (organic export production) was probably enhanced in this oligotrophic environmental setting (low percentages of *C. pelagicus*, Fig. 8), possibly because of the proximity to land at the time of deposition. The generally high content of epifaunal benthic foraminiferal taxa (63-98% in the Adelholzen Beds, 21-74% in the Stockletten) underlines the high oxygenation level at the seafloor.

All samples from the section contain very rich calcareous nannoplankton assemblages with dominance of small reticu-

lofenestrids, *R. dictyoda* and *C. floridanus*. Small reticulofenestrids generally dominate nannoplankton assemblages along continental margins and high amounts of *R. minuta* can be interpreted as indicative of a warm, well stratified water column. Low percentages of *C. pelagicus* point to even more oligotrophic paleo-environments and are in good agreement with the foraminiferal interpretations. The cluster analysis distinguished between four major assemblages that mainly reflect the successive transgressive stages. Furthermore, the correlation between the calculated BFAR-derived pPP with the coordinate 1 of nannoplankton nMDS and TOC is obvious (Fig. 10). The rough coordinate 1 trend (Fig. 10, rightmost collumn) starts with generally positive values (except basal upper Adelholzen Beds), became most negative in the top upper Adelholzen Beds and the basal Stockletten, and finally turned back to positive values during deposition of middle to upper Stockletten. pPP and nMDS-values run largely parallel and indicate that nannoplankton assemblages as well as BFAR represent surface nutrient conditions.

The comparison of the above listed results points to at least five "events" in the upper half of the Adelholzen Section (Fig. 10) that were related to paleoceanographic changes and resulted in characteristic planktic and benthic foraminifera and calcareous nannoplankton assemblages. The main parameters that governed the assemblages were nutrient supply for primary producers as well as for consumers, stratification, and related oxygenation of bottom waters. The first event happened in the middle part of the Upper Adelholzen Beds within the marls with Discocyclina around sample AH-89, the second occurred in the upper part of the Upper Adelholzen Beds at the transition from the marls with Discocyclina to the marly brown sands around sample AH-101, the third is the most prominent and is located in the basal Stockletten shortly before the stratigraphic gap at sample AH-113, the fourth happened in the middle part of the Stockletten (AH-125), and the last one a little further up-section (AH-129). These "events" may be subdivided into three different types:

1) Type 1 is characterized by strongly increased planktic and benthic accumulation rates, high percentages of *C. pelagicus*, and relatively low percentages of *R. minuta*. In this case, increased amounts of nutrients in surface waters enabled primary producers such as *C. pelagicus* to thrive and resulted in extraordinary high planktic foraminiferal accumulations rates. Since the stratification indicator *R. minuta* occurs only with moderate (comparatively low) percentages, good vertical mixing of nutrient enriched deeper (bottom?) water with surface waters took place. As a consequence, also benthic foraminiferal accumulation rates increased moderately but distinct (Fig. 8), and productivity indicators reached higher percentages (Turrilinids, Uvigerinids; Fig. 5). This "event" is the strongest productivity change in the investigated record. It happened directly after the climatic optimum phase (sample AH-113) and may be interpreted as a response (increased vertical mixing with subsequent increased nutrient supply after cooling) to the breakdown of

the stable conditions (stratified water column) during the assumed climatic optimum phase before.

2) The second type is characterized by moderate increase in planktic and benthic accumulation rates and percentages of *C. pelagicus*, and relatively low percentages of *R. minuta*. This type is similar to Type 1 but is less pronounced, in particular with respect to the increases in *C. pelagicus* and planktic foraminiferal accumulation rates. Furthermore, relatively high contents of Gyroidinoids and Lenticulinids point to well oxygenated bottom waters during these phases of moderately increased surface productivity. This pattern has been observed at two levels: samples AH-101 and AH-129. A sample from the level below AH-129 (AH-125) is also characterized by extremely low accumulation rates and high percentages of agglutinated taxa, particularly pointing to perturbations of the deeper parts of the water column.

3) Contrary to the first two types, the third type is characterized by coeval decrease in planktic and benthic accumulation rates, relatively low or minimal contents of *C. pelagicus*, and of increased or maximal contents of *R. minuta*, respectivly. In this case, low surface productivity is combined with stratification and results in accordant assemblages that indicate slight oxygen deficiency at the sea floor (increased contents of Bolivinids, Turrilinids, reduced contents of Gyroidinoids, Lenticulinids). These conditions prevailed around samples AH-89 and AH-125.

In addition to the five events, a possible sixth one marks the beginning of the increase in foraminiferal accumulation rates and derived parameters. This is accompanied by a strong negative nMDS coordinate 1 value, slight TOC increase, and an increase in planktic *Pseudohastigerina* percentages, but no significant changes in the benthic assemblages (Figs. 5, 8, 10). Therefore, we added a question mark for this level (glauconitic sands) in Fig. 10. It may just indicate the acceleration of the deepening.

We conclude that increased vertical mixing of the water column provided nutrients for increased foraminiferal ARs and pPP (sample AH-129) after a phase of stagnation with very low pPP and oxygen depletion at the sea floor (sample AH-125) in the early Priabonian. Similarly, a lack of vertical mixing was apparently responsible for decreased foraminiferal ARs and pPP at some stage during deposition of the upper Adelholzen Beds (AH-89).

8.5 Supraregional context

By global comparison, the reported changes of foraminiferal assemblages, organic flux, and pPP can be interpreted as the regional "shallow" site expressions of eccentricity paced and comparatively modest hyperthermals. Sexton et al. (2011) report a number of such events from the Middle Eocene. These showed more rapid recoveries of the carbon cycle than the extreme Lower Eocene hyperthermals (e.g., Paleocene-Eocene Thermal Maximum with massive release of greenhouse gases; Zachos et al., 2008; Bijl et al., 2009; Stap et al., 2010) and were related to different driving mechanisms (surficial carbon redistribution) similar to younger periods. However, the tempo-

ral resolution at Adelholzen is too low to verify this hypothesis.

Our findings show, to a certain degree, the global influence for the environmental changes at the northern margin of the Tethyan Ocean: increasing relative abundance of cold or deep water inhabitants (*C. pelagicus* among calcareous nannofossils, *Subbotina* spp. among planktic foraminifera) correspond to the general cooling during the Middle to Late Eocene. However, regional subsidence and periods of vertical mixing or stratification apparently modified the global trends and became more important for the specific conditions that resulted in the sedimentary succession and the fossil assemblages found in Adelholzen.

9. Conclusions

- The sedimentary record of the Adelholzen Section covers large parts of the Lutetian and Priabonian Stages, while the intermediate Bartonian Stage is completely missing. This 4.34 My stratigraphic gap within the Stockletten encompasses large parts of planktic foraminiferal zone E11, the entirety of E12, and large parts of E13 or the upper part of nannoplankton zone NP16 and the entire NP17. Analysis of subsequent foraminiferal assemblages indicates stressful environmental conditions that may point to dysoxic conditions in the lower parts of the water column.
- Deepening started during deposition of the upper Adelholzen Beds (E10, NP15c) and culminated in the Stockletten (E14/15, NP20). Calculated paleo-water depth estimates range from 50 m (middle neritic) near the base of the section to 480 m in the Stockletten (upper bathyal). Larger benthic foraminifera indicate the light exposed portion of the Adelholzen Section. Macrofossils found in the lower to upper Adelholzen Beds confirm the paleo-water depth estimates.
- Peaks in planktic and benthic foraminiferal accumulation rates point to periods of increased pPP. The most prominent event at the base of the Stockletten was shortly after the assumed climatic optimum phase during the deposition of the marly brown sand. Planktic assemblages were dominated by oligotrophic *Acarinina* with increasing amounts of meso- to eutrophic *Pseudohastigerina*, *Parasubbotina*, and *Globorotaloides*. Benthic assemblages show gradual changes with increasing paleo-water depth from typical shallow water assemblages with nummulitids towards deep water assemblages with uniserial taxa and infaunal genera. Relative peaks of low-oxygen tolerant opportunistic taxa indicate periods of reduced oxygen supply and, in combination with increased ARs, periods of high food supply.
- The results of the statistical analyses of calcareous nannoplankton assemblages reflect the successive stages of vertical mixing, nutrient availability, possibly paleotemperatures, and pPP. They are in good agreement with the results obtained from foraminiferal assemblages.
- Calculated pPP was low during deposition of the lower and middle Adelholzen Beds, increased in the upper Adelholzen Beds and reached peak values in the lower Stockletten (late Lutetian). The values correspond to those of the cen-

ters of modern tropical-subtropical anticyclonic gyres. Consequently, we interpret the entire section at Adelholzen as a highly oligotrophic succession.

- The combination of assemblage composition, accumulation rates, and derived parameters (C-flux, pPP) enabled the identification of several distinct paleoceanographic events. The changes affected nutrient availability, food supply, and bottom water oxygenation in different ways and may possibly be related to modest hyperthermals with surficial carbon redistribution mechanisms.

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Holger GEBHARDT[1)*)], Stjepan ĆORIĆ[1)], Robert DARGA[2)], Antonino BRIGUGLIO[3)], Bettina SCHENK[1)], Winfried WERNER[4)], Nils ANDERSEN[5)] & Benjamin SAMES[1)3)]

[1)] Geologische Bundesanstalt, Neulinggasse 38, A-1030 Wien, Austria;

[2)] Naturkundemuseum Siegsdorf, Auenstr. 2, D-83313 Siegsdorf, Germany;

[3)] Universität Wien, Institut für Paläontologie, Althanstraße 14, A-1090 Wien, Austria;

[4)] Bayerische Staatssammlung für Paläontologie und Geologie und GeoBioCenterLMU, Richard-Wagner-Str. 10, D-80333 München, Germany;

[5)] Leibniz Laboratory for Radiometric Dating and Stable Isotope Research, Christian-Albrechts-Universität Kiel, Max-Eyth-Str. 11, D-24118 Kiel, Germany;

[*)] Corresponding author, holger.gebhardt@geologie.ac.at