# COCCOLITHOPHORID EVOLUTIONARY BIODIVERSITY AND ECOLOGY NETWORK

## CODENET

TMR Network ERBFMRX CT97 0113

Final Report

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**CONTENTS**

## 1. RESULTS OF THE NETWORK

### 1.1 INTRODUCTION

Coccolithophorids form a major component of the oceanic microplankton and consequently are of great interdisciplinary interest. For marine biologists, they are one of the main open ocean primary producers. For biogeochemists, they play key roles in the global carbon, carbonate and sulphur cycles For marine geologists, coccoliths constitute the single most important component of deep-sea oozes and chalks and provide key floral, isotopic, and biomarker signals for interpreting global change in the geological record. For palaeontologists, their exceptional fossil record makes them an outstanding biostratigraphic group and gives them unusual potential for testing evolutionary hypotheses.

This convergence of interests has meant that coccolithophorids are the subject of intensive research, however, most research has focussed on application of coccolithophorid to solve problems, whist many fundamental aspects of their biology have been understudied. The CODENET network project was designed to redress this balance, on the one hand we aimed to exploit the very extensive knowledge of coccolithophorids to address broad questions such as the pattern of evolution in phytoplankton. On the other hand we aimed to refine knowledge of the phylogeny and ecology of the group to provide basic scientific understanding to inform research applications of the group in oceanography, palaeoceanogrpahy and global change research.

The project had a basic four dimensional structure (figure 1) with 8 research teams* carrying out co-ordinated research on 6 key species spanning the evolutionary biodiversity of coccolithophorid focussed on 15 discrete research tasks contributing to 3 work areas. Network efficiency was provided was provided by the common focus on selected species which lead to maximal use of cultures and sharing of samples. Network effectiveness was provided by synthesis of results from disparate research tasks to solve larger questions in the three work areas. In this report the research undertaken is first reviewed by research task, then selected highlights are discussed in more depth, finally we review the degree to which the objectives given in the proposal have been met in each research area.

* The eight initial teams included several participants from other laboratories (e.g. University College London participants in the NHM team, U. Erlangen participants in the AWI team and U. Milano participants in the VUA team). Subsequently the CODENET project was extended by agreement to include participants from,, U. Bremen (K-H Baumann, B. Boeckel, C. Sprengel) and U. Oviedo (H. Stoll). These participants carried out research directly focussed on the project attended workshops, including the mid term review, contributed to joint publications, and acknowledged CODENET in their work. Contributions from these teams are included in this report.

### 1.2 SUMMARY OF RESEARCH UNDERTAKEN, BY RESEARCH TASK

See also figure 2 for an indication of personnel involved in each task and total number of man months committed by each team.

**RT1. Culture isolation and maintenance (U. Caen, NHM, ETHZ)**

The core objective here was to isolate 5-10 strains of each of the key species. This was significantly exceeded with a total of 178 strains of these species isolated and an additional 61 strains of 10 other species, several of which had never previously been isolated. The U. Caen team played the lead role here but were assisted by virtually all teams, notably NHM, ETHZ, CSIC, and MNHN-UL. Culture material from the CODENET collection and previous work (Algobank collection) was provided by the U. Caen team to all participants underpinning a very wide range of research. Culture maintenance was primarily carried out at U. Caen with back-up collections held at ETHZ (1998-9) and NHM (1999-2001).

NB CODENET species isolations: *G. oceanica* - 67 strains + sister taxon *E. huxleyi* (33 strains, 2 varieties); *C. leptoporus* - 65 strains inc. large, ?large and intermediate morphotypes + sister taxon *O. fragilis* (21 strains); *C. pelagicus* 17 strains inc. temperate and arctic varieties; *H. carteri* 12strains inc. *H. c. carteri* and *H. c. hyalina* varieties; *S. pulchra* 14 strains inc *S. p. pirus* and *S. p. oblonga* varieties; *U. sibogae* 4 strains inc. *U. s. sibogae* and *U. s. foliosa* varieties + sister taxon *U. hulburtiana* (1 strain).

**RT2. Life-Cycle study (U. Caen, CSIC, NHM, ETHZ, AWI)**

This was a key success area of the project with major breakthroughs from both culture studies of life-cycle transitions and field observations.

Induction of life-cycle changes proved elusive despite extensive experimentation at U. Caen. However, constant monitoring of the growing culture collection enabled identification of cultures spontaneously undergoing phase changes in 4 of the 6 CODENET species and one other species. These allowed key observations on the life-cycle pattern and process to be made. Critically, flow cytometry (NIOZ) and nuclear staining experiments (U. Caen) confirmed that the alternate heterococcolith and holococcolith bearing phases are respectively haploid and diploid. Unexpected complimentary field observations of "combination coccospheres", bearing both holococcoliths and heterococcoliths, provided a rich source of additional data on life-cycle associations. Numerous publications have featured this work (Cros et al. 2000, Sprengel & Young 2000, Cortes et al. 2000, Renaud & Klaas 2001, Geisen et al. subm, Cortes & Bollmann in press, Cros in prep).

**RT3. Molecular genetics (AWI)**

This research task involved four discrete sub-tasks.
A. Plastid genome studies - testing of hypothesis of abnormally large genome based on observations of *Isochryis galbana*. This challenging hypothesis was rigorously tested, and ultimately disproved (Saez et al 2001).
B. Broad scale phylogenetic studies using slow evolving genes. The success of the culture isolation program (RT1) allowed this project to exceed objectives with the first multi-species molecular phylogeny of coccolithophorids being created. This has yielded a rich data set to refine knowledge of evolutionary relationships and a framework for interpreting much other data. In combination with geological data (RT15) it has yielded remarkably promising molecular clock data.
C-D Fine-scale phylogenetic studies using fast evolving genes. Some significant problems were encountered in this area (e.g. with microsatellites) and ultimately only a sub-set of the planned approaches proved productive. The successful techniques (tufA, ITS) have, however, produced excellent results and in combination with other studies drastically revised our conception of genotypic variation in coccolithophores.

**RT4. Lipid biomarker composition and palaeothermal calibration (NIOZ) and other palaeoproxies (VUA, U. Oviedo)**
Work on the long-chain alkenone biomarkers synthesised by coccolithophores compromised three main components, broadly as planned. (1) Survey of occurrence and variability of the biomarkers across coccolithophorid biodiversity, using the full range of species available in the COENET and Caen cultures. (2) Testing/calibration of the $U_k^{37'}$ palaeothermometer using material from culture experiments (RT9), cruisework (RT11) and other selected sample sets (RT12-14). (3) Investigation of the alkenone biomarker as a maximally constrained compound for reconstruction of palaeo CO2 levels from carbon stable isotopes.
The suitability of the CODENET framework for this type of palaeoproxy testing rapidly became evident and so three further geochemical palaeoproxies, all on coccolith carbonate were studied (1) oxygen and carbon stable isotopes (VUA) (2) Mg/Ca ratios - a potential palaeothermometer (VUA); (3) Sr/Ca ratios, a potential indicator of palaeoproductivity (U. Oviedo). Each of these proxies was investigated using a combination of culture, oceanographic, and geological samples. Key to this was the fact that the culture experiments were already being carried out by partners in the project and that special oceanographic sampling was carried out by other partners in the network (geological sample sets are relatively easy to obtain and consequently are often the only ones used). Results publication include Stoll et al. (in press a-c), Ziveri et al (in prep.) In parallel much experimentation was carried out to develop a methodology for separating specific coccolith fractions from sediment samples (Stoll & Ziveri, in press).

**RT5. Photosynthetic pigment studies (CSIC)**
High Performance Liquid Chromatography (HPLC) analysis of pigment composition is used in oceanography as a tool for estimating the biomass and taxonomic composition of phytoplankton populations. It hence is an oceanographic proxy analogous to the palaeoproxies analysed in RT4. Kees van Lenning, the YVR at CSIC worked primarily on this task.
The main sub-projects were (1) Refinement of analytical protocols (Latasa et al. 2001); (2) Application and refinement of *Chemtax* technique using large data sets of oceanographic samples. (3) Survey of pigment composition across coccolithophorid diversity (van Lenning et al. in prep a,b). In total the distribution of 24 pigment types was mapped out in 92 culture strains resulting in recognition of a complex interplay of phylogenetic and ecological factors in determining pigment composition.

**RT6. Coccolith ultrastructure analysis (NHM)**
High Resolution Scanning Electron Microscopy, Atomic Force Microscopy (Henriksen et al. in prep.) and analytical Light Microscopy have been used to produce revised models of the ultrastructure and crystallography of the coccoliths of the CODENET species and other key taxa. This has lead to reassessment and refining of biomineralisation models (Young et al. 1998) and of morphology based taxonomy.

**RT7. TEM fine structural studies (U. Caen)**
Cytological studies were carried out on the CODENET species and additional key species isolated for the first time, notably *Algirosphaera robusta* (a species which shows very unusual features especially related to biomineralisation - Probert et al. in prep.). These studies combined with critical literature review allowed a range of key cytological characters to be mapped out against phylogeny. They also underpin contributions of the U. Caen team to life-cycle studies.

**RT8. Phylogenetic synthesis (NHM, AWI, U. Caen, CSIC)**
This task was always to be the last stage of the research and is in fact still in hand. To facilitate this the AWI team has been able to extend employment of the YVR Alberto Saez for 9 months beyond the end of the contract, using institutional resources. Synthesis work includes (1) integration of data from molecular genetics, morphology and palaeontology to produced a revised classification of the coccolithophorids (see also RT16 below) - broadly speaking molecular genetic data has confirmed the family and generic level groupings of the traditional taxonomy but provided much new data on the relationships between them. (2) Mapping out of cytological, biomarker and pigment characters to distinguish ecological adaptations from

stable phylogenetic characters. This has revealed evidence of a previously unsuspected pattern of convergent evolution toward open ocean adaptation. (3) Derivation of a molecular clock from integration of molecular genetic and palaeontological divergence time estimates.

**RT9. Physiological characterisation (NHM, ETHZ, U. Caen, MNHN-UL, CSIC)**
Growth experiments were carried out on all the CODENET species to determine variability in growth rates and temperature tolerances and provide samples for other studies. Experiments were carried out at ETHZ (*G. oceanica* and *C. leptoporus*), U. Caen (most species), NHM - in collaboration with U. Caen and MNHN-UL (*S. pulchra, C. pelagicus, C. leptoporus, U. sibogae, H. carteri*). Samples from these experiments were used for RT4 (NIOZ, VUA, U. Oviedo), RT5 (CSIC) and RT10 (NHM, ETHZ, MNHN-UL). These experiments are labour intensive and proved valuable as training exercises, with at each site students being involved (e.g. Alexandra Duarte Silva MNHN-UL; Aude Houdan U. Caen; Daniela Schmidt ETHZ; Blair Steel NHM,).

**RT10. Morphological work on cultured samples (NHM, ETHZ, MNHN-UL)**
Morphometrics was used to analyse variation In coccolith morphology in the samples grown in culture. Approximately 20->100 samples were analysed per species with the basic data set comprising: (1) Single samples grown under approximately uniform conditions (17C, early log phase, nutrient saturated medium) from all isolated strains. (2) A large suite of samples from 2-3 strains grown under varying conditions. Sub-task distribution: NHM + MNHN-UL *C. pelagicus*; NHM - *U. sibogae, H. carteri* and *S. pulchra*. ETHZ *C. leptoporus* and *Gephyrocapsa*. A key general conclusion was that culture conditions has remarkably little effect on coccolith morphology, and especially on morphometric parameters.

**RT11-14, sample-based studies**
These research tasks differ from those above in that they are based on oceanographic and geological samples sets rather than algological cultures. Most of the teams have long experience in work on this type of sample set and indeed a prime aim of the CODENET project was to carry out fundamental research to underpin such activities. Within these areas our research can be approximately classified into two types of projects: (a) focussed communal projects involving limited sets of key samples studied by researchers from many teams. These were used particularly for methodology development, palaeoproxy calibration and study of intraspecific variation. (b) Individual projects, primarily carried out by research students, and often at least partially in the context of other programmes. These projects provided much data and insights for the CODENET project. In addition the CODENET project was able to greatly extend its training role through interaction with an extended family of young researchers who gained an insight into multidisciplinary research at a European level they might otherwise have missed, not least through participation in workshops. Finally many CODENET YVRs were involved in supervising such projects giving them valuable teaching experience. NB (1) Only students directly affiliated to a CODENET team and doing directly relevant research are noted below, although several other students contributed to and benefited from the network. (2) Conservative estimates of man month contributions of these students are included in the tables. (3) Other student projects were based on the culture-based research tasks, as noted above.

**RT11. Study of plankton assemblages - ecological characterisation (NHM, ETHZ, VUA, CSIC, MNHN-UL)**
Communal studies: Two short cruises were arranged by the MNHN-UL team for the CODENET project. These provided an initial communal sample set, allowed intercalibration of counting methodologies (Bollman et al. in press) and allowed us to establish a set of sampling protocols for combined collecting for alkenones (RT4), pigments (RT5), coccolith carbonate (RT4), coccolith assemblages (RT11) and cultures (RT1). Subsequently this approach was applied by smaller teams on a succession of cruises.
Individual research projects:
Lluisa Cros (PhD CSIC) Coccolithophorid ecology in the NW Mediterranean..
Mara Cortes (PhD, ETHZ) Coccolithophore ecology at the HOT station ALOHA, Hawaii.
Alexandra Duarte-Silva (MNHN-UL) Coccolithophore assemblages off Lisbon,
Marc Hockfield (MSc UCL/NHM) *Emiliania huxleyi* blooms.
Elisa Malinverno (PhD Milano/VUA) Productivity and vertical distribution of coccolithophores in the Ionian Sea.
Emma Williamson (MSc UCL/NHM) Coccolithophorid ecology in the Alboran Sea (MATER samples).

**RT12. Sediment trap studies - flux rates and seasonal succession (VUA, ETHZ,U. Bremen)**
Communal studies: The VUA team made available sample sets from selected sediment traps for integrated analysis of intraspecific variation and palaeoproxy testing. In particular samples from offshore Somalia were used for an integrated study involving virtually all teams (Ziveri et al in prep). Methodology papers included Young & Ziveri (2000), Ziveri & Young (1999).
Individual research projects:
Claudia Sprengel (PhD and subsequent PostDoc, U. Bremen) Coccolith calcite fluxes in the Canaries area (CANIGO project).
Alexandra Broerse (PhD VUA) Coccolith calcite fluxes in selected sediment traps and estimation of global coccolith fluxes (GEM project).
Ali Bairbakhish, (Diploma ETHZ), Analysis of coccolithophores in oceanic sedimentary trap samples: from HOT (Hawaiian Ocean Time-series station).

**RT13. Holocene sediment samples - global biogeography (VUA, ETHZ, MNHN-UL, U. Bremen).**
Communal studies: (a) The ETHZ group selected a set of well constrained samples for this task, they were prepared, in parallel with the geological sample set at a series of workshops held in ETHZ during 1998 and distributed them to other teams for morphometric analysis. Joint experiments on quantitative preparation peparation techniques at these workshops lead to two papers, Bollmann et al. (1999) and Geisen et al. (2000). (b) The VUA team compiled a database of published and unpublished Holocene assemblage analyses to review biogeography of the species (Ziveri et al. in prep.).
Individual research project:
Babette Boeckel (PhD, U. Bremen) Holocene coccolithophore assemblages in the South Atlantic (including morphometric study of CODENET species).

**RT14. Geological sample studies - microevolution and ecological response (NHM, ETHZ, VUA, MNHN-UL, U. Bremen).**
Communal studies: As with the Holocene samples a communal sample set was identified and selected by the ETHZ team (in collaboration with the NHM team), prepared at the ETHZ workshops and distributed between the participants. The sampling was based on a time slice approach with samples being selected from 8 ODP sites at 0.5Ma spacing covering the Pliocene and Pleistocene. These provided an overview of geological variability for direct comparison with the patterns of extant variability.
Individual research projects:
Barbara Balestra (PhD Firenze/VUA) Coccolithophorid paleoceanography in the Denmark Strait. (teams VUA, NIOZ).
Babette Boeckel (PhD, U. Bremen) Coccolithophore flux and assemblage development in the South Atlantic in the Late Pleistocene 150 ka (including morphometric study of CODENET species)
Samantha Gibbs (PhD U. Cambridge/NHM) Coccolithophore palaeoceanography in the Late Pliocene (including microevolutionary study of *C. leptoporus*).
Jorijntje Henderiks, (PhD, ETHZ) Last Glacial-Interglacial Paleoceanography of the Eastern Boundary Current System, Canary Islands Basin. (including biotic palaeoproxy development for *C. leptoporus* and *Gephyrocapsa*)
Anna Lototskaya (PhD VUA) N. Atlantic climate change 150,00-1000,000 years BP.
Aurea Narciso (Masters, MNHN-UL) *Coccolithus pelagicus* morphological variation in the last 4Ma (including contribution to the communal study of *C. pelagicus*).

**RT15. Macroevolutionary studies - divergence times of the lineages (NHM, ETHZ).**
Database analyses (ETHZ) and critical review of the literature (NHM) have been used to provide maximally constrained palaeontological estimates of divergence times.

**"RT16" Synthesis and revision of the taxonomy of extant coccolithophorids (NHM, ETHZ, VUA, CSIC, AWI).**
This additional research task was not in the proposal but was undertaken for the following reasons (1) Our research on life-cycles, phylogeny and intra-specific variation have all had taxonomic implications - forcing revisions of the previous, rather well-established taxonomy. (2) Detailed study of plankton samples, by the CSIC team in particular, lead to recognition of numerous undescribed species. (3) The network teams included a high level of taxonomic expertise (notably Annelies Kleijne VUA, Lluisa Cros CSIC) and the network framework provided an ideal structure for communal work on taxonomy, also involving participants from U. Copenhagen and U. Tubingen. (4) It became increasingly apparent from the experiences of the many researchers in RT12-14 that the existing literature was difficult to use and constituted a barrier to wider research. So a workshop was organised in Amsterdam in Oct 1999 on coccolithophorid taxonomy and subsequently the relevant enthusiasts got together regularly at CODENET meetings. Outcomes have included EMIDAS, an online WWW image reference collection (http://www.emidas.ETHZ.ch), preparation of an Atlas of Mediterranean Coccolithophores (Cros & Fortuno in press), a Guide to Extant Coccolithophore Taxonomy (Young et al. in prep. - and draft copies have been used as a working identification manual) and several specialist papers (Cros 2000, Kleijne et al. in press, Ostergaard et al. in prep.)

## 1.3 SELECTED SCIENTIFIC HIGHLIGHTS

### A. EVIDENCE FOR HAPLO-DIPLONTIC LIFE-CYCLES CHARACTERISED BY DISCRETE BIOMINERALISATION MODES

**Background:** There are two basic types of coccoliths, holococcoliths and heterococcoliths, with very different ultrastructures, reflecting significantly different biomineralisation modes (e.g., Young et al. 1999). Because coccolithophores are classified primarily by coccolith morphology, this differentiation has been used as a major classification criterion; Jordan & Green (1994) list 123 heterococcolithophorid species in 13 families and 65 holococcolithophorid species in a single family. However, holococcolith and heterococcolith stages are known to occur in the life-cycle of *Coccolithus pelagicus*, from classic observations of Parke & Adams (1960), subsequently confirmed by other work. Detailed life-cycle observations were only available from a very few haptophytes, none of which form holococcoliths. Synthesising this data Billard (1994) suggested that haplo-diplontic life-cycles were pervasive in haptophytes, that organic scale morphology was indicative of ploidy stage and that heterococcoliths and holococcoliths were possibly formed on diploid and haploid stages, respectively. Testing these hypotheses and exploring their implications was a key objective of the CODENET project (figure 3).

**New observations:** A wealth of new data on life-cycles, unexpectedly, came from work on plankton samples by Lluïsa Cros (CSIC Barcelona). She observed numerous combination coccospheres containing both holococcoliths and heterococcoliths, which we interpret as recording a transition between life-cycle phases. More than a dozen consistent pairings of holococcolith and heterococcolith "species" have now been observed, coming from 5 different heterococcolith families, and including 4 of the CODENET species. These results are documented and discussed in a paper with authors from three other CODENET teams (Cros et al. 2000). Further examples have also been found both by Cros and other CODENET workers (Young et al. 1999, Sprengel & Young 2000, Cortes & Bollmann in press, Cros & Fortuno in press, Geisen et al. subm).

The culture studies of life-cycles was somewhat inhibited by an inability to induce phase changes. Extensive experimentation by Ian Probert and Aude Houdan (PhD student) of the Caen team failed to reveal any triggers for phase changes. However, continuous monitoring of cultures at U. Caen and the NHM resulted eventually in detection of phase changes in 5 species (*Coccolithus pelagicus, Gephyrocapsa oceanica, Calcidiscus leptoporus, Syracosphaera pulchra* and *Coronosphaera mediterranea*) including 4 of the CODENET species. These observations confirmed and extended the independent observations from the field samples. These cultures were further used to examine the process of phase transition, and to test the ploidy level hypothesis. This was done first using first by using nuclear staining and semi-quantitative light microscope observations then by flow cytometry (at NIOZ, in collaboration with Hanno Kinkel). This confirmed that the holococcolith phase has half the DNA content of the heterococcolith phase.

Culture experiments were then conducted, at U. Caen, to investigate physiological differentiation of the phases within single species and determine trophic modes. These showed that the hapld phase is lower growing and mixotrophic, i.e. able to both photosynthesise and ingest particulate organic matter. We hypothesise that this is an adaptation to low nutrient conditions.

**Implications:** This work has radically changed our basic understanding of coccolithophorid biology, some obvious implications include: (1) Taxonomy and Biodiversity - the species-level taxonomy of coccolithophores has been progressively revised as new combinations were found. This also prompted review of the taxonomic significance of different aspects of holococcolith morphology and ultrastructure. (2) Ecology and Physiology - the widespread occurrence of this life-cycle type indicates that it must be ecologically adaptive and indeed an essential part of their ecology. We are reviewing distribution of holococcolithophores vs. heterococcolithophores in general and of the pairings indicated by combination cells in particular. Initial results suggest the holococcolithophores are living in shallower and more oligotrophic waters and so that the life-cycle may be a nutrient/energy resource exploitation strategy. (3) Macroevolution - the distribution of holo-hetero life-cycles across coccolithophorid phylogeny can be reviewed using both classic stratophenetic data (Young et al. 1999) and new molecular genetic data (unpubl. work of Medlin & Saez and of collaborators in Tsukuba). Both analyses suggest that the families with this life-cycle type had a common origin close to that of the coccolithophores (Late Triassic, ca 230Ma). Evidently discrete calcification modes have been maintained in the two life cycle phases over a very long period. However, calcification is itself a clear characteristic of the coccolithophores, suggesting that in part it is likely that it occurs by common molecular genetic and biochemical pathways in the two phases. This poses interesting questions about the nature of evolution in organisms with haplo-diplontic life-cycles.

In all three of these areas our work has both produced significant advances in understanding and opened up promising new fields for future research.

**B. MOLECULAR PHYLOGENY AND MOLECULAR CLOCK**

The prime focus of molecular genetic work in the latter part of the project, by Alberto Saez (AWI), was investigation of the phylogenetic relationships of coccolithophorids, using the culture collection developed during the project. For this work one or a few strains of all available coccolithophorid species have been studied. Two genes have been sequenced for most strains; 18S rRNA which is the prime gene for investigating deep phylogenetic relationships and a chloroplast gene, tufA. Having two genes provides testing of relationships, and since tufA is a faster evolving gene it provides better resolution of recently evolved species than 18S rRNA. Additionally a third and even more variable gene, ITS, was successfully sequenced from the *Coccolithus* and *Pleurochrysis* strains, and investigative work was carried out on the application of the AFLP genetic fingerprinting technique.

**Large-scale phylogeny**

Our new 18S rRNA tree provides the first multi-species molecular phylogeny of coccolithophorids. It strongly supports the previous results, from broader studies of haptophytes including a few coccolithophorids (Edvardsen et al. 2000, Fujiwara et al. 2001), that the coccolithophorids originated once, but with an early divergence into two groups, the Isochrysidales (which includes some secondarily non-calcifying genera), and the rest of the coccolithophores. In addition it provides much new information on relationships within the coccolithophorids.

The classical, morphology/palaeontology based classification of coccolithophorids is generally well supported, in particular there is a good correspondence with the phylogeny of Young & Bown (1997), Young et al. (1999), based on coccolithophorid ultrastructure and stratophenetics..

Our work has also shown that the subdivision into Isochrysidales vs. other coccolithophorids is paralleled by two major characters. First the production of lipid biomarkers is a shared characteristic of the Isochrysidales (Hanno Kinkel of the NIOZ team screened a large set of species to test this). Second calcification in the haploid phase (holococcolith production) occurs exclusively in the residual clade of other coccolithophorids. Since diploid phase (heterococcolith) calcification is a shared characteristic of the two clades it is parsimonious to hypothesise that this calcification mode evolved first with transfer of calcification to the haploid phase occurring subsequently. this runs counter to predictions that the simpler extra-cellular calcification of holococcoliths had evolved first. It is supported, however, by evidence of different biomineralisation modes occurring in the haploid phase. The co-occurrence of two biomineralisation modes in single species and the evolutionary stability of this differentiation across the haploid/diploid divide makes this a highly promising system for future functional genomic research on biomineralisation.

By contrast with these relatively simple patterns, pigment types provided a much more complex pattern Closely related taxa consistently showed similar pigment compositions but almost all individual pigments showed disjunct occurrences relative to phylogeny - i.e. individual pigments and even pigment associations occurred repeatedly in unrelated groups of taxa. Closer analysis of the data showed that these groupings were related to ecology and in particular that there was a consistent differentiation between coastal and open oceanic taxa. For example the oceanic species are characterised by the pigment HfX (19'-hexanoyloxyfucoxanthin) but in the coastal species this replaced by Chl $c_1$ (chlorophyll $c_1$). The combined ecological-evolutionary signal suggests to us that ecological adaptations reflected in structure of light-harvesting antenna were genetically coded, rather than being temporary conditions related to external growth factors and/or physiological state of cultures.

**Molecular clock (figure 4)**

All 18S phylogenetic trees have shown a high level of correspondence between divergence times based on palaeontological data and base-pair distance from molecular data. Consequently we are confident that it will be possible to construct a rather well-constrained molecular clock for the group. This work is still in progress but analysis based on a preliminary linearised tree of 18S data has produced extremely encouraging results. There is an excellent correlation between molecular genetic estimations of relative divergence and the geological estimates of absolute divergence time. This result contrasts with much experience of molecular clocks of major discrepancies between geological and molecular genetic estimates. We believe that this may primarily reflect the fact that we have restricted our calibration set to divergence times which are tightly constrained geologically, and so that the underlying potential of molecular clocks may be significantly greater than has been inferred from less well-constrained studies. The molecular clock analysis has also provided unexpected insights to the nature of the Cretaceous/Tertiary boundary extinctions. It is well established that approximately 90% of coccolithophore species went extinct during this event, which is thought to have been caused by a meteorite impact . The time calibrated molecular phylogeny indicates that a significant number of coastal clades, with very poor fossil records, must have survived the Cretaceous/Tertiary and in at least some cases were ancestral to Tertiary oceanic lineages. This combined with critical review of the fossil record has lead us to infer that extinction rates in oceanic coccolithophorids may have been nearer 99% than 90% with recolonisation occurring from the coastal environment. This hypothesis would also be consistent with the known record of other phytoplankton groups.

**C. SPECIES MODELS - EVIDENCE OF FINE-SCALE GENOTYPIC VARIATION**

This work area was particularly tightly focussed on the CODENET species with separate case studies being carried out on each of them. These were collaborative exercises involving in particular culture isolation, molecular genetic study, laboratory culture experiments, detailed qualitative morphological work and morphometric work on a mix of culture, oceanographic and geological samples. Each case study was very different but some strong patterns emerged (figure 5).

*Umbilicosphaera sibogae* var. *sibogae* vs *U. sibogae* var. *foliosa*
**Background**: Two varieties have traditionally been recognised in this species based largely on coccosphere characters. *U. s. sibogae* has large colonial coccospheres containing 2-4 cells whilst *U. s. foliosa* has simple coccospheres containing a single cell. There are correlative differences in coccolith morphology but it had been speculated that these were a consequence of the different coccosphere morphology. Hence alternative hypotheses were that these varieties were life-cycle stages of a single species or discrete taxa.
**Our results**: All data indicates that these are discrete species. This includes morphometric evidence that the coccolith morphotype do not intergrade, recognition of additional qualitative differences. Absence of transitions in culture and molecular genetic evidence of significant divergence (5-20Ma). Nonetheless the two taxa cluster together on all trees so clearly are closely related, as suggested by the coccolith morphology. The implication is that two closely related species have adopted very different ecological strategies and adaptations (broadly *U. s. sibogae* is oligotrophic and *U. s. foliosa* mesotrophic).

*Calcidiscus leptoporus*
**Background**: This species had been carefully studied from geological and oceanographic samples (e.g. Kleijne 1993, Knappertsbusch et al. 1997) and tentatively subdivided into small, intermediate and large morphotypes. These, however, strongly overlapped, leading again to alternative hypotheses of ecophenotypic or genotypic control.
**Our results**: This species has been particularly intensively studied in the project (Baumann & Sprengel 2000, Renaud & Klaas 2001, Henderiks & Renaud 2001, Renaud et al. in press, Gibbs et al. in press, Quinn et al. subm. Quinn et al. in prep.). Initial results from oceanographic and culture studies produced conflicting data, however, subsequently data from holococcolith morphology (Geisen et al. subm.) and combined morphological and molecular genetic study of a large collection of culture isolates (Quinn et al. in prep.) proved that the variation was predominantly genotypic and provided the key for reinterpretation of previous data. The large form appears to be a warm water eutrophic species and the intermediate form a mesotrophic species of broad temperature tolerance.

*Gephyrocapsa oceanica* and related species
**Background**: For this species-group there was a strong working model of subdivision into 6 closely related species with discrete ecologies and more or less discrete morphologies (Bollmann et al. 1997).
**Our results**: Culture studies were limited due to a failure to isolate most of the morphotypes, however those which were cultured showed strong morphological stability, with no transitions into other morphotypes. Moreover detailed testing of the hypothesis of differential ecologies of the morphotypes through derivation of a temperature transfer function based on the distribution of these morphotypes and testing in geological studies provided excellent results (Bollmann et al. subm.).

*Coccolithus pelagicus*
**Background**: This species was known to have evolved rapidly in the recent geological past and to show anomalous ecological distributions but was regarded as a single rather variable species.
**Our results:** Pooling of data between teams lead to the recognition that there were discrete arctic and temperate-upwelling populations of the species and that these had markedly different size ranges and temperature preferences. The two sub-types were cultured following targeted sampling missions. Culture studies then showed that the differentiation was stable under laboratory conditions and molecular genetics demonstrated that they were discrete, but closely related taxa (Young et al in prep. Saez et al. in prep.).

*Syracosphaera pulchra*
**Background**: This species has unusually high morphological complexity and was considered a particularly well-defined species. It was selected to provide a control study in degree of variation possible in a single species.
**Our results**: Detailed study of geological and oceanographic samples yielded more complex and variable morphological patterns than predicted, but these were initially interpreted as essentially noise, i.e. random population-level variation. Then combination coccosphere evidenced provided striking evidence from holococcolith morphology that the species in fact consists of at lest two discrete sub-taxa (Geisen et al subm.). Re-examination of the morphometric data from oceanographic and culture samples suggests that there may be a slight differentiation in mean size of the heterococcoliths, testing of the predictions from this, using molecular genetics, is in progress.

*Helicosphaera carteri*
**Background**: This species produces morphologically variable coccoliths even on single specimens. Palaeontologists have, however, successfully used fine morphovariants for biostratigraphy leading to a discordance between biological and palaeontological species concepts and a suggestion that in this species sympatric evolution of a phenotypically plastic population might lead to gradualistic change in range of morphological variation within a single species.
**Our results:** Morphometric analyses again produced ambiguous, difficult to interpret patterns. Our key result came from culture isolation of a disputed morphovariant – *H. carteri* var *hyalina*. Contrary to expectations the coccolith morphology has proven stable in culture indicating again that a subtle morphological variant is under genotypic control.

**Synthesis**

The common thread in these different studies is that fine scale morphovariants have repeatedly been shown to be stable genotypically differentiated sub-taxa with discrete ecologies, rather than ecophenotypes. This provides a critical framework for understanding the autecology of modern coccolithophores, for developing assemblage-based palaeoproxies of environmental change and interpreting microevolutionary patterns.

**D. PALAEOPROXY STUDIES**

Palaeoceanography is primarily based on study of biotic and geochemical proxies which provide records of fluctuations in environmental parameters such as temperature and productivity through the geological record. The single most important coccolithophophorid-based proxy is the "uk37" palaeothermometer based on degree of saturation of alkenones produced by coccolithophores. A core -objective of the CODENET project was development and testing of this proxy using samples derived from culture experiments, oceanographic sampling, sediment traps and well-constrained geological samples (project of Hanno Kinkel, NIOZ). A parallel project was development of a technique for determining past fluctuations in atmospheric $CO_2$ ratios based on carbon isotope ratios of the same alkenone biomarkers. During the course of the project we exploited the same synergies to extend our work to study of three other geochemical palaeoproxies. First, oxygen isotope ratios of coccolith carbonate were studied by Patrizia Ziveri (VUA) in order to develop their potential as a palaeothermometer. Second, Sr/Ca ratios of coccolith carbonate were studied by Heather Stoll (U. Oviedo) in order to test their potential as a proxy or palaeoproductivity. Third Mg/Ca ratios were examined as a potential palaeothermometer. [N.B. H. Stoll was not contractually a part of the CODENET project, but was co-opted as an additional core-collaborator].

For biotic proxies - i.e. those based on assemblages of fossils or morphological variation of individual species - our key work was the intraspecific variation studies outlined above. This has shown that conventional taxonomy has lumped morphotypes with discrete ecologies and that this is one key factor responsible for the relatively disappointing results of previous attempts to develop biotic palaeoproxies from coccolithophores. The *Calcidiscus* and *Gephyrocapsa* systems are already roiducin promising results (Bollmann et al. subm., Henderiks & Renaud 2001). The *Umbilicosphaera sibogae* and *Coccolithus pelagicus* systems are very promising. Taken together these four systems together with better established systems such as *Florisphaera profunda* should allow robust coccolithophore-assemblage based palaeoproxies of temperature and productivity for the last 1-2million years.

**Results from coccolith carbonate studies**

Culture experiments run by Christine Klaas (ETH), Ian Probert (Caen) and Markus Geisen and Blair Steel (NHM) provided an excellent sample set to test and calibrate new proxies from minor elements and stable isotopes and assess the range of variations across different species. These culture samples have demonstrated important effects of coccolithophore growth rates on coccolith Sr/Ca ratios in several different species, but have also indicated that temperature may exert an additional influence on coccolith Sr/Ca. This study, the first published for multiple species and the first article-length treatment of minor element partitioning in coccoliths from culture studies, was accepted into a special volume of *Global and Planetary Change*.

Culture samples are also revealing that the variable non-equilibrium “vital effects” in oxygen isotope fractionation across different species show a close relationship with cell division rates. This result has important implications for the origin of “vital effects” in coccolithophores as well as potential for a palaeoceanographic proxy. (fugure 6, Ziveri et al. in prep.)

Culture samples were also used to evaluate whether coccolith Mg/Ca ratios have potential as palaeotemperature indicators (Mg/Ca is being employed extensively in foraminifera as a palaeotemperature proxy). This first look at coccolith Mg/Ca, while promising, demonstrated that the high Mg content in coccolith organic matter complicates precise analysis of Mg/Ca in coccolith calcite (Stoll et al. in press).

One previous limitation on using coccoliths for palaeoproxy work was the inability to separate out samples dominated by a single or small number of related species, since minor element and isotopic chemistry may vary among species. We have developed two separation methods based on differential settling velocities which have been very successful in obtaining monospecific coccolith fractions from a variety of sediments. Separation of the very small coccoliths of the ecologically important deep-photic species *Florisphaera profunda* has been a particularly encouraging success. We have used these separated samples to identify the degree of chemical heterogeneity among different species in two different oceanographic settings (Stoll & Ziveri subm.). Application of this method to resolve anomalies in the palaeoproxy records and to investigate the palaeoecology of selected species is planned for future research.

**Developments**

The CODENET project has provided an ideal framework for testing of these palaeoproxies with high recognition within the palaeoceanographic community. This was reflected in the organisation of a special session at the European Geophysical Congress (Nice, April 2001) co-chaired by P. Ziveri. In addition both H. Kinkel and H. Stoll obtained permanent positions to continue their work and P. Ziveri has been awarded a university post-doctoral fellowship at VUA and has a pending research application for development of the work. The work also formed the basis of a UK (NERC) grant awarded for work testing the causes of anomalous "coccolithophore blooms" detected by satellites in late winter in the Bering Sea.

**1.4 REVIEW OF SUCCESS IN ACHIEVING KEY OBJECTIVES**

All the participants regard the CODENET project as highly successful, exceeding our predictions in most areas and yielding many additional unexpected results. Nonetheless, it is appropriate to review the results relative to the stated objectives for each work area, as given in the research proposal and contract.

**Work area 1. Evolutionary biodiversity:** A study of diversity of coccolithophorid biology relative to higher level phylogeny.

Key synthetic objectives (reproduced from the contract);

• *Determine the major patterns of biodiversity in coccolithophorid life-cycles, biomarker composition, photosynthetic pigments, cytology and plastid genome.*

• *Re-evaluate the phylogeny of the coccolithophorids using separate and combined analyses of: molecular genetic, morphological, biochemical and palaeontological data.*

• *Calculate divergence times of groups and rates of evolution, including molecular clock calibrations.*

• *Reconstruct the sequence of major evolutionary steps in coccolithogenesis, lipid biochemistry, plastid evolution, and life cycle differentiation.*

To a certain extent these are all open-ended objectives. Nonetheless, in each case the progress has certainly been considerable and it is true to say that the project has resulted in major advancements of knowledge.

**Work area 2. Microevolution and species-level variation:** A study of microevolutionary pattern and process, species concepts, and the significance of fine-scale genotypic diversity.

Key synthetic objectives (reproduced from the contract);

• *Evaluate which aspects of variation represent genotypic vs. ecophenotypic or ontogenetic variation.*

• *Determine whether intra-specific variability in morphology, physiology and biochemistry are correlated, defining discrete sub-species.*

• *Determine whether microevolution occurs by (sub-)species selection or by effectively sympatric evolution within ocean-scale populations.*

As outlined in the highlights section progress in this area was extremely strong, useful new data was derived for each of the species a clear pattern emerged and these objectives were met.

**Work Area 3. Ecology:** An investigation of the prime constraints on coccolithophorid ecology and the ecological significance of biodiversity within the coccolithophorids.

Key synthetic objectives (reproduced from the contract);

• *Determine whether coccolithophorids as a group occupy a distinctive ecological niche, and if so characterise it.*

• *Determine which aspects of intra- or inter-specific assemblage variation are most valuable for palaeo-ecological calibrations and develop palaeoecological proxies.*

• *Determine the extent to which coccolithophorid carbonate accumulation rate is affected by species composition and evolution.*

Niche characterisation is a complex question, on the one hand it has become clear that coccolithophorids have competitive advantage in stratified seas and our work on life-cycles strongly suggests that the haplo-diplontic life cycle is an adaptation in part to this. Conversely it is clear that coccolithophorids occupy a broader range of environments and that many basic aspects of their biology are still poorly known. For example the phylogenetic work highlighted the likely importance of coastal species in evolution of the coccolithophorids and highlighted likely ecological adaptations in this group in terms of pigments and arguably coccolith and scale characters, this however defines more questions than it resolves.

The palaeoproxy work easily exceeded the objectives through (1) the development of geochemical proxies and (2) the intraspecific variation work identifying distinction of fine scale taxa as the key to developing assemblage-based (i.e. floristic) proxies.

Coccolith carbonate accumulation rates were extensively studied in the sediment trap and palaeontological projects using new quantitative methods most notably by PhD students at U. Bremen, VUA and ETHZ. The importance of species composition analysis for quantification of accumulation rates has been amply proven but the deeper questions of causality are still to be resolved.

## 1.5 PRINCIPAL NETWORKING AND CO-ORDINATION ACTIVITIES

### 1.5.1 Scientific collaboration

As the network developed scientific collaboration between the teams, and especially the young researchers has become increasingly developed and complex. This occurred through exchange of samples, numerous short research visits, pooling of results, and work on joint publications. The following scientific areas provide an interesting set of examples of the different ways in which collaboration has occurred (figure 7)

*A. Culture isolation, and culture collection maintenance.*

Here a core activity has been undertaken primarily by one team, U. Caen, for the benefit of the network as whole. Assistance has come (1) from other teams (NHM, ETHZ) assisting in the isolation work and maintenance of duplicate cultures, and; (2) from numerous teams assisting by facilitating or undertaking water sampling for culture isolation. Subsequently, virtually all teams have used the culture collection in one way or another.

Similar patterns of collaboration have been seen with one team undertaking a task for the benefit of the network as a whole with assistance from others in, for instance, cruisework sampling and meeting organisation.

*B. Molecular phylogeny*

In this case the deliverable has been a scientific result rather than a communal resource, and the responsibility has been exclusively with one team, AWI. The work, has nonetheless, been carried out in close collaboration with the Caen team, who have provided the material from cultures. Subsequently the value of the work was greatly enhanced by parallel study of other aspects of phylogenetic diversity throughout the network. As a result collaborative interpretation of results is maximising the benefit of disparate studies.

This is perhaps the clearest single example but the general trend of altruistic collaboration and resultant enhancement of research results was pervasive within the network.

*C. Holococcolith evidence for cryptic speciation.*

In this area the network brought together researchers who made complimentary observations which combined add up to a significant new insight. Advances of this type cannot easily be predicted or planned but are a major value-added benefit of network research.

A similar style of collaboration, with pooling of complimentary data has been evident throughout the field of fine-scale taxonomy.

*D. Geochemical palaeoproxy studies.*

Here we have a classic type of multidisciplinary study, with different teams undertaking parallel studies on common sample sets. What is rather unusual is that the same set of workers used very different sample sets provided by a wide range of collaborators. Each team was able to carry out their particular research very efficiently and the combined result was highly effective. Finally, as indicated by the feedback line, the results of the specialist studies provided new insights on the studies samples. Consequently, the network has achieved an enviable reputation within the field as an example of collaborative research.

*Summary.*

Collaborations have occurred in a range of ways, both planned and unplanned. A common end result, however, has been that the network structure has produced a very significant multiplier effect with all participants contributing to and benefiting from the collaboration and major advances being made. We would strongly recommend the network model.

**1.5.2 SUMMARY OF CODENET MEETINGS, AND WORKSHOPS**

Our original plans were essentially limited to annual meetings although with the intention to develop additional meetings in accordance with need. As outlined below and in figure 8, the opportunities presented by the network lead to a succession of workshops being organise, particularly through the action of the young researchers. In particular an early spring series of meetings was organised to compliment the main summer workshops. During the course of the program meetings were held at each of the participating institutes and almost all the YVRs gained experience in meeting organisation. In these notes network funded young visiting researchers are indicated by underlining.

**November 1997 - Advance planning workshop. VU-Amsterdam.**

Organisers: Jan van Hinte, Patrizia Ziveri, Jeremy Young.

Participation - 12 scientists, from all teams.

This one day workshop was held before formal commencement of the project. It allowed the scientists in charge to meet and focussed on plans for recruitment of YVRs, planning of early collaborations, and particularly culture acquisition.

**February 1998 - CODENET geological projects planning workshop at INA7 Conference in Puerto Rico**

Organisers: Jeremy Young (NHM), Amos Winter (Puerto Rico)

Participation - NHM (2), ETHZ (2), VUA (1), CSIC (1), Lisbon (1), NIOZ (1)

The International Nannoplankton Association (INA) is the professional society for nannoplankton research and their application in industrial biostratigraphy. Many CODENET participants were attending, so the opportunity was taken to send additional participants and organise a half-day workshop. This played a valuable role in planning the geological projects during the year. In addition, Mario Cachao gave an oral presentation introducing the project to the scientific community and other participants gave technical presentations related to the project.

**2-4 June, 15-26 June, 17-24 July 1998 - ETHZ sample preparation workshops,**

Organisers: Joerg Bollman, Sabrina Renaud (ETHZ)

Participation - NHM, ETHZ, VUA, Lisbon

A succession of sample preparation workshops were held in ETHZ Zurich in order to refine quantitative sample preparation techniques (Bollmann et al. 1999, Geisen et al. 2000) and prepare sample sets for network research projects [RT13, 14].

**18th-22nd Sept. 1998 - First Annual CODENET network workshop, Blagnac France.**

Organisers: Jan van Hinte, Sandra Broerse, Patrizia Ziveri (VUA), Jeremy Young (NHM).

Participation - 28 scientists, including all YVRS NHM (3), ETHZ (3), VUA (4), Caen (2), AWI (2), CSIC (3), Lisbon (2.5), NIOZ 2), Bremen (5), + invited colleagues from Firenze, Kiel and Bremen

This workshop was especially important, since it was the first opportunity for all the participants to get together, co-ordinate their activities and turn a set of good intentions into active collaborations and research programs.

Presentations by each participant team outlined their objectives and specialist interests. Research talks covered various key areas of science. Master class training sessions were given on culture techniques (Caen, NHM) and organic geochemistry (NIOZ), these proved both effective and popular. Overviews of the principal objectives of the project provided a focus for planning of the research tasks and lead to workshop sessions for this. A positive development was that the YVRs and other key younger participants took responsibility to actively plan the next phase of network research, and decided to organise an additional workshop in Easter 1999. Overall the workshop left participants with a clear appreciation of the significant work needed to realise the objectives of the network, but with a strong commitment to fulfil it.

**5-9 October 1998 - ETHZ Calcareous nannofossil short course**

Organisers: Joerg Bollman, Hans Thierstein, Katharina von Salis (ETHZ)

This course was organised to provide specialist training in nannofossil taxonomy and methodology. it focussed on SEM techniques, image analysis and taxonomy of the CODENET species. 6 scientists attended, mostly from outside the network but with interest in contributing to the network objectives.

**10-12 February 1999 - Culture methods training workshop, Caen**

Organisers: Ian Probert (Caen), Christine Klaas (ETHZ), Chantal Billard (Caen)

Participation - 14 scientists, NHM (2), ETHZ (3), VUA (2), AWI, NIOZ, CSIC (2), Caen (3).

Culture work was a core activity for the network and this workshop provided training in techniques. All YVRs attended and several other young post-docs. 2 days of work included both practical and theoretical sessions.

**1-2 March 1999 - Taxon focussed workshop on *Coccolithus pelagicus*, Bremen**

Organisers: Karl-Heinz Baumann (U. Bremen), Jeremy Young (NHM).

Participation - NHM, Lisbon, VUA, Bremen (3), + visit to AWI Bremerhaven

Small workshop to exchange results from detailed studies on biogeography and intraspecific variation of *C. pelagicus*. Joint publication from this is in preparation and several new research initiatives were set in motion. Also, visit by participants to molecular genetics laboratory at AWI Bremerhaven.

**18-20th March 1999 - Spring CODENET workshop, NIOZ Texel**
Organisers: Hanno Kinkel, Gerard Versteegh (NIOZ), Patrizia Ziveri (VUA)
Participation - 27 scientists, including all YVRs and also many scientists from outside core teams.
Workshop planned by the YVRs to (1) provide additional network integration and (2) allow more outside scientists to contribute (Blagnac was rather expensive/exclusive). One day of open contributions, with very high scientific standard; morning of YVR presentations on results of first year's work; afternoon workshop session focused on offer from Lisbon of short cruise in June, accepted.

**July 1999 - NIOZ Flow Cytometry Workshop**
Organiser: Marcel Veldhuis (NIOZ)
Participants: Hanno Kinkel (NIOZ), Ian Probert (Caen), Kees van Lenning (CSIC), Patrizia Ziveri (VUA)
Informal workshop to provide training in flow cytometry for relevant YVRs and hands on experience of organic geochemical techniques. Followed by longer research visit by IP and KvL.

**2nd-5th September 1999 - Second Annual CODENET network workshop, Blagnac France**
Organisers: Jan van Hinte, Patrizia Ziveri (VUA), Jeremy Young (NHM)
Participation - 30 scientists, including all YVRs, NHM (3), ETHZ (3), VUA (4), Caen (2), AWI (2), CSIC (3), Lisbon (2.5), NIOZ 2), Bremen (5), Oviedo (1) + guest participants from Tsukuba Japan (2)
Major workshop. Attended by all YVRs, many scientists in chief, other team members and guests. Research presentations by all YVRs and most guests; review and workshop sessions on progress against objectives; training sessions on Molecular Genetics (V. Huss & A. Saez AWI) and Cladistics (R. de Jong, Leiden). General conclusion that the network needed some refocusing but was being *very* productive.

**16th September 1999 - Amsterdam, Coccolith Ecology Training Workshop.**
1 day training workshop organised by Patrizia Ziveri (VUA) and given by Dr. R. Jordan (Yamagata University) during research visit to VUA (& other CODENET teams). Attended by CODENET participants from VUA, NHM, NIOZ and Bremen. Most participants stayed for 1-2 more days for informal research collaboration.

**3rd-6th October 1999 - Woods Hole Alkenone Workshop**
CODENET Participants: Gerald Ganssen (VUA), Joan Grimalt (CSIC) Hanno Kinkel (NIOZ) and Gerard Versteegh (NIOZ).
This was a major NSF workshop focussed on work needed to realise the potential of the Alkenone palaeothermometer. The CODENET presentations had considerable impact.

**15th-16th October 1999 - Amsterdam Taxonomy Workshop**
Organisers: Patrizia Ziveri (VUA), Jeremy Young (NHM)
Participation - 11 scientists, from NHM, ETHZ, VUA, Caen, CSIC, Bremen, + Tuebingen
Short workshop to investigate potential for collaboration on synthesis of coccolith taxonomy and to provide opportunity for taxon buffs to get together. General discussions, demonstration of EMIDAS WWW database by ETHZ team, specialist workshop on *Syracosphaera* taxonomy. Decisions to collaborate on development of EMIDAS, on a Guide to Coccolithophore Taxonomy and various specific publications.

**29-31 February 2000 - Mid term review meeting, NHM**
Organisers: Jeremy Young, Markus Geisen (NHM)
Participation - 18 CODENET scientists + 3 person EU team, including all YVRs, NHM/UCL (3), ETHZ (2), VUA (3), AWI (2), NIOZ (2), CSIC (2), Caen (2), Bremen (1), Oviedo (1).
This was the formal mid term review meeting, held on 30th February, with Prof. D. Guy-Ohlsen as the external assessor. The meeting went well and we benefited both from the comments of the assessor and from our own review of the activity. Both the formal report on the network and informal comments were generally very positive. Additional network activities around the formal review meeting were:

- *Pre-meeting one day research workshop* for the network to review progress, especially valuable since all YVRs and one senior representative of each team was present.
- *Post-meeting one day training workshop* for the YVRs on science funding and grant applications – presentations by Heather Stoll (U. Oviedo), Vanessa Pike (Research Consulting Office, NHM) and Jeremy Young (NHM).
- *Post-meeting research visits* to the NHM by Ian Probert (4 days), Hanno Kinkel (4 days) and Patrizia Ziveri (1 day).

**16-20 June 2000 -Summer publications workshop, Blagnac France**
Organisers: Patrizia Ziveri, Jan van Hinte (VUA), Jeremy Young (NHM)
Participation – 17 scientists, including all YVRs; NHM (3), ETHZ (4), VUA (5), AWI (1), NIOZ (1), CSIC (2), Caen (2), Lisbon (1).
This workshop was arranged to facilitate joint publication of results since the extensive network of collaborations meant that we had numerous projects where several participants needed to collaborate on joint publications. The workshop was informally organised with the emphasis on different sets of

collaborators working together in their own time. In total some 20 mss, at widely varying stages of preparation, were worked on. A particular feature was that we were able to bring together a group of young researchers with special interest in nannoplankton taxonomy who worked together exceptionally intensively (Mara Cortes ETHZ, Lluisa Cros CSIC, Annelies Kleijne VUA).

**8-10th Sept 2000 - 3rd Annual CODENET workshop, Tagungshaus, Bredbeck, Germany**

Organisers: Karl-Heinz Baumann (Bremen), Jeremy Young (NHM)

Participation – 28 scientists, including all YVRs; NHM (5), ETHZ (2), VUA (3), AWI (2), NIOZ (2), CSIC (3), Lisbon (3), Caen (1), Bremen (4), Oviedo (1) + 2 outside guests (Doan Nhu Hai, Copenhagen, Ulf Rogalla, BGR Kiel).

This workshop preceded the International Nannoplankton Association conference in Bremen, at which numerous presentations from CODENET participants were made to a broad scientific audience with special interest in coccolithophores. The workshop was organised by the University of Bremen team in a secluded conference retreat in woodland outside Bremen. Presentations included extended informal reports of research results by the young researchers without rigorous timetabling (a notably successful format), a keynote talk by Linda Medlin (AWI) on molecular clock interpretations of phytoplankton evolution, and a training session by sedimentologists from Bremen on sediment trap research. The meeting was notable for the high level of new results presented and for the very open communication.

**11th-15th Sept 2000 - 8th International Nannoplankton Association Conference (INA8), Bremen, Germany**

CODENET participation, 25 scientists, 20 presentations.

The CODENET team made a major impact at this meeting, with the very substantial body of new science presented fulfilling the promise of the launch at INA7 in 1998.

**14th -17th Feb 2001 - Barcelona PostDocs Workshop, ICM Barcelona, Spain**

Organisers: Kees van Lenning, Lluisa Cros (CISC), Jeremy Young (NHM)

Participation - 20 scientists, including all YVRs; NHM (3), ETHZ (1), VUA (2), AWI (1), NIOZ (1), CSIC (5), Caen (1), Lisbon (1), Bremen (2) + 3 outside guests from local institutes

This workshop was arranged to provide update on progress between the YVRs and other key participants and to broaden training of YVRs in a range of oceanographic topics, exploiting the facilities of the Instituto de Ciencias del Mar. The former objective was met through a day of relatively informal presentations and workshops, the latter through 2 days of guest lectures and visits to scientific facilities.

**30th March 2001 - Symposium on the use of coccolithophore-based proxies in palaeoceanography at 26th European Geophysical Society General Assembly, Nice, France**

Organisers: Patrizia Ziveri, Anthony Rossell-Melle and Maureen Conte

CODENET Participation Barbara Balestra (Firenze/VUA), Babette Boeckel (Bremen), Mario Cachao (Lisbon), Gerald Ganssen (VUA), Jorijntje Henderiks (ETHZ), Hanno Kinkel (NIOZ), Elisa Malinverno (Milano/VUA), Heather Stoll (U. Oviedo), Peter Westbroek (U. Leiden), Jeremy Young (NHM) Patrizia Ziveri (VUA).

The extensive work on calibration of coccolith based palaeoceanographic proxies lead to PZ co-organising this symposium, in which 13 out of 20 talks were given by CODENET participants. The value was enhanced by it preceding a similar symposium of planktonic foram derived palaeoproxies, there was very positive exchange between these two sessions.

**25th-29th August 2001 - CODENET Final Workshop, Blagnac, France**

Organisers: Patrizia Ziveri, Jan van Hinte (VUA), Jeremy Young (NHM)

Participation: 25 scientists, including all YVRs; NHM (4), ETHZ (3), VUA (4), AWI (2), NIOZ (1), CSIC (2), Lisbon (1), Caen (2), Bremen (2), + 3 outside guests (Trevor Bailey, Sasha Tozzi, U. Rutgers, USA, Jette Ostergaard, Copenhagen).

This final CODENET workshop concentrated on synthesis of results and continuing work on publications. Presentations included review and update talks by the YVRs, overview talks by several of the senior scientists, and a series of regular research presentations by guests and other participants. In place of our usual training workshops we undertook an excursion to the Biarritz K/T boundary section in order to provide the non-geologists with experience of field geology. Finally the workshop ended with a spectacular party, and thunderstorm.

**10-15th Feb 2002 - Coccolithophores from cellular processes to global impact conference. Monte Verita, Ascona, Switzerland**

Organisers : Patrick Quinn, Hans Thierstein (ETHZ), Jeremy Young (NHM)

This post-project conference is being organised using the conference facility of ETH Zurich to provide a synthesis of the CODENET results in the context of broader research on coccolithophores. A high profile set of keynote speakers have been arranged from both within and outside the CODENET project.

**1.5.3 CRUISES WITH SIGNIFICANT CODENET TEAMS AND RESEARCH VISITS**

The constraints of network funding meant that cruisework could not be pre-planned in detail, but rather had to rely on an opportunistic approach. As outlined below this proved very successful with the teams regularly involved in cruisework making opportunities available to the other teams. The notes also cover joint laboratory work where it involved groups of participants, but not the innumerable short visits by individual YVRs.

**April 1999 - CODENET 1 Cruise, Lisbon**

Organiser : Christine Klaas (ETHZ), Mario Cachao (MNHN-UL)

Participants: Joerg Bollmann (ETHZ), Christine Klaas (ETHZ), Sabrina Renaud (ETHZ), Ian Probert (Caen), plus many from Lisbon.

One day cruise for water sampling for culture isolation and exploration of potential for collaborative cruisework. Followed by extended visit by CK. Many lessons learnt for subsequent multi-participant cruise.

**14-15 June 1999 - CODENET 2 Cruise, Lisbon**

Organisers: Mario Cachão (MNHN-UL), Hanno Kinkel (NIOZ), Jeremy Young (NHM)

Participation: Markus Geisen (NHM), Hanno Kinkel (NIOZ), Christine Klaas (ETHZ), Kees van Lenning (CSIC), Ian Probert (U. Caen), Heather Stoll (U. Oviedo), Jeremy Young (NHM), Patrizia Ziveri (VUA), plus many from Lisbon.

Two one day cruises were carried out along a transect across the Portuguese Shelf. These provided common sample sets for intercalibration experiments; a well constrained investigation of coccolith ecology across a productivity gradient; a special sampling opportunity for novel techniques; and training in cruisework and cruise organisation.

**14-21 July 1999 Icelandic Field Sampling Trip**

Participants: Ian Probert (Caen), Kerstin Muller (NHM), Hafstein Gudfinsson (Icelandic Marine Research Institute)

Field sampling for plankton and culture isolation, targeted on isolation of Arctic variant of *C. pelagicus*. Several strains of this species were successfully isolated and numerous filter samples collected from a mixed coccolithophore-diatom bloom (to be studied at NHM & UCL).

**25th Oct - 6th Nov 1999 MATER Cruise, in Alboran Sea**

Participants: Kees van Lenning (CSIC) Germà Cervera Payà (CSIC), Andy Howard (NHM), Markus Geisen (NHM), Sandra Broerse (VUA) + many others from MATER project

At very short notice, berths became available on a MATER cruise in the Alboran Sea organised by CSIC. A rapidly assembled CODENET team (with logistic support from across the network) was able to carry out intensive sampling following the protocols developed on the CODENET II cruise. Large sample sets collected. Sampling of Deep Chlorophyll Maximum for culture isolations yielded 49 successful cultures, including many very useful ones.

**15th - 26th November 1999 CODENET Japan visit.**

Hosts: M. Kawachi, I. Inouye, M-H Noel (Tsukuba), H. Okada (Sapporo), R. Jordan (Yamagata)

Participants: Ian Probert (Caen), Jeremy Young (NHM), Markus Geisen (NHM), Patrizia Ziveri (VUA)

Research visit to Japanese colleagues working in fields very closely related to CODENET (50% funded by hosts). Activities included 2 day open workshop on "The State of Research on Coccolithophorids in Europe and Japan" (31 participants), research visits to Sapporo and Yamagata, field sampling trip from Tsukuba. Core outcomes: decision to launch semi-formal collaboration program, data exchange with Sapporo, many new isolations from fieldwork, including *H carteri*.

**February-March 2000 NHM culture experiment**

An extended culture experiment was carried out on the ecophysiology of *Coccolithus pelagicus* at the NHM. This was a collaborative activity between the Caen, NHM and Lisbon teams. From Caen, Ian Probert provided cultures and helped set up the experiment. Alexandra Duarte Silva of Lisbon visited for one month to obtain training in culture and morphometric techniques, and carry out the bulk of observations for her masters degree and Mario Cachao visited for a short period to obtain familiarisation with the techniques used. Fabrizio Tremolada (U. Milano – research group associated with VUA) continued observations as part of a training visit.

**July 2000 MARE cruise**

The NIOZ and VUA teams were able to organise CODENET participation on a Dutch cruise in the South Atlantic investigating warm core eddies. Sandra Broerse (VUA) and Claire Findlay (NHM) participated, collecting samples for a range of participants. A particular success was collection of samples for culture isolation, after the cruise Markus Geisen and Ian Probert made 30 successful isolations from the samples, including several target species.

**Aug 2000 Barcelona mini-cruise**

Kees van Lenning and Lluisa Cros of CSIC Barcelona have organised numerous nearshore sampling trips for Ian Probert (Caen) in August they extended this with charter of a small vessel for a one day sampling

mission from the CSIC Blanes research station (near Barcelona). Ian Probert (Caen), Markus Geisen (NHM), Jeremy Young (NHM), and Babette Boeckel (Bremen) reorganised their holiday plans to join them for this mission and four days of associated work.

**Sept 2000, *Meteor* research cruise M48-4 off Namibia.**
The Bremen team invited Markus Geisen (NHM) to join Claudia Sprengel (Bremen) on this cruise so that intensive nannoplankton sampling could be carried out. This was further facilitated by sponsorship from British Airways "Assisting Conservation" scheme. Sampling included 18 depth transect stations, 79 surface water nannoplankton samples, 18 fine fraction calcite samples for stable isotope work (for VUA), and 13 samples of concentrated sea water for isolation work (for U. Caen).

**Feb 2001, Bering Sea Cruise**
Alexandra Broerse (NHM) participated in a research cruise to the Bering Sea to determine the nature of anomalous bright water patches which had been identified as coccolithophore blooms. The material collected was subsequently analysed by CODENET researchers at the NHM, VUA, U. Caen and NIOZ.

### 1.5.4 NETWORK CO-ORDINATION ACTIVITIES (OTHER THAN WORKSHOPS)

**WWW Site**
The CODENET web site (www.nhm.ac.uk/hosted_sites/ina/CODENET) was established early in the project life as a tool for providing both information for interested outsiders and network co-ordination. It has been updated throughout the project and now includes over 100 separate pages. These include information on the project, advance information on network activities, reports of these activities, details of the participants, abstracts, etc.
Additional WWW resources directly linked to the CODENET site, were produced by other teams including: a major online database of coccolithophorid images EMIDAS produced by the ETHZ team (http://www.emidas.ETHZ.ch); and an online bibliography, produced by H. Stoll (U. Oviedo - http://www.williams.edu/Geoscience/faculty%20pages/Heather/CODEbibh.htm)

**Electronic mailing list**
An electronic mailing list was hosted, by the NHM, for the network. This was used to inform participants of research progress and network activities and for some general discussion.

**Reports**
Annual and Mid Term Reports were completed (by the co-ordinator) for the commission and used as benchmarks for reviewing progress. Additionally abstract and report volumes were produced (edited by Patrizia Ziveri, VUA) for the Blagnac workshops.

**Posters**
Large format posters were produced, by Markus Geisen (NHM), providing overviews of the project objectives and workplan (1998) and progress around the mid term mark (early 2000). Copies of these were given to all teams and were displayed at numerous international conferences and smaller meetings.

**1.6 ASSESSMENT OF BENEFITS OF WORKING TOGETHER AT COMMUNITY LEVEL TO THE PARTICIPANTS**

The essential feature of this project was to unite a range of different specialists in research on a particular group of organisms. In principle the range of disciplines involved - phycology, molecular genetics, palaeoceanography, systematics, organic geochemistry could have been found in many of the European countries. However, attempting to carry out this research in one country would have required serious compromises as either second rate teams would have been involved or teams would have had to work outside their core specialisation. Hence working at European level enabled us to bring together a significantly stronger and more enthusiastic set of teams than would have been possible on a national level. As a result the research was able to proceed rapidly and efficiently. The network has received a high level of recognition in Europe and special interest from Japan and the USA. More generally all participants valued the opportunity to work at a European level and the variety of cultural and scientific traditions brought to the network greatly enhanced the experience.

Both the direct scientific benefits of collaborating at European level and the less tangible cultural benefits were actually realised as a result of the flexible network structure.

**1.7 INTERACTIONS WITH INDUSTRY**

This has mostly consisted of communication of results through presentations at joint academic-industrial meetings. In particular there was strong representation at meetings of the European Geophysical Society, European Union of Geoscientists, International Nannoplankton Association, American Society of Limnologists and Oceanographers, American Geophysical Union. Results will not be directly commercialised but the insights into the basic biology of these organisms will underpin future applied research on coccolithophorids in the fields of biostratigraphy, marine resource management and aquaculture.

**1.8 ASSESSMENT OF THE CONTRIBUTION MADE BY THE NETWORK TO THE TRAINING AND MOBILITY OF YOUNG RESEARCHERS**

Eight young researchers were directly funded by the network. Of these six were employed essentially through the life of the network whilst one, Sabrina Renaud, left ETHZ part way through to take up a CNRS research post at U. Lyon. She was replaced by Pat Quinn (from U. Sheffield) who proved an invaluable addition to the project. All the YVRs carried out excellent research and in several cases this was directly recognised by the host teams extending their employment contracts. As a result the total period of YVR employment (281 months) significantly exceeds the contractual obligation (252 months). The YVRs worked together enthusiastically and maximised the opportunities available to them to do so. In particular the YVRs organised a sequence of additional workshops and undertook numerous short research visits. As a result of the numerous scientific contacts and collaborations combined with more formal training sessions all the YVRs gained experience in the full range of approaches included in the project.

These benefits were extended by inclusion in all the teams of additional nationally funded young researchers who strongly participated in the project. This included graduate students, masters students, PhD students, and post doctoral researchers.

# FACTUAL INFORMATION ON EACH PARTICIPANT

Contract Number: ERBFMRXCT97 0113

Reporting Period: 45 months ending September 2001

| | |
|---|---|
| Name of the network participant<br><br>Their scientific speciality[1] | The Natural History Museum<br><br>L-35 E-22 E-23 |
| Name of the scientist in charge | Dr Jeremy R. Young |
| Number of individual researchers contributing to the joint activities of the network | 14 |
| Total number of man-months spent on the project | 99 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]: | |
| - name and nationality (ISO Code) | Markus Geisen DE |
| - date of birth | 22/08/1971 |
| - start date and duration of the appointment in months | 30/03/1998, 42 months |
| - category of researcher | Doctoral student |
| - scientific speciality[1] | E-22 |
| - list of publications in refereed journals | YOUNG J.R. & GEISEN M. (1998) Using spreadsheets to produce stacked histogram, stacked line and spindle charts. *Journal of Micropalaeontology*, **17/2**, 104.<br>BOLLMANN, J., BRABEC, B., CORTÉS, M. & GEISEN, M. (1999). Determination of absolute coccolith abundances in deep-sea sediments by spiking with microbeads and spraying (SMS-method). *Marine Micropaleontology*, **38**, 29-38<br>GEISEN M., BILLARD C., BROERSE A.T.C., CROS L., PROBERT I., AND YOUNG J. R. (submitted). Life-cycle associations involving pairs of holococcolithophorid species : Intraspecific variation or cryptic speciation? Submitted to *European Journal of Phycology*.<br>GEISEN, M, BOLLMANN, J., HERRLE, J. O., MUTTERLOSE J. & YOUNG J. R., (2000). Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. *Micropaleontology*, **45**, 437-442.<br>GEISEN M., PROBERT I, & YOUNG J.R. (in press). Coccolithophores for exhibition. *Journal of Nannoplankton Research.*<br>STOLL, H.M., ZIVERI, P., GEISEN, M., PROBERT, I., AND YOUNG, J.R. (in press). Potential and limitations of Sr/Ca ratios in coccolith carbonate: new perspectives from cultures and monospecific samples from sediments. *Philosophical Transactions of the Royal Society, London* |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]: | |
| - name and nationality (ISO Code) | Markus Geisen DE |
| - date of birth | 22/08/1971 |
| - destination, start date and likely duration of their secondment in months | ETHZ<br>2-6-98 1.5 months (total, of four shorter secondments)<br><br>U. Bremen |
| - category of staff | 1/4/2000, 1 month<br><br>Doctoral student |

Notes:

Annex B

**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

**Reporting Period: 45 months ending September 2001**

| | |
|---|---|
| Name of the network participant<br>Their scientific speciality[1] | ETHZuerich<br>L35, E22 |
| Name of the scientist in charge | Prof. H. Thierstein |
| Number of individual researchers contributing to the joint activities of the network<br>Total number of man-months spent on the project | 8<br>80 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]:<br>- name and nationality (ISO Code)<br>- date of birth<br>- start date and duration of the appointment in months<br>- category of researcher<br>- scientific speciality[1]<br>- list of publications in refereed journals | <br>Patrick Quinn GB<br>14/05/1971<br>18/08/1972<br>13 months<br>Post doctoral researcher<br>E22, E23<br>QUINN, P. S., THIERSTEIN, H. R., BRAND, L. E. AND WINTER, A., (submitted). Experimental evidence for the species character of *Calcidiscus leptoporus* morphotypes, *Marine Micropaleontology*. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff | Sabrina Renaud FR<br>14/05/1971<br>01/01/1998<br>24 months (left 31/12/99 to take permanent post at CNRS Lyon)<br>Post doctoral researcher<br>L35 E22<br>RENAUD, S. AND KLAAS, K., (2001). Seasonal variations in the morphology of the coccolithophore *Calcidiscus leptoporus* off Bermuda (N. Atlantic), *Journal of Plankton Research*, 23 (8), 779-795.<br>RENAUD, S., ZIVERI P. AND BROERSE, A. T. C., (submitted). Seasonal and geographical variations of the coccolithophore *Calcidiscus leptoporus*: Differential fitness of morphotypes in a multidimensional ecological space. *Marine Micropaleontology*. |

Notes:

Annex B

**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

**Reporting Period: 45 months ending September 2001**

| | |
|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Vrije Universiteit Amsterdam<br>L35 E22 E23 |
| Name of the scientist in charge | Gerald Ganssen |
| Number of individual researchers contributing to the joint activities of the network | 10 |
| Total number of man-months spent on the project | 88.5 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]: | |
| - name and nationality (ISO Code) | Patrizia Ziveri IT |
| - date of birth | 06/11/63 |
| - start date and duration of the appointment in months | 1/10/98<br>36 months |
| - category of researcher | Post Doctoral Researcher |
| - scientific speciality[1] | E22 E23 |
| - list of publications in refereed journals | ZIVERI P., YOUNG J. R. & van HINTE J.E. (1999). Coccolithophore export production and accumulation rates. In "On the determination of sediment accumulation rates". Bruns P. and Hass C. H. (Eds), *GeoResearch Forum*, 5, 41-56.<br>BROERSE, A.T.C., ZIVERI, P., AND HONJO, S., (2000) Coccolithophore ($CaCO_3$) flux in the Sea of Okhotsk: seasonality, settling and alteration processes, *Marine Micropaleontology*, 39 (1-4): 179-200.<br>YOUNG, J.R. AND ZIVERI, P., (2000) Calculation of coccolith volume and its use in calibration of carbonate flux estimates, *Deep-Sea Research*, II, 47, 9-11: 1679-1700.<br>ZIVERI, P., BROERSE, A.T.C., VAN HINTE, J.E. AND HONJO, S., (2000) The fate of coccoliths at 48°N 21°W, Northeastern Atlantic. *Deep-Sea Research*, II, 47, 9-11: 1853-1875.<br>ZIVERI, P., AND THUNELL, R., (2000) Coccolithophore export production in Guaymas Basin, Gulf of California: Response to climate forcing. *Deep-Sea Research*, II, 47, 9-11: 2073-2100.<br>BROERSE, A.T.C., ZIVERI, P., VAN HINTE, J.E. AND HONJO, S., (2000) Coccolithophore export production, seasonal species composition and coccolith $CaCO_3$ fluxes in the NE Atlantic (34°N, 21°W and 48°N, 21°W) *Deep-Sea Research*, II, 47, 9-11: 1877-1905.<br>ZIVERI, P., RUTTEN, A., DE LANGE, G., THOMSON, J. AND CORSELLI, C., (2000) Present-day coccolith fluxes recorded in central eastern Mediterranean sediment traps and surface sediments, *Palaeogeography, Paleoclimatology and Palaeoecology*, 158, 3-4: 175-195.<br>RUTTEN, A., DE LANGE, G.J., ZIVERI, P., THOMSON, J., VAN SANTVOORT, P., COLLEY, S. AND CORSELLI, C., (2000) Recent terrestrial and carbonate fluxes in the pelagic eastern Mediterranean; a comparison between sediment trap and surface sediments, *Palaeogeography, Paleoclimatology and Palaeoecology*, 158, 3-4:197-213<br>STOLL , H. AND ZIVERI, P. (in press). Methods for separation of monospecific coccolith samples from sediments. *Marine Micropaleontology*.<br>STOLL, H.M., ZIVERI, P., GEISEN, M., PROBERT, I., AND YOUNG, J.R. (in press). Potential and limitations of Sr/Ca ratios in coccolith carbonate: new perspectives from cultures and monospecific samples from sediments. *Philosophical Transactions of the Royal Society, London*<br>RENAUD, S., ZIVERI P. AND BROERSE, A. T. C., (submitted). Seasonal and geographical variations of the coccolithophore *Calcidiscus leptoporus*: Differential fitness of morphotypes in a multidimensional ecological space. *Marine Micropaleontology*. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff<br><br>NB SECONDMENT<br>A. T. C. Broerse (postdoctoral researcher) worked at the NHM and Southampton for 6 months from 15th Jan 2001 on a CODENET-related project, but her salary at this time was paid by a UK grant. | |

Annex B
**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

**Reporting Period: 45 months ending September 2001**

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|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Université de Caen Basse Normandie<br>L32, L25 |
| Name of the scientist in charge | Pr. Chantal Billard |
| Number of individual researchers contributing to the joint activities of the network<br>Total number of man-months spent on the project | 4<br>68.5 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]:<br>- name and nationality (ISO Code)<br>- date of birth<br>- start date and duration of the appointment in months<br>- category of researcher<br>- scientific speciality[1]<br>- list of publications in refereed journals | <br>Ian Probert, GB<br>03/12/68<br>1//01/98, 45 months<br>Post Doctoral Researcher<br>L35, L32, E23<br>GEISEN M., BILLARD C., BROERSE A.T.C., CROS L., PROBERT I., AND YOUNG J. R. (submitted). Life-cycle associations involving pairs of holococcolithophorid species : Intraspecific variation or cryptic speciation? Submitted to *European Journal of Phycology*.<br>GEISEN M., PROBERT I, & YOUNG J.R. (in press). Coccolithophores for exhibition. *Journal of Nannoplankton Research*<br>STOLL, H.M, KLAAS, C., PROBERT, I. P.,RUIZ-ENCINAR, J., GARCIA-ALONSO, J.I. (in press). Calcification rate and temperature effects on Sr partitioning in coccoliths of multiple species of coccolithophorids in culture**.** *Global and Planetary Change***.**<br>STOLL, H.M, RUIZ-ENCINAR, J., GARCIA-ALONSO, J.I., ROSENTHAL, Y., KLAAS, C., AND PROBERT, I. (in press). A first look at paleotemperature prospects from Mg in coccolith carbonate: cleaning techniques and culture measurements. *Geochemistry, Geophysics, Geosystems*.<br>STOLL, H.M., ZIVERI, P., GEISEN, M., PROBERT, I., AND YOUNG, J.R. (in press). Potential and limitations of Sr/Ca ratios in coccolith carbonate: new perspectives from cultures and monospecific samples from sediments. *Philosophical Transactions of the Royal Society, London*<br>+ 8 mss in prep. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff | |

Notes:

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**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

**Reporting Period: 45 months ending September 2001**

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|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Alfred Wegener Institute - Bremerhaven<br>L22, L32, L35 |
| Name of the scientist in charge | Linda Medlin |
| Number of individual researchers contributing to the joint activities of the network<br>Total number of man-months spent on the project | 4<br>56 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]:<br>- name and nationality (ISO Code)<br>- date of birth<br>- start date and likely duration of the appointment in months<br>- category of researcher<br>- scientific speciality[1]<br>- list of publications in refereed journals | <br>Alberto Garcia-Saez, ES<br>22/10/65<br>01/03/98, 43 months<br>Post Doctoral Researcher<br>L22, L23, L35<br>SÁEZ A. G., ENGEL H., MEDLIN L. AND HUSS V. A. R. (2001). Plastome size and a possible heterogeneous base composition of nuclear DNA from *Ochrosphaera* (Prymnesiophyta). *Phycologia*, **40**: 147-152.<br>+ 5 mss in prep. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff | |

Notes:

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**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

**Reporting Period: 45 months ending September 2001**

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|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Consejo Superior de Investigaciones Cientificias-ICM<br>L35 E23 |
| Name of the scientist in charge | Prof. Marta Estrada |
| Number of individual researchers contributing to the joint activities of the network | 10 |
| Total number of man-months spent on the project | 89 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]: | |
| - name and nationality (ISO Code) | Kornelis van Lenning, NL |
| - date of birth | 02/04/64 |
| - start date and likely duration of the appointment in months | 01/04/98, 42 months |
| - category of researcher | Post Doctoral Researcher |
| - scientific speciality[1] | L35 |
| - list of publications in refereed journals | LATASA et al. (2001) *Chromatographia*, **53**, pp. 385-391.<br>Van LENNING ET AL. (in prep for *J. Phycol.*) Pigment analysis and genetic characterisation of the Pavlovales (Haptophyte).<br>Van LENNING ET AL. (in prep for *J. Phycol.*) Variable pigment patterns among cultured haptophytes versus current taxonomy and phylogenetic relationships.<br>Van LENNING ET AL. (in prep for *Limnol. Oceanogr.*) Distribution and pigment composition of *Prochlorococcus* populations in the coastal upwelling influenced Canary region. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]: | |
| - name and nationality (ISO Code) | |
| - destination | |
| - date of birth | |
| - start date and likely duration of their secondment in months | |
| - category of staff | |

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**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

Reporting Period: 45 months ending September 2001

MNHN-UL

| | |
|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Museu Nacional de Historia Natural da Universidade de Lisboa<br>E22, E23, L35 |
| Name of the scientist in charge | Mario Cachao |
| Number of individual researchers contributing to the joint activities of the network<br>Total number of man-months spent on the project | 7<br>54.5 |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]:<br>- name and nationality (ISO Code)<br>- date of birth<br>- start date and likely duration of the appointment in months<br>- category of researcher<br>- scientific speciality[1]<br>- list of publications in refereed journals | |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff | <br>Alexandra Duarte Silva<br>NHM<br>13/06/1975<br>1/3/2000 – 1 month<br>research student |

**TMR RESEARCH NETWORKS**
**INFORMATION ON EACH PARTICIPANT**

Contract Number: ERBFMRXCT97 0113

Reporting Period: 45 months ending September 2001

| | |
|---|---|
| Name of the network participant<br>Their scientific speciality[1] | Nederlands Insituut voor Onderzoek der Zee<br>E22, E23 |
| Name of the scientist in charge | Jaap Sinninghe-Damste |
| Number of individual researchers contributing to the joint activities of the network<br>Total number of man-months spent on the project | 9 (inc 3 at U. Bremen*)<br>90 (inc 37 at U. Bremen) |
| For each researcher *whose salary or fellowship is financed* by the network contract[3]:<br>- name and nationality (ISO Code)<br>- date of birth<br>- start date and duration of the appointment in months<br>- category of researcher<br>- scientific speciality[1]<br>- list of publications in refereed journals | <br>Hanno Kinkel DE<br>06.03.1968<br>01/07/1999 36<br>Post Doctoral Researcher<br>E-22, E-23<br>BAUMANN, K.-H., M. CEPEK AND H. KINKEL (2000). Coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity. Use of Proxies in Paleoceanography - Examples from the South Atlantic. G. Fischer and G. Wefer. Berlin, Heidelberg, Springer.<br>DITTERT, N., K.-H. BAUMANN, T. BICKERT, R. HENRICH, R. HUBER, H. KINKEL AND H. MEGGERS (2000). Carbonate dissolution in the deep sea: Methods, quantification and paleoceanographic application. Proxies in paleoceanography. G. Fischer and G. Wefer. Berlin Heidelberg, Springer-Verlag.<br>KINKEL, H., K.-H. BAUMANN AND M. CEPEK (2000). Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability. *Marine Micropaleontology, **39**,* 87-112. |
| For each researcher or support technician seconded under the network contract to another participant for one month or more[4]:<br>- name and nationality (ISO Code)<br>- destination<br>- date of birth<br>- start date and likely duration of their secondment in months<br>- category of staff | |

* The University of Bremen team has been formally included in the CODENET project as part of the NIOZ team, through revision of the contract .

Annex C

# TMR RESEARCH NETWORKS
# STATISTICAL SUMMARY

Contract Number: ERBFMRXCT97 0113.

Reporting Period: 45 months ending. 30/09/2001

| | |
|---|---|
| Total number of individual research staff contributing to the joint activities of the network during the reporting period | 67 |
| For those researchers whose salaries or fellowships have been financed by the contract:<br><br>- Total number of such researchers whose appointments started during the reporting period<br><br>- Total number of such researchers working for the network at the end of the reporting period<br><br>- Number of man-months provided by these young researchers during the reporting period | <br><br>8<br><br>6<br><br>281 |
| For all researchers or support technicians seconded for one month or more from one team of the network to another during the reporting period[1]:<br><br>- Number<br><br>- Number of man-months involved | <br><br>3 (+ numerous shorter visits)<br><br>3.5 (ca 12 including shorter visits) |
| Number of coordination meetings and workshops held during the reporting period involving all network participants and number of participants at each. | 9<br>Sept 98, Blagnac France, 28 participants.<br>Feb 99, Caen, 14 participants.<br>March 99, NIOZ, 27 participants.<br>Sept 99, Blagnac, 30 participants<br>Feb 00, NHM, 18 participants.<br>June 00, Blagnac France, 17 participants.<br>Sept 00, Bremen, 28 participants<br>Feb 01, ICM Barcelona, 20 participants<br>Aug 01, Blagnac France, 25 participants. |
| Joint publications during the reporting period[2]:<br><br>- Total number<br><br>- Number in refereed journals (please send a copy of each in annex) | <br><br>20 published, in refereed journals (includes 2 co-edited special issues).<br>2 submitted.<br>14near submission |

Notes:

a. Seconded staff are those who spend at least one month working at one of the other teams in the network, while remaining in the employment of the seconding team.

b. Joint publications are publications by researchers from at least two of the network participants. Please avoid double counting from one reporting period to the next.

## 3. JOINT PUBLICATIONS

Publications resulting from the CODENET project and involving participants from two or more CODENET teams. Network funded young visiting researchers are indicated by underlining.


BAIRBAKHISH, A.N., BOLLMANN, J., SPRENGEL, C., & THIERSTEIN H.R (1999): Disintegration of aggregates and coccospheres in sediment trap samples. *Marine Micropaleontology*, **37**, 219-223. (CODENET Participants ETHZ ANB, JB, HRT, Bremen-CS)

BOLLMANN, J., BAUMANN K.-H. AND THIERSTEIN, H. R., (1998). Global dominance of *Gephyrocapsa* coccoliths in Late Pleistocene: Selective dissolution, evolution, or global environmental change?, *Paleoceanography*, **13**, 517-529. (CODENET Participants ETHZ-JB, HRT, Bremen-KHB)

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# Summary Report

| | |
|---|---|
| **Network acronym** | CODENET |
| **Title** | Coccolithophorid evolutionary biodiversity and ecology network |
| **Contract number** | ERBFMRXCT9701113 |
| **Contractual period** | Start date 1998-01-01, end date 2001-09-31. Duration 45 months |
| **Co-ordinator** | Young, Jeremy, The Natural History Museum, Cromwell Road, London, SW7 5BD, GB, 44-171-938-8996, 44-171-938-9277, jy@nhm.ac.uk |
| **Other participants** | Thierstein, Hans, Geologisches Institut, Eidgenössische Technische Hochschule, Zürich, CH<br><br>Ganssen, Gerald, Vrije Universiteit Amsterdam, Faculteit der Aardwetenschapen, Amsterdam, NL<br><br>Billard, Chantal, Université de Caen Basse-Normandie, Caen, FR<br><br>Medlin, Linda, Alfred-Wegener-Institute for Polar & Marine Research, Bremerhaven, DE<br><br>Estrada, Marta, Consejo Superior de Investigaciones Cientificias - Instituto de Ciencias del Mar, Barcelona, ES<br><br>Cachao, Mario, Museu Nacional de Historia Natural da Universidade de Lisboa, Lisboa, PT<br><br>Sinninghe Damste, Jaap, Nederlands Instituut voor Onderzoek der Zee, Texel, NL |

**Objectives**

This project was an integrated multidisciplinary study of six coccolithophorid species addressing fundamental aspects of high level biological diversity within the group, micro-evolutionary pattern and process, and their ecological adaptation and impact.

Coccolithophorids are a major component of the oceanic microplankton of great interdisciplinary interest. For marine biologists, they are one of the main open ocean primary producers. For biogeochemists, they play key roles in the global carbon, carbonate and sulphur cycles For marine geologists, coccoliths constitute the single most important component of deep-sea oozes and chalks. We united this group of interests, via a programme involving geologists, biochemists and biologists to understand current biodiversity within the coccolithophorids, to explore microevolutionary pattern and process within the group and to reveal their adaptive responses to environmental change. We selected six keystone taxa and studied their

- Molecular genetics (AWI)
- Lipid and pigment chemistry (NIOZ, CSIC)
- Life-cycles (U. Caen)
- Cytology (U. Caen)
- Coccolith ultrastructure (NHM)
- Phylogenetic relations (NHM, AWI)
- Physiological responses to varying growth conditions (NIOZ, NHM, ETHZ, CSIC, U. Caen)
- Seasonal distribution, and biogeography (NHM, ETHZ, VUA, CSIC, MNHN-UL)
- Morphometric variability at present day and in the fossil record (NHM, ETHZ, FdA-VUA, CSIC, MNHN-UL).
- Contribution to modern and ancient fluxes of carbonate from the plankton to the sediment archive (VUA, U. Bremen).

Each of these tasks constituted a discrete sub-project for which the network provides an ideal framework, via provision of cultures, pooling of experience and direct interaction with related sub-projects. These individual sub-projects were integrated into three major work areas to answer specific questions concerning

1) The diversity within coccolithophorids and the characterisation of stable genetically controlled aspects of that diversity.
2) How and why species evolve.
3) The ecological adaptations within the group.

This research contributed greatly to our knowledge of this key algal group and substantially advanced our conceptual understanding of evolutionary biodiversity and ecology in the world's oceans today and in the past.

**Partnership**
The project united eight first rate European teams with diverse specialisations but a common interest in coccolithophorids. Our focus on six key species provided a basic framework for uniting the different research strands, and this was reinforced through common use of culture strains, joint cruisework, and co-ordinated laboratory experiments. Most importantly the individual studies provided complimentary data on phylogeny, intraspecific variability and ecological adaptation enabling us to address larger scale questions than would otherwise be possible.
*Broader participation*: In addition to the eight lead institutes, workers from many other institutes participated in the project. In particular a team from the University of Bremen lead by Dr Karl-Heinz Baumann, and Heather Stoll of University of Oviedo participated as, in effect, additional teams. Other participants contributing to the project came from: Bochum University, Bristol University, Cambridge University, Erlangen University, U. Firenze, Instituto Hidrografico and IPIMAR (Lisbon), Leiden University, U. Milano, Tsukuba University and NIES, University College London, Southampton University.

**Applications**
Specialist studies in the network contributed to knowledge across the spectrum of disciplines involved, including for example:
a. The application of molecular genetics to phytoplankton studies
b. Calibration and development of the Uk37 palaeothermometry technique
c. Phytoplankton pigment characterisation;
d. Palaeoceanographic and climate change information retrieval from calcareous nannofossils.
Many of these techniques have direct or indirect application within industry, notably the petroleum geology industry, so relevant results of the project have been communicated at joint industrial-academic meetings.

**Training aspects**
The network funded seven three year+ visiting researcher posts (in total 282 man months). In addition the teams included a number of other, nationally funded, young post doctoral researchers, PhD and MSc students. All these participants both learnt the specialist techniques of their host institutes and benefited from working on an international multidisciplinary project.
Training opportunities were maximised through short exchange visits, workshops and advanced training courses, aimed at ensuring that all participants gain familiarisation with the full range of research methodologies employed in the project, including: molecular genetics, organic geochemistry, biological oceanography, algal culture isolation and growth, oceanographic sample collection and analysis especially of sediment traps, image analysis and phylogenetic analysis techniques.

**Results and achievements**
These are being reported in the scientific literature and on our web site.
Significant achievements have been made in all the main research areas of the project, including:

- Establishment of a large new collection of isolated strains of the target species, and several other coccolithophorid species (ca 200 strains in total).
- First isolation of phytoplankton species from the deep photic zone.
- Production of first multi-species 18 sRNA and TufA tree for the coccolithophorids and high-quality molecular clock based on integration of this with palaeontological data.
- Discovery that oceanic coccolithophores have evolved repeatedly from coastal species, including a major recolonisation event following the end Cretaceous extinctions. Demonstration that this has caused repeated adaptations of the pigment composition which provides new insight to the ecophysiology of the photosynthetic apparatus.
- Use of integrated cruisework and laboratory experiments for parallel development and testing of a range of novel techniques in pigment analysis, organic biomarker study, geochemical proxies and phytoplankton distribution.
- Proof that coccolithophorids have an unusual two phase life-cycle with discrete asexually reproducing haploid and diploid phases characterised by different coccolith types. New understanding of coccolithophorid life-cycles and biomineralisation based on discovery of combination coccospheres and culture studies.
- Development of detailed models of intraspecific variation in the key species through integrated laboratory and field studies. Discovery of numerous sibling species and cryptic speciation, development of model of sub-species selection based on this.
- Production of an open access reference database of nannoplankton images EMIDAS.

**Keywords:**
Marine biology, palaeontology, phycology, molecular genetics, organic geochemistry

**Network Home Page**
http://www.nhm.ac.uk/hosted_sites/ina/CODENET/details.htm

# NETWORK BUDGET SUMMARY 1998-2001 (excluding ETH Zürich)

| PAYMENTS | Allocation in contract | reallocations | Allocation (after reallocations) | advance | 1st annual | 2nd Annual | 3rd annual | Total paid | Allocation remaining (after reallocatio) |
|---|---|---|---|---|---|---|---|---|---|
| 1. NHM | 227792.4 | -3323.83 | 224469 | 68312 | 45369 | 56184 | 26956 | 196821 | 276 |
| 3. FdA-VUA | 264600 | 3323.83 | 267924 | 79350 | 24644 | 90989 | 55892 | 250875 | 170 |
| 4. U. Caen | 188038 | 13000.00 | 201038 | 56390 | 47229 | 49374 | 31198 | 184192 | 168 |
| 5. AWI | 250179 | | 250179 | 75026 | 47137 | 54082 | 55948 | 232193 | 179 |
| 6. CSIC | 202680 | | 202680 | 60781 | 32160 | 37746 | 32202 | 162889 | 397 |
| 7. MNHN-UL | 57600 | | 57600 | 17274 | 10326 | 11984 | 6939 | 46523 | 110 |
| 8. NIOZ | 241000 | -13000.00 | 228000 | 72273 | 31056 | 52167 | 35783 | 191278 | 367 |
| TOTAL | 1431889.4 | | 1431889 | 429406 | 237921 | 352526 | 244919 | 1264771 | 1671 |
| % Of BUDGET | | | | 30.0 | 16.6 | 24.6 | 17.1 | 88.3 | 1 |

N.B. Budget reallocations between partners
1. 3323.83 euros were reallocated from the NHM to the VUA budget in 1998 to compensate VUA for expenses met on behalf of the network as a whole.

2. 13000 euros were reallocated from the NIOZ to the U. Caen budget in 2001 to allow U. Caen to continue employment of the YVR Ian Probert while he undertook collaborative experiments

| COSTS | Allocation (after reallocations) | Costs incurred (from annual cost statements) | | | | | Overspend (allocation total costs incurred) |
|---|---|---|---|---|---|---|---|
| | | 1998 | 1999 | 2000 | 2001 | Total | |
| 1. NHM | 224469 | 46960 | 68115 | 58309 | 50913 | 224297 | -1 |
| 3. FdA-VUA | 267924 | 26492 | 104835 | 93314 | 66302 | 290943 | 230 |
| 4. U. Caen | 201038 | 48542 | 59224 | 59278 | 35456 | 202499 | 14 |
| 5. AWI | 250179 | 48884 | 67186 | 90892 | 53688 | 260650 | 104 |
| 6. CSIC | 202680 | 33575 | 48362 | 60512 | 60235 | 202684 | |
| 7. MNHN-UL | 57600 | 10729 | 15001 | 14984 | 18571 | 59285 | 16 |
| 8. NIOZ | 228000 | 32739 | 64790 | 67629 | 63986 | 229144 | 11 |
| TOTAL | 1431889 | 247921 | 427512 | 444919 | 349151 | 1469502 | 376 |
| % Of BUDGET | | 17.3 | 29.9 | 31.1 | 24.4 | 102.6 | |

NB Overspends - these were incurred by the participants in the knowledge that they would not be reimbursed by the EU.

**SUBDIVISION OF COSTS BY CATEGORY**

| YEAR | PERSONNEL COSTS | NETWORK COSTS | DIRECT COSTS | OVERHEADS | TOTALS |
|---|---|---|---|---|---|
| 1998 | 150186 | 30049 | 27872 | 39813 | 249919 |
| 1999 | 244292 | 58931 | 62164 | 62126 | 429511 |
| 2000 | 251955 | 52913 | 78053 | 61997 | 446919 |
| 2001 | 189862 | 59584 | 56932 | 42774 | 351152 |
| TOTALS | 836296 | 201477 | 225021 | 206709 | 1469503 |
| % | 56.9 | 13.7 | 15.3 | 14.1 | |

NB Cost adjustments

1. The NHM figures for 2000 included an adjustment to previous costs of -961ecu, following recovery of VAT, this has been deducted from the direct costs declared.

2. The NIOZ figures for 2001 included an adjustment to previous costs of +14453ecu, following reassessment of social costs of employment of the YVR, this has been added to the personnel costs declared.

# CODENET COST STATEMENTS 2002

**SUMMARY COST STATEMENT TO BE COMPLETED BY THE NETWORK COORDINATOR**

**(ECU only)**

for the period from 1 Jan 2002 to 30 Sept 2002
Project Short Title: CODENET
Contract N_: ERBFMRXCT97 0113

| NAME OF PARTNER[1] | Personnel Costs | Networking Costs | Other Direct Costs | Overheads | VAT and Adjustments | **TOTAL** |
|---|---|---|---|---|---|---|
| 1. NHM | 24553 | 12433 | 8063 | 5864 | 0 | 50913 |
| *2. ETHZ** | 31850 | 4651 | 9123 | 0 | 0 | 45624 |
| 3. FdA-VUA | 40163 | 7119 | 7969 | 11050 | 0 | 66302 |
| 4. U. Caen | 30746 | 4088 | 0 | 622 | 0 | 35456 |
| 5. AWI | 34156 | 4275 | 13379 | 1879 | 0 | 53688 |
| 6. CSIC | 24604 | 19772 | 5820 | 10039 | 0 | 60235 |
| 7. MNHN-UL | 0 | 8000 | 7476 | 3095 | 0 | 18571 |
| 8. NIOZ | 21187 | 3896 | 14226 | 10225 | 14453 | 63986 |
| **TOTAL** (exc ETHZ): | 175409 | 59584 | 56932 | 42774 | 14453 | 349151 |

* ETHZ is separately funded, from Swiss national research funds and so is not included in the totals.

The signed original copy of each Participant's Cost Statement is attached.

Certify by the Network Co-ordinator on behalf of the Participants as reasonable for the work under the contract.

Name: Dr. Jeremy R. Young

Signature:

Date: 23rd January 2002

14 The Contractor should appear as the first partner in the list, followed by the Associated Contractors given in the order shown in Part A of Annex I to the Contract.

If a Participant does not submit a Cost Statement, insert "no statement" in the column "VAT and Adjustments". If the Cost Statements for any Participant cover more than one reporting period, indicate the number of periods in the column "VAT and Adjustments"; separate Cost Statements should be submitted for each period.