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The evolution of *Eucoronis fridtofjanseni*, n. sp. and its application to the Neogene biostratigraphy of the Norwegian-Greenland Sea

ABSTRACT

Eucoronis fridtofjanseni, n. sp. is abundantly preserved in hemipelagic sediments of the Norwegian-Greenland Sea ranging in age from approximately 8 to 10.5 Ma. Its first and last appearances are abrupt, and it is easily distinguishable from other constituents of the high latitude radiolarian subfauna. Moreover, its stratigraphic range can be conveniently used to establish a new range zone within the radiolarian biozonation. *Eucoronis fridtofjanseni* evolved from a secondary branch of the *Corythospyris* lineage. A single dichotomy occurred in this lineage in the Middle Miocene and eventually gave rise to *Eucoronis* morphology with *Corythospyris jubata* and *Clathrospyris sandellae* as intermediate species. These intermediates represent a reversal of the major evolutionary trend with the development of complex skeletal forms from a simpler precursor. The evolutionary cycle regresses to a simple lattice design in *E. fridtofjanseni*. Both *E. fridtofjanseni* and the stem lineage acquired pairs of large sagittal lattice pores on the front and back of the lattice shell. *Eucoronis* is emended.

INTRODUCTION

Eucoronis fridtofjanseni, n. sp. has special significance for 2 reasons. First, this species represents an example of convergence in which a high latitude lineage has evolved, apparently independently, to a skeletal morphology similar to that of contemporaneous equatorial species. Second, the stratigraphic range of *E. fridtofjanseni* defines the boundaries of a new biostratigraphic zone (biozone) in a previously unzoned interval (interzone) of the radiolarian zonal scheme for the Norwegian-Greenland Sea (Bjørklund, 1976). Consequently, the present paper has the triple purpose of describing the new species, discussing its evolution and providing a definition for the *E. fridtofjanseni* Range zone.

A system of form genera is employed in this paper. In an earlier revision of the Trissocyclidae, Goll (1968, 1969) proposed 4 phyletic genera to include all the species in this family. Such an extreme reduction in the number of genera resulted in broad complex generic definitions that have not been easy to interpret by other specialists. Moreover, the frequent development of homeomorphs in evolutionarily quite distinct lineages creates havoc with broad phyletic genera. In more recent contributions, Goll (1976, 1978, 1979) has used a larger number of smaller, more concisely defined genera that have only limited evolutionary significance. Such a system benefits from simplicity, but species that are members of the same lineage may be assigned to different genera as successive skeletal transformations occur.

Eucoronis fridtofjanseni is a member of the Trissocyclidae, a nas-sellarian family that is represented by only 2 species each in Holocene Antarctic and subarctic Pacific sediments, whereas approximately 25 trissocyclid species presently inhabit tropical waters. This low diversity for the Trissocyclidae in the Antarctic appears to have persisted throughout the Cenozoic (Chen, 1975). Sediments from the subarctic Pacific older than Pliocene are either barren of siliceous microfossils (Kling, 1973) or contain only rare, moderately preserved radiolarians (Ling, 1973), and it is not possible at the present time to document the full course of trissocyclid evolution in this region. Surface sediments of the deep Arctic Basin are largely barren of siliceous microfossils (Herman, 1969), and sediments unequivocally older than Late Pleistocene have not been sampled, with the exception of a single, small occurrence on the Alpha Cordillera (Ling, McPherson and Clark, 1973). Moreover, there is no published record of trissocyclids in Arctic plankton [the 2 species identified as *Aegospyrus* sp. and *Tholospyris gephyristes* by Hülsemann (1963) are not trissocyclids], and our knowledge of the present and past distributions of these organisms in the central Arctic region is completely lacking.

The situation is considerably different in the Norwegian-Greenland Sea, however, where radiolarians in the plankton have been thoroughly reported (Cleve, 1899; Jørgensen, 1905). Holocene sediments of this basin complex have been extensively cored, and sediments containing siliceous microfossils as old as Early Eocene have been drilled by the Deep Sea Drilling Project (Talwani et al., 1976, 1978). The same two modern trissocyclids that occur in the North Pacific, *Lophospyris pentagona* (Ehrenberg) and *Triceraspyris?* sp. Ling (1973, 1974) are also present in the Norwegian-Greenland Sea, but they occur in much lower frequencies and occupy distinctively different provinces. Neither of these species has a direct ancestry in this basin dating back before Pliocene time, however. Trissocyclids are abundant in the siliceous oozes older than Early Pliocene, and the family is represented by a single lineage that has *Corythospyris fiscella* as its ancestral species (Goll, 1978). From Eocene to Early Miocene time, this lineage was monotypic, evolving slowly as a series of morphs that have not yet been adequately examined. The last remnants of this lineage eventually disappeared in Norwegian-Greenland Sea sediments of Late Pliocene age.

The *Corythospyris* lineage appears to have undergone a single cladogenesis in the Middle Miocene that involved a major skeletal transformation to *Clathrosopyris sandellae* Goll, 1979a. *Clathrosopyris sandellae* then gave rise to *Eucoronis fridtofjanseni* in the Late Miocene, and it is on the latter evolution that this paper is focused. The secondary lineage, which consists of only *C. sandellae* and *E. fridtofjanseni*, is relatively short-ranging. Both species are abundantly preserved in lower Upper Miocene sediments, and the disappearance levels of both species in the Norwegian-Greenland Sea are essentially coincident at about 8 Ma.

STRATIGRAPHY

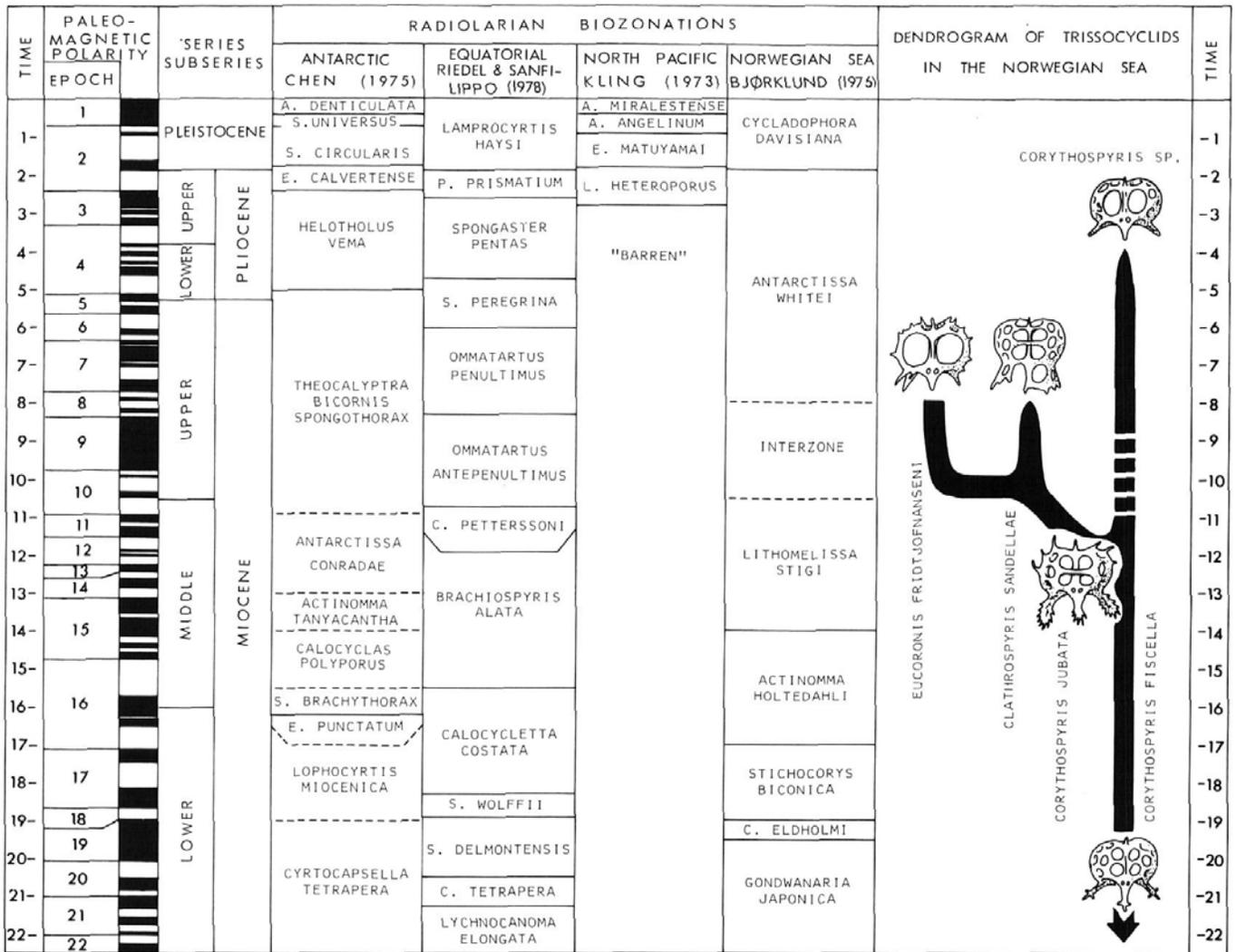
Tertiary marine planktonic microfossil assemblages of the Norwegian-Greenland Sea were essentially unknown before 1974, when *Glomer Challenger* (DSDP Leg 38) drilled 17 holes in the sea floor on and north of the Iceland-Faeroe Ridge (Talwani et al., 1976, 1978). Drilling sites were selected primarily to provide information bearing on the complex tectonic history of this region, and most of the holes were only discontinuously cored. Sediments recovered from this drilling are varied in nature, and include thick turbidites and sections deposited subaerially and at neritic depths. Poorly sorted sandy muds of presumably glacial marine origin form the uppermost unit in each hole, but hemipelagic sediments with major ooze components were penetrated below this unit in sites on the Vøring Plateau (Sites 338-343) as well as 2 other sites, one

on the Iceland-Faeroe Ridge (Site 336) and the other on the Iceland Plateau (Site 348). The provincial nature of the microfossils in these sections poses special problems because these can not be confidently correlated with tropical and temperate biozonations or chronostratigraphic units. These problems are compounded by the restricted occurrence of calcareous microfossils in Norwegian-Greenland Sea sediments. Foraminifera and calcareous nannofossils are abundant in only the Oligocene sediments, and their restricted diversity is a further obstacle to accurate correlation. Siliceous microfossils are generally well preserved in the hemipelagic sediments, and series/subseries boundaries were assigned largely on the basis of Neogene diatoms and Paleogene silicoflagellates by intermediate correlation with North Pacific sections. Eleven papers dealing with marine microfossils in Leg 38 recovery have been published in Talwani et al. (1976, 1978).

The radiolarian biozonation proposed by Bjørklund (1976) was new, and based on the stratigraphic ranges of species that have not been reported from other regions. Therefore, its relationship to the standard Cenozoic chronostratigraphic units could be determined only by comparison with other fossil biozonations (Schröder et al., 1976). If this correlation with absolute time is correct, the Norwegian-Greenland Sea radiolarian biozonation can be compared with the radiolarian biozonations for the Antarctic and Pacific (text-fig. 1). The stratigraphic range of *Eucoronis fridtofjanseni* is restricted to the Upper Miocene, and consequently only the Neogene portions of these biozonations are shown in text-figure 1. The radiolarian biozonation of Bjørklund (1976) is not complete, as there is an interzone in the lower Upper Miocene, in which the radiolarian assemblage was regarded too homogeneous to provide biostratigraphic control. Re-examination of this material, however, reveals that the stratigraphic range of *E. fridtofjanseni* is ideally suited to defining a new biozone to fill this former interzone.

The base of the *Eucoronis fridtofjanseni* Range-zone is defined as the first appearance of *E. fridtofjanseni* and is coincident with the top of the *Lithomelissa stigi* Zone of Bjørklund (1976), which hitherto had been undefined. The last consistent occurrence of the nominate taxon marks the top of the *E. fridtofjanseni* Range-zone, which is coincident with the base of the *Antarctissa whitei* Zone. The definition of the *A. whitei* Zone must be emended to a partial range zone, because early specimens of *A. whitei* are at variance with the original description of this species (Bjørklund, 1976), and the base of its biostratigraphic range is uncertain.

Sediments assignable to the *E. fridtofjanseni* Range-zone were recovered only in 3 of the Leg 38 drilling



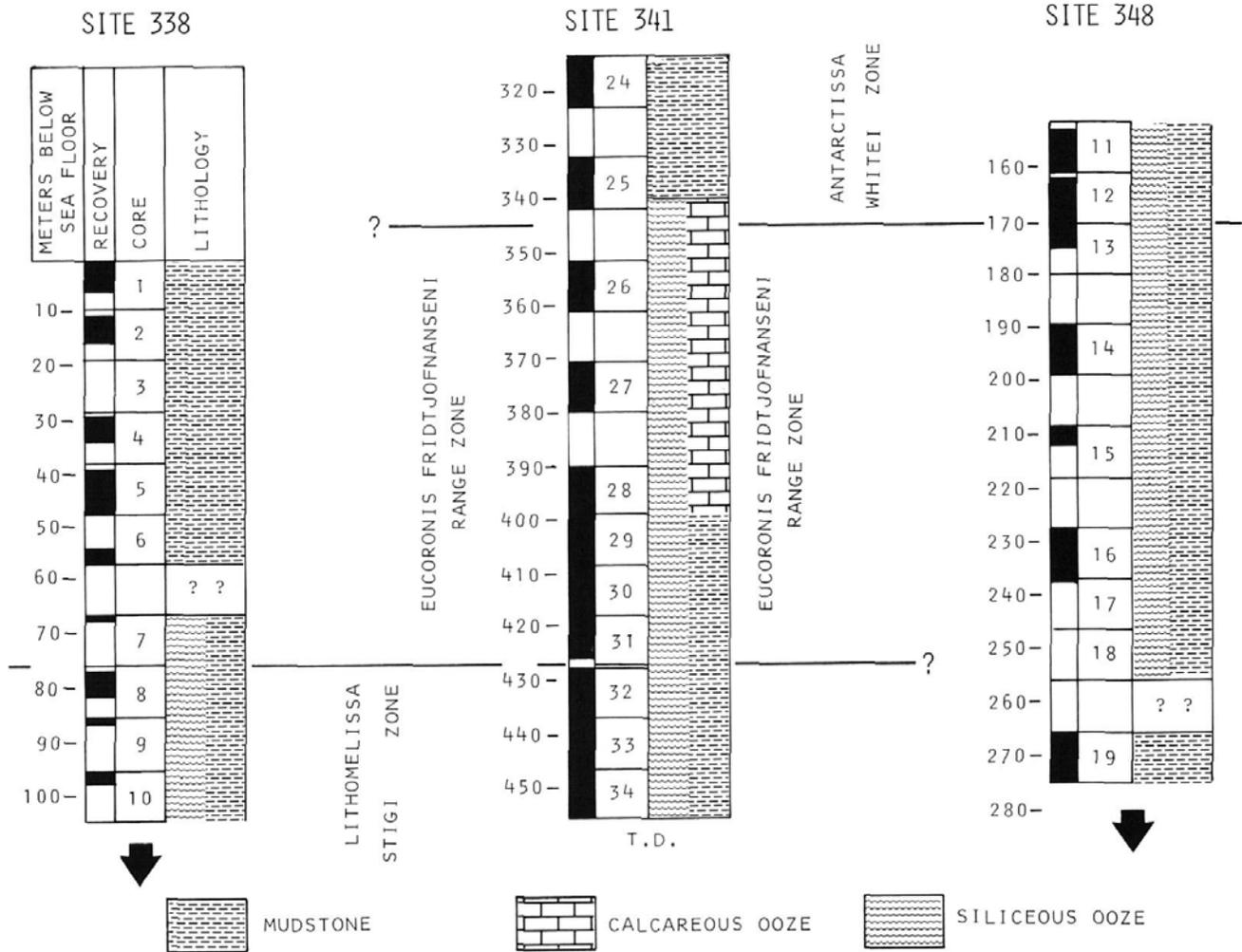
TEXT-FIGURE 1
 Chart comparing absolute time, paleomagnetic stratigraphy and 4 radiolarian biozonations with dendrogram of the Neogene trissocyclid lineage in Norwegian-Greenland Sea sediments. Paleomagnetic stratigraphy is from LaBrecque, Kent and Cande (1977). Ages of equatorial Pacific zonal boundaries follow Bjørklund and Goll (1979).

sites (338, 341, 348), and both the base and top of the zone are present only in the recovery from Site 341. This site serves as the type locality (Vøring Plateau, latitude 67°20.10'N., longitude 06°06.64'E., water depth 1439 m). The type section includes cores 26 to 31 and ranges from 351.5 to 427.5 m below the sea floor. However, there is a 9.5 m uncored interval between cores 25 and 26, and conceivably the true thickness of the type section may extend somewhat higher than 351.5 m.

The stratigraphic ranges in the type section of the taxa discussed in this paper, as well as certain accessory species described by Bjørklund (1976), are shown in table 1. The frequency of occurrence designations: + (present), R (rare), C (common), A (abundant), VA (very abundant), D (dominant) are defined by

Bjørklund and Goll (1979). Because the total number of Radiolaria from our samples on microscope slides varied over a wide range, we normalized these frequency designations to values equivalent to counts of 25,000 specimens. *Eucoronis fridtofjanseni* is common to dominant in all but 2 of the samples that we have examined from the type section, and the species is easily distinguished from the 2 other concurrent trissocyclids.

The correlation proposed here for Sites 338, 341 and 348 is shown in text-figure 2. The state of preservation of siliceous microfossils deteriorates in the middle of core 25 at Site 341, and the lithology grades into a calcareous mud in this core. Only the base of the *E. fridtofjanseni* Range-zone can be recognized at Site 338 (core 7), which consists of siliceous hemipelagic



TEXT-FIGURE 2

Proposed correlation of the 3 DSDP Leg 38 sites of Norwegian-Greenland Sea in which *Eucoronis fridtjofnanseni*, n. sp. occurred. *Abbreviation*: T. D., terminated drilling. Arrows below depicted recovery of Sites 338 and 348 indicate that additional cores were recovered from underlying sedimentary sections.

sediments separated from the overlying calcareous mudstones by a 9.5-m coring discontinuity. These overlying calcareous mud units at Sites 338 and 341 were interpreted as being of glacial marine origin and less than 3 m.y. in age by the shipboard scientific party. Consequently, hiatuses of 4.5 to 7 m.y. were drawn at the base of these units (Schröder et al., 1976, fig. 17). There is no evidence to support this interpretation however, and we conclude that the calcareous muds may represent encroachment by a prograding continental margin. If this scenario is correct, the sections at Sites 338 and 341 are reasonably continuous, and core 26 (Site 341) represents the true top of the *E. fridtjofnanseni* Range-zone. The "glacial" unit is much thinner at Site 348 (cores 1-5) and siliceous microfossils of Late Miocene to Pliocene age occur in variable concentrations in cores 6-18. The concentration and diversity of radiolarians are far too low

to distinguish biozones in the diatomaceous sediments of cores 16-18, but the upper part of the *E. fridtjofnanseni* Range-zone is present in cores 13-15, and well-formed specimens of *A. whitei* occur in core 12.

EVOLUTION

The Neogene portion of the trissocyclid lineage treated here is shown in text-figure 1. The major stock of this lineage, *Corythospyris fiscella* Goll, 1978, has maintained rather stable skeletal morphology since Eocene time. The species displays typical *Corythospyris* test design: a small, finely perforate lattice shell with 3 simple or trifurcate basal spines, a prominent pair of secondary lateral pores on the front of the lattice shell, and a small pair of sagittal lattice pores on the back of the lattice shell below the vertical spine (Goll, 1978, pl. 5, figs. 5-21). Its species-diagnostic characteristic

This morph, labelled simply *Corythospyris* sp. in text-figure 1, replaces *C. fiscella* in Upper Miocene sediments and has a sporadic occurrence in the lower part of the type section (table 1). The abundance of *Corythospyris* sp. increases markedly in core 26 (Site 341), and the species is the terminal member of the stem lineage in the Norwegian-Greenland Sea. The exact level of the last occurrence of *Corythospyris* sp. can not be determined at this time, because of poor opal preservation in core 9 and low recovery in core 10 at Site 348, but the species must have disappeared from the Norwegian-Greenland Sea about 4–6 Ma. Both *Corythospyris* sp. and *C. fiscella* are comparatively small trissocyclids. The width of the lattice shell ranges from 60 to 77 μm (Goll, 1978).

The origins of *Clathrospyris sandellae* are not confidently understood, but we conclude that this species evolved from *C. fiscella* commencing in the Middle Miocene. Massive, thick-walled specimens of *C. fiscella* appear for the first time in the *Gondwanaria japonica* Zone (core 15, Site 338). This morph is in sharp contrast to the delicate thin-walled lattice shells that characterize other species of *Corythospyris* from both high and low latitudes. Two other skeletal transformations are associated with thick wall development on these specimens. The basal spines are progressively larger, more massive and broaden distally to form an irregularly sulcate web. Irregularly distributed spines are present on the top and sides of the lattice shell of some specimens, which were assigned to the new species *Corythospyris jubata* by Goll (1978). *Corythospyris jubata* represents the first stage in the lineage dichotomy that eventually gave rise to *Eucoronis fridtjofnanseni*. The species is short-ranging and has its last occurrence below core 32 at Site 341. We have not yet made a detailed examination of this portion of the lineage, but specimens of *C. jubata* are approximately 20–25% larger in overall size than their immediate precursor. Lattice shell widths range from 76 to 95 μm (Goll, 1978).

Clathrospyris sandellae Goll retains the 6 pairs of sagittal lattice pores that characterize *Corythospyris fiscella* and *C. jubata*, but otherwise the species comprises a diverse assemblage of skeletal types that are distinctively different from *Corythospyris* morphology. A short lattice shell segment below the cephalis is present on some specimens (pl. 1, figs. 17, 20; pl. 2, figs. 12, 14; pl. 3, figs. 1, 2, 5, 6), and other specimens have instead an irregular number of simple basal spines (pl. 1, fig. 19; pl. 2, figs. 11, 13, 16, 17; pl. 3, figs. 3, 8). Goll (1978) attempted to use the presence or absence of such a postcephalic lattice segment as a species-specific criterion to distinguish *Clathrospyris camelopardalis* from *C. sandellae*. However, we con-

clude that there is no systematic difference between these morphs, which are here collectively referred to as *C. sandellae*. Lattice bars are massive, circular in cross section and border subpolygonal lattice pores. The lattice shell is only slightly campanulate on some specimens (pl. 2, fig. 11; pl. 3, fig. 3), whereas other specimens bear a chaotic profusion of short lattice spines (pl. 2, fig. 12; pl. 3, figs. 1–2), and still others have robust tubercles at the junctions of 2 or more lattice bars (pl. 1, fig. 17; pl. 2, figs. 14, 16, 17). At high magnification, clusters of fine spicules are observable on the surfaces of these tubercles (pl. 2, fig. 18) that resemble the fine structure of the axobate of *C. sandellae* (pl. 2, fig. 15), *E. fridtjofnanseni* (pl. 2, fig. 5) and many other trissocyclids. A trissocyclid (*Acanthodesmiidae*, gen. et spp. indet.; Kling, 1973, pl. 8, fig. 8) similar to and perhaps identical with the tuberculate morph *C. sandellae* is preserved in Upper Miocene sediments (*Cannartus petterssoni* Zone) from DSDP Site 173 in the eastern North Pacific. A broad size range is associated with this polytypic skeletal development. Lattice shell widths of *C. sandellae* range from 84–171 μm .

The evolutionary affinities between *C. sandellae* and *E. fridtjofnanseni* are more secure because of the observation of many intermediates. Lattice shells of *E. fridtjofnanseni* are irregularly spinous, and some specimens of this species that appear to be at an early evolutionary stage have remnants of thoracic lattice (pl. 1, fig. 8; pl. 2, fig. 9). Consequently, we conclude that *E. fridtjofnanseni* evolved from the portion of the polytypic *C. sandellae* population that possessed both of these structures. The first stage of the transformation from *C. sandellae* to *E. fridtjofnanseni* involves separation of the front of the cephalic lattice from the sagittal ring. This free portion of the cephalis is rapidly lost, and only traces of its presence are preserved on some individuals (pl. 1, figs. 14, 15; pl. 2, fig. 10). This loss of lattice results in specimens with a large pair of sagittal lattice pores on the front of the lattice shell that occupies the complete height of the sagittal ring (pl. 1, figs. 14–16). The back of the lattice shell remains unchanged, however (pl. 1, fig. 13). These latter specimens have the skeletal characteristics of neither *C. sandellae* nor *E. fridtjofnanseni*, and they are referred to here simply as intermediate specimens. As this evolution progressed, cephalic lattice became restricted to a narrow lateral band that is joined only to the top of the sagittal ring and the extreme sides of the basal ring. This step completes the transition to the stable *E. fridtjofnanseni* morphology. Large sagittal lattice pores are present on both the front and back of the cephalis, and the regular configuration of 6 pairs of sagittal lattice pores, which is diagnostic for *C. sandellae* and *C. fiscella*, is completely disrupted. There is no

uniformity in the number of lattice bars that are joined to the sagittal ring, but many specimens have 3 such pairs of lattice bars, and the lateral portion of each lattice hemisphere is reduced to a single outwardly convex lattice bar (pl. 1, figs. 6–8, 10, 11; pl. 3, figs. 25–26). Skeletons of *E. fridtjofnanseni* retain the robust, massive lattice bars of *C. sandellae*, and the sculptured axobates of the 2 species are similar (compare pl. 2, figs. 5 and 15). The thoracic lattice observed on some "primitive" specimens of *E. fridtjofnanseni* is almost entirely lost in more "advanced" populations, but many specimens retain a single, or pairs of, secondary lateral pores on the front of the skeleton (pl. 1, figs. 10, 11; pl. 3, figs. 21, 25). The development of *E. fridtjofnanseni* morphology represents a stabilization of skeletal design compared to the polytypic nature of *C. sandellae*. The overall size of the skeleton of *E. fridtjofnanseni* is remarkably uniform. The maximum width of the lattice shell ranges from 115–121 μm .

Eucoronis fridtjofnanseni has an abrupt first appearance in the recovery from Site 341 (table 1). The species is absent in core 32 and abundant to dominant in core 31. In a normal stratigraphic succession with constant sedimentation, one would expect the frequency of a new species to increase gradually in progressively younger sediments, at least within the recovery of one core. Although the nature of its first appearance is a positive attribute for *E. fridtjofnanseni* as a zonal index species, such an extreme change in frequency of occurrence between 2 samples no more than 3 m apart suggests that the true history of the first appearance of *E. fridtjofnanseni* is not accurately represented here. There may be a hiatus between these two cores, but there is no other evidence for such a sedimentary structure. More probably, mechanical reworking of younger material down core as a result of drilling disturbance has affected the recovery in core 31.

Alternatively, this recovery may be a reasonably accurate reflection of the actual faunal succession here. The Miocene-Pliocene sections at Sites 338, 341 and 348 contain high concentrations of terrigenous silt and clay (35–75%) and volcanic ash is variably present (table 1). The concentration of radiolarians in our samples from Site 341 fluctuates broadly, and the relative frequencies of individual species also undergo wide changes in abundance. For example, *Hexalonche* sp. A (Bjørklund, 1976) experiences a brief but dramatic dominance in cores 31 and 32, and there is a single abundant occurrence of *Spongotrochus glacialis* Popofsky, 1908 in core 29 (table 1). There are other species not shown in table 1 that have similarly broad occurrence variations. The occurrence of *C. sandellae* also displays great variability at site 341,

being both absent and very abundant in different samples from cores 28 and 29. These observations suggest that the water-masses overlying the Vøring Plateau were quite unstable during this interval of time, with shifting properties that lead to short term blooms of certain species. *Eucoronis fridtjofnanseni* is less variable in its occurrence in Site 341 sediments, and this relative uniformity in the radiolarian fauna may be partly responsible for its high relative frequency. The percentage of *E. fridtjofnanseni* in a two-species subset, including only *C. sandellae*, is shown in column 12 of table 1 to demonstrate the abundance of the former species compared with that of its precursor.

Eucoronis fridtjofnanseni may have been introduced fully formed into the Norwegian-Greenland Sea at the beginning of the Late Miocene. Such an interpretation is supported by its abrupt first occurrence, but the species has not been reported from other localities. We conclude that *E. fridtjofnanseni* must have evolved endemically in the Norwegian-Greenland Sea with *C. sandellae* as its precursor because of the morphological affinities previously discussed. Possibly, the Vøring Plateau was not the locality over which the earliest stages of this evolution took place. Intermediate specimens occur in the type section as high as core 28, and it is apparent that this evolution was not "instantaneous," but transpired over an interval of perhaps 1.5 m.y., unless this recovery is badly mixed.

CONVERGENCE

Reduction of skeletal lattice is the most pervasive evolutionary trend in the Trissocyclidae. This transformation by loss of skeletal elements from ancestors with complex lattice shells to descendant species with simple tests has occurred repeatedly in this group, and the end result may have been the evolution of the so-called "naked" nassellarians. *Eucoronis* morphology represents an advanced stage of this progression, but it is not the simplest skeletal configuration in the Trissocyclidae. *Zygocircus* (as emended by Goll, 1979) is characterized by skeletons consisting only of the sagittal ring or both the sagittal and basal rings. The trend toward loss of lattice is commonly associated with increased regularity in the arrangement of the remaining structural elements (for example, *Trissocyclus stauropora* Haeckel). *Eucoronis* is characterized by chaotic spine development, however, and the regularity of the few lattice components is not exceptional. The variable lattice development of the precursor to *E. fridtjofnanseni*, *C. sandellae*, has been described earlier.

Eucoronis morphology can be explained as an adaptation to living in warm, low salinity surface water. Directional selection in this environment logically favors reduced density of the total living organism

(protoplasm + skeleton). The massive construction of the skeleton of *E. fridtofjanseni* suggests that reduction of mass was not the primary adaptation here. However, both *E. fridtofjanseni* and *C. sandellae* were eventually superseded in the Norwegian-Greenland Sea by trissocyclids with skeletons composed of much more delicate lattice elements.

We have not observed *E. fridtofjanseni*, in sediments from regions other than the Norwegian-Greenland Sea. The species may have lived in the subarctic Pacific, although there is no evidence of its existence in the nonsiliceous Upper Miocene sediments of that region. The species is clearly not present in sediments underlying the northern transition plankton province of the Pacific (DSDP Site 34). If we assume, therefore, that *E. fridtofjanseni* was a polar species, then it follows that *Eucoronis* morphology evolved independently in this region. *Eucoronis* species have existed continuously in tropical oceans since Early Miocene time [*E. circumflexa* (Goll)]. Yet, these high- and low-latitude populations were probably not contiguous. Three equatorial *Eucoronis* specimens that were contemporaries of *E. fridtofjanseni* are shown in plate 1, figures 1-3. The general similarity in skeletal architecture between these specimens and *E. fridtofjanseni* is obvious, although the tropical species are characterized by more delicate lattice construction. There are other aspects of skeletal morphology in which they differ as well. The primary lateral elements, which divide the basal ring into 2 pairs of basal pores on most nassellarians, are extremely slender processes or reduced to short spines on these tropical *Eucoronis* species (pl. 1, fig. 1). For most nassellarians, the basal pores are the primary cephalic apertures through which protrude the lobes of the protoplasmic central capsule (see for example, *Tetraspyris tetracorethra* Haeckel, 1887, pl. 53, fig. 19 and *Lampromitra coronata* Haeckel, 1887, pl. 60, fig. 7). Atrophy of the primary lateral elements on tropical *Eucoronis* species may be associated with the evolution of the shape of the central capsule. Haeckel (1887, pl. 82, fig. 4) illustrated *Eucoronis challengerii* with a small spherical central capsule. The basal pores are not the major apertures of *Eucoronis*, but *E. fridtofjanseni* does not show a similar reduction in the development of the primary lateral bars (pl. 1, fig. 4; pl. 2, figs. 6, 7).

Is the evolution of *E. fridtofjanseni* from its *Clathrospyris* precursor somehow related to the evolution of *Corythospyris* sp. from *C. fiscella*? One can only speculate on this possibility, but the evolutionary trends are similar in both lineage branches. *Eucoronis fridtofjanseni* and *Corythospyris* sp. are quite different morphologically, and most taxonomists regard them as reproductively isolated populations, although we have

proposed that these morphs have had a recent common ancestry. Goll (1976, 1979) and Bjørklund and Goll (1979) have argued that radiolarians of quite disparate skeletal design are capable of hybridization. *Eucoronis fridtofjanseni* essentially replaced *Corythospyris* sp. in the Norwegian-Greenland Sea during the early Late Miocene, but *Corythospyris* sp. occurs in sediments of this age in the North Atlantic (DSDP Site 116). Both species developed pairs of large sagittal lattice pores on the front and back of the lattice shell at approximately the same time. Possibly, interaction between *E. fridtofjanseni* and *Corythospyris* sp. served as the linkage mechanism between the evolution of high- and low-latitude *Eucoronis*.

CONCLUSIONS

Whatever the forcing function that has driven the evolution of *E. fridtofjanseni*, the rapid convergence within this high latitude lineage toward a morphology homologous to a skeletal design common for tropical trissocyclids is quite remarkable. From the frequency of *E. fridtofjanseni* in sediments at Site 341, it is apparent that this species flourished in the Norwegian-Greenland Sea for approximately 2.5 m.y. Ultimately, however, the species was not successful, and the abrupt and approximately simultaneous extinction of *E. fridtofjanseni* and *C. sandellae* is enigmatic. Both of these extinctions followed the reappearance of *Corythospyris* sp. in Site 341 sediments with common or abundant frequencies. Presumably, *Corythospyris* sp. was reintroduced into the Norwegian-Greenland Sea from the North Atlantic as the Iceland-Faeroe Ridge subsided (Thiede, 1979). Intrusion of North Atlantic water may have altered the physical-biological balance of the Norwegian-Greenland Sea in a manner to which *C. sandellae* and *E. fridtofjanseni* were not adapted. Possibly, competition may have been responsible for the extinction of these 2 species. High latitude faunas are characterized by low diversity, and this region may not have been able to support 3 trissocyclids. Although *E. fridtofjanseni* and *C. sandellae* were endemic to the Norwegian-Greenland Sea, *Corythospyris* sp. appears to have been a member of a larger, more broadly distributed population that may have had better survival potential.

Many interesting questions can be drawn from the available data on *E. fridtofjanseni*. Answers to these questions will require observation of this species from other Arctic and subarctic regions, as well as from the Norwegian-Greenland Sea. The present study is based mainly on a single section (Site 341) that may not be complete. New information on the evolution of *E. fridtofjanseni* must await additional drilling or piston coring in localities where Miocene sediments can be penetrated.

SYSTEMATICS

Kingdom PROTISTA Haeckel, 1866
Phylum PLASMODROMA Doflein, 1901
Subphylum SARCOMASTIGOPHORA Honigberg and Balamuth, 1963
Superclass SARCODINA Hertwig and Lesser, 1874
Class ACTINOPODEA Calkins, 1909
Subclass POLYCYSTINA Ehrenberg, 1838
Order NASSELLARIA Ehrenberg, 1875
Superfamily PLAGIACANTHOIDEA Hertwig, 1879, emend. Goll, 1979
Family TRISSOCYCLIDAE Haeckel, 1881, emend. Goll, 1968

Genus *Eucoronis* Haeckel, 1881, **emend.** Goll and Bjørklund, 1979

Eucoronis HAECKEL, 1881, p. 445; 1887, pp. 976–977.—
CAMPBELL, 1954, p. D108.—PETRUSHEVSKAYA, 1971, p. 267.

Emended diagnosis: The genus *Eucoronis* includes trissocyclids with a simple, sparsely trellised lattice shell consisting of a single irregularly spinous chamber. One or more arches of lattice are joined to the top of the sagittal ring and lateral surfaces of the basal ring, and frame a large pair of sagittal lattice pores on both the front and the back of the lattice shell. There is no regular thorax nor systematically disposed basal spines, and the lattice shell does not enclose the top of the sagittal ring.

Type species: *Eucoronis perspicillum* Haeckel, 1887, by subsequent designation of Campbell, 1954.

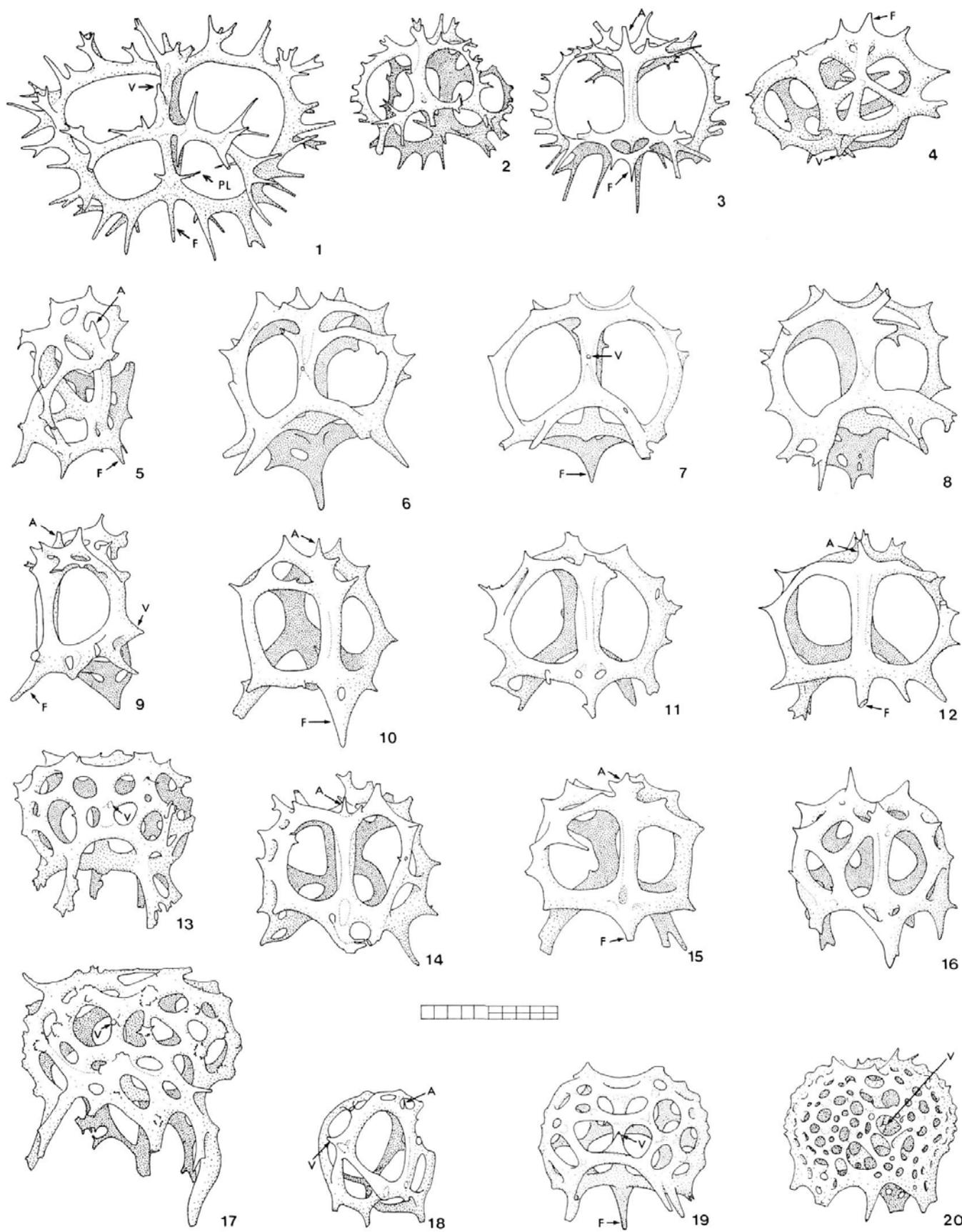
Remarks: Haeckel (1887) assigned *Eucoronis* to the suborder Stephoidea on the basis of its possession of a sagittal ring and the absence of a "complete" lattice shell. The stephoids were subdivided into 4 families, of which Coronida was defined as having 2 additional rings: the horizontal basal ring and the frontal ring. Our emendation of *Eucoronis* is close to the sense of Haeckel's Coronida, with 2 exceptions. Haeckel (1887) further subdivided the Coronida into 4 subfamilies based on the basal ring and its enclosed basal pores: Zygostephanida, Acanthodesmida, Eucoronida and Trissocyclida. Haeckel apparently erected the first 2 of these subfamilies to accommodate specimens that were so oriented that certain critical structures were not visible. These subfamily definitions are based on the absence of the basal ring and median bar, respectively, and we have never observed nassellarians fitting these descriptions. The Eucoronida (2 basal pores) and Trissocyclida (4 basal pores) are generally consistent with our emendation of *Eucoronis*. The number of basal pores depends on the degree of development of the primary lateral processes, as we have described in an earlier paragraph. Consequently, we have lumped a number of Haeckel's (1887) genera into this single taxon. We have not formally synonymized under *Eucoronis* any of the 7 generic names Haeckel included in Eucoronida and Trissocyclida be-

PLATE 1

All figures × 250
Scale bar = 100 μm

(A, apical spine; F, frontal spine; PL, primary lateral process; V, vertical spine)

- 1 *Eucoronis challengerii* (Haeckel)
Oblique back-basal view, DSDP 77B-15-cc.
- 2–3 *Eucoronis* sp.
2, oblique back view, DSDP 77B-15-cc; 3, front view, DSDP 77B-17-cc.
- 4–12 *Eucoronis fridtofjanseni*, Goll and Bjørklund, n. sp.
4, basal view, paratype USNM 258901, DSDP 341-28-3, 79–81 cm; 5, oblique front-left side view, DSDP 341-27-3, 14–16 cm; 6–7, back views of two specimens from DSDP 341-28-3, 79–81 cm; 8, back view, DSDP 341-27-3, 14–16 cm; 9, right side view of specimen with a broken lattice shell exposing the sagittal ring, DSDP 341-27-3, 14–16 cm; 10, oblique front view, DSDP 341-27-5, 82–84 cm; 11, front view, DSDP 341-27-cc; 12, front view, DSDP 341-27-3, 14–16 cm.
- 13–16 Specimens having skeletons intermediate between those of *Eucoronis fridtofjanseni*, n. sp. and *Clathrospyrus sandellae* Goll
13, back view showing small sagittal lattice pores, DSDP 341-31-5, 17–19 cm; 14, front view, DSDP 341-31-5, 17–19 cm; 15, front view, DSDP 341-27-3, 14–16 cm; 16, front view, DSDP 341-31-cc.
- 17–20 *Clathrospyrus sandellae* Goll
17, back view of specimen with large tubercles and postcephalic lattice, DSDP 341-28-cc; 18, left side view of specimen with broken lattice shell exposing the sagittal ring, DSDP 341-28-3, 79–81 cm; 19, back view of specimen with campanulate lattice shell, DSDP 338-7-cc; 20, back view of specimens showing partial lattice development above the sagittal ring, DSDP 341-26-cc.



cause 6 of the type species are unidentifiable for a variety of reasons, and the seventh type species, *Trisocyclus stauropora* is clearly neither a coronid nor referable to *Eucoronis* in our emended sense.

Eucoronis includes species with or without a sternal bar, and the nature of the axobate is variable. A profusion of short lattice spines is diagnostic for the genus.

This emendation of *Eucoronis* represents a further dismantling of *Giraffospyris* as a phyletic genus as it was interpreted by Goll (1969, fig. 2). Goll (1979) transferred *Giraffospyris haeckelii* (Bütschli, 1882) to *Zygocircus*. We here transfer *Giraffospyris circumflexa* Goll, 1969 and *Giraffospyris angulata* (Haeckel, 1887) to *Eucoronis*. Furthermore, *Giraffospyris laterispina* (Goll, 1969) must also be transferred to *Eucoronis*, although specimens of this species bear only minor lattice spine development and the species is not perfectly consistent with our definition of *Eucoronis*.

Stratigraphic range: *Eucoronis hertwigi* (Bütschli, 1882) is the oldest known representative of the genus. This species was described from the Oceanic Formation of Barbados, but its stratigraphic range is not known more precisely than Upper Eocene. *Eucoronis* does not have a continuous occurrence in tropical sediments, however. The next oldest species, *Eucoronis circumflexa*, has its first appearance in the Lower Miocene, and the genus is continuously represented in younger sediments.

***Eucoronis fridtofjanseni* Goll and Bjørklund, n. sp.**

Plate 1, figures 4–12; plate 2, figures 1–10; plate 3, figures 14–26

Diagnosis: A species of *Eucoronis* characterized by a massive lattice shell with short stout lattice spines and well-developed primary lateral bars.

Name: In honor of Fridtjof Nansen, a Norwegian equally famous as oceanographer and humanitarian.

Description: Thick-walled sagittal ring equidimensional and D-shaped (pl. 1, fig. 9; pl. 3, figs. 16–17) or tall and subrounded (pl. 3, fig. 18); 78–100 μm high and 63–78 μm thick. Front of sagittal ring bears a broad external longitudinal ridge between the apical and frontal spines (pl. 2, fig. 10; pl. 3, figs. 14, 21, 23, 25). Back of sagittal ring between apical and vertical spines has slight furrow on some specimens (pl. 1, fig. 6) and is circular in cross section on others (pl. 2, figs. 1, 4). Short, simple apical spine obscure on most specimens (pl. 1, figs. 5, 9–10, 12). Robust vertical spine arises from approximate mid-point of back of sagittal ring height, quite prominent on some specimens (pl. 1, fig. 9; pl. 2, figs. 3–4). Frontal spine 22–45 μm long, simple on some specimens (pl. 1, figs. 9, 12), but most specimens have secondary lateral bars joined to short frontal bar to form 1 or 2 prominent basal pores on the front of the skeleton, and free spine projects downward from distal end of frontal bar (pl. 1, figs. 4, 6, 10–12; pl. 3, figs. 21, 25). Primary lateral bars are stout, well-developed, joined to median bar of sagittal ring and back lateral surfaces of basal ring, frame 2 additional pairs of large basal pores (pl. 1, fig. 4; pl. 2, figs. 6–7). Small tuberculate axobate projects downward from median bar at point of juncture with primary lateral bars. Summit of axobate bears a field of extremely fine

PLATE 2

Scanning electronphotomicrographs

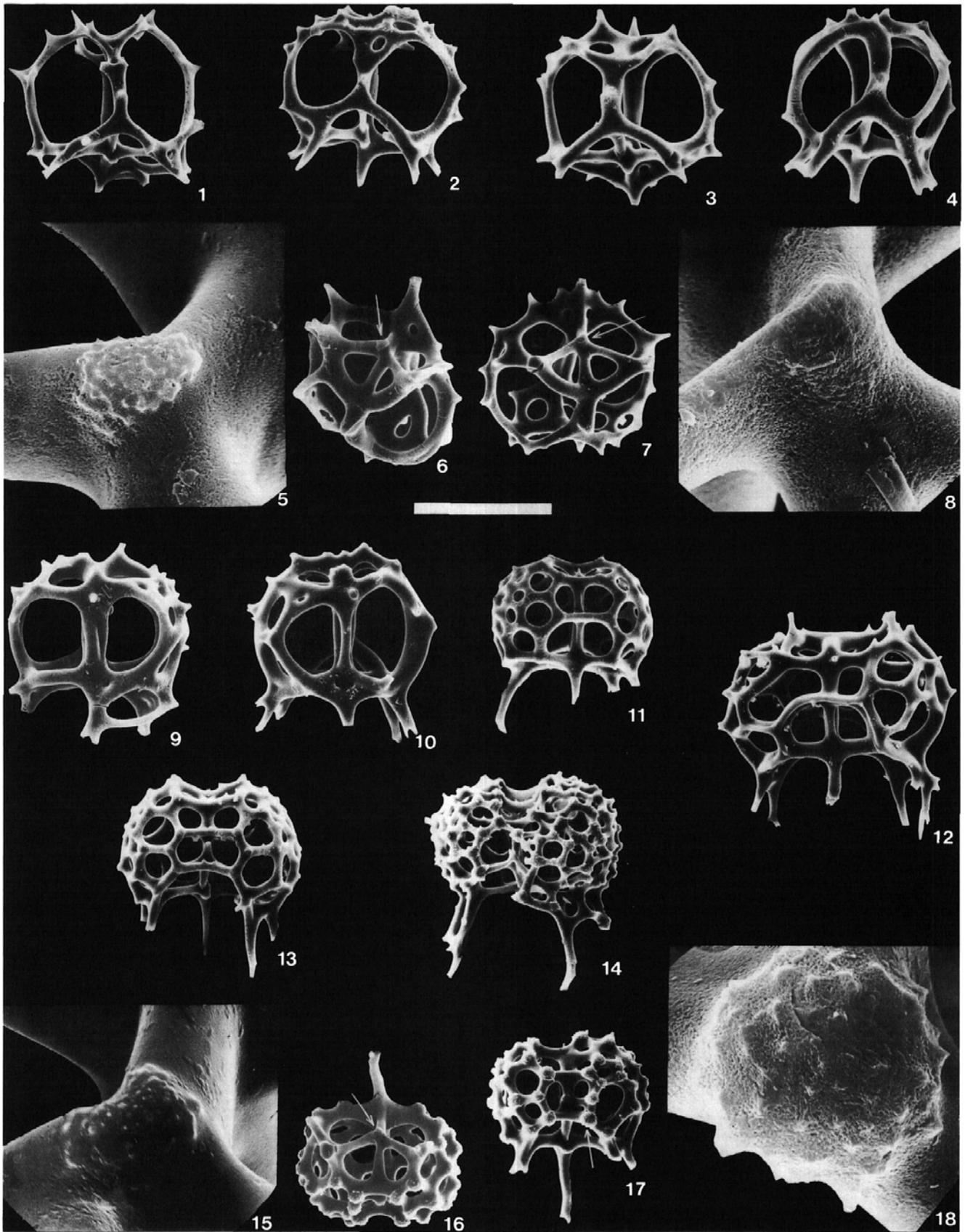
(Figures 5 and 8, $\times 2500$, scale bar = 10 μm ; figures 14 and 18, $\times 3750$, scale bar = 6.7 μm ; all other figures $\times 250$, scale bar = 100 μm .)

1–10 *Eucoronis fridtofjanseni*, Goll and Bjørklund, n. sp.

1, back view, DSDP 341–28–3, 79–81 cm; 2–4, back views of three specimens, DSDP 341–27–3, 14–16 cm. 5–8, oblique basal views of two specimens, DSDP 341–27–3, 14–16 cm; 5, close-up of sculptured axobate; 6, same specimen, arrow indicates location of figure 5; 7, specimen with smooth axobate, arrow indicates location of figure 8; 8, same specimen, close-up of axobate. 9–10, front views of two specimens displaying an early stage of lattice development, DSDP 341–27–3, 14–16 cm.

11–18 *Clathrospyris sandellae* Goll

11, front view of specimen with relatively smooth lattice shell, DSDP 341–28–3, 79–81 cm; 12, front view of large spinous specimen, DSDP 341–29–cc; 13–14, back views of two specimens having remnants of secondary lattice development over the cephalic pores, DSDP 341–28–3, 79–81 cm. 15–18, basal and back views of specimen with large lattice tubercles, DSDP 341–28–3, 79–81 cm; 15, close-up of sculptured axobate; 16, same view, arrow indicates location of figure 15; 17, back view, arrow indicates location of figure 18; 18, close-up of lattice tubercle.



microspicules on most specimens (pl. 2, fig. 5), but 1 specimen has been observed with a smooth axobate (pl. 2, fig. 8). No sternal bar or tertiary lateral bars.

Lattice shell discoidal, height and width approximately equidimensional, 115–121 μm in diameter, slightly constricted by top of sagittal ring. Lattice shell consists only of basal ring and a sparse trellis of lattice arches spanning the lateral portions of the basal ring and top of the sagittal ring. Oval basal ring 95–102 μm wide, 70–78 μm thick (pl. 1, fig. 4). Lattice shell does not extend below basal ring on most specimens, but remnants of thoracic lattice occur on rare specimens (pl. 1, fig. 9). Variable number of short simple basal spines project from basal ring (pl. 2, figs. 6–7). Many specimens have a single pair of stout, spinous, outwardly convex lattice bars projecting from lateral margins of basal ring and branching near contact with top of sagittal ring to form a variable number of pairs of small apical sagittal lattice pores. Additionally, these lattice arches frame a pair of large, round to D-shaped, sagittal lattice pores 60–82 μm in maximum diameter on each of the front and back of the lattice shell. No sternal bar.

Dimensions based on measurements of 50 specimens from DSDP Site 341, core 28, sections 1 and 2.

Holotype: USNM 258897, DSDP Site 341, core 27, section 3, 14–16 cm; England Finder 033/2; plate 3, figures 25–26.

Paratypes: USNM 258898, DSDP Site 341, core 27, section 3, 14–16 cm; England Finder N30/0; plate 3, figures 14–15. USNM 258899, DSDP Site 341, core 27, section 3, 14–16 cm; England Finder 035/0; plate 3, figures 19–20. USNM 258900, DSDP Site 341, core 27, section 3, 14–16 cm; England Finder N31/1; plate 3, figures 23–24. USNM 258901, DSDP Site 341, core 28, section 3, 79–81 cm.; England Finder T53/1; plate 1, figure 4.

Remarks: The axobate of *Eucoronis fridtofjanseni* is faintly visible when viewed by bright field light microscopy, but the details of its construction can only be observed by SEM. This structure is regarded as having great value for tracing trissocyclid evolution, but it is not ideally suited as a genus level taxonomic criterion because it can not be routinely observed on conventional slide preparations. The absence of a microspicule field on the axobate of one specimen (pl. 2, figs. 7–8) is perplexing. The pitted composition of this specimen appears to represent a slightly weathered surface from which the surface coating has been dissolved, revealing the inner microspherulitic opal texture. In contrast, the smooth outer surface of the specimen shown on plate 2, figure 5 is essentially intact and the microspicule field is preserved. Hence, the absence of such a field on the former specimen may be a function of the degree of weathering. The axobates of *E. fridtofjanseni* and *Eucoronis angulata* (Goll, 1972, pl. 63, fig. 3) are quite similar in structure.

PLATE 3

All figures $\times 250$
Scale bar = 100 μm

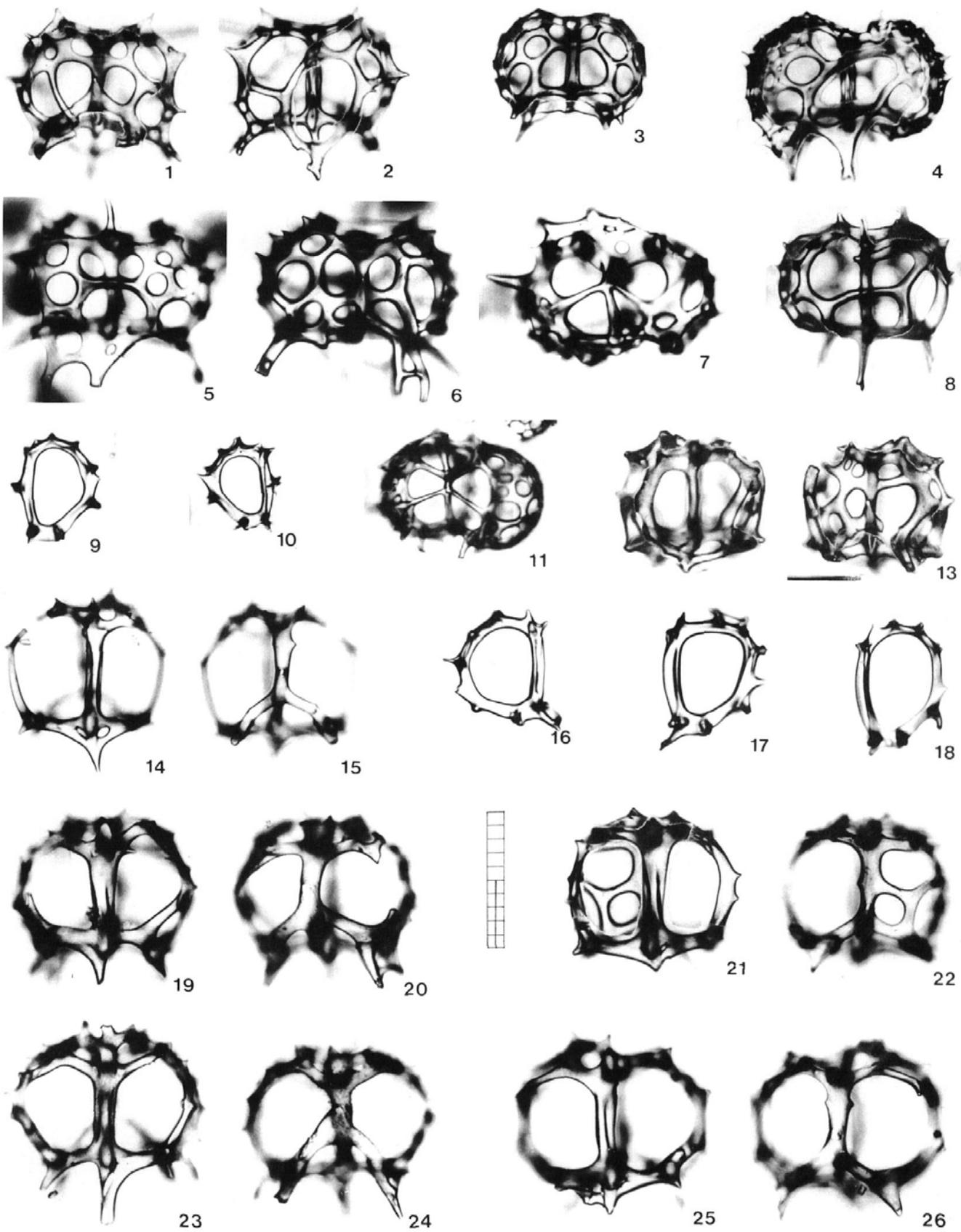
1–11 *Clathrospyrus sandellae* Goll

1–2, back and front views, respectively, of spinous specimen, DSDP 341–31–cc; 3, front view of small smooth specimen, DSDP 341–27–3, 14–16 cm; 4, front view, DSDP 341–26–4, 13–15 cm; 5–7, front, back and basal views, respectively, of same specimen, DSDP 341–26–4, 14–16 cm; 8, front view, DSDP 341–29–6, 100–102 cm; 9, right-side view of sagittal ring, DSDP 341–29–3, 120–122 cm; 10, left-side view of sagittal ring, DSDP 341–29–6, 100–102 cm; 11, basal view, DSDP 338–8–2, 53–55 cm.

12–13 Front and back views, respectively, of a specimen displaying skeletal characteristics intermediate between those of *Eucoronis fridtofjanseni*, n. sp. and *Clathrospyrus sandellae*, DSDP 341–31–cc.

14–26 *Eucoronis fridtofjanseni* n. sp.

14–15, front and back views of paratype USNM 258898, DSDP 341–27–3, 14–16 cm; 16, left-side view of sagittal ring, DSDP 341–30–1, 100–102 cm; 17, right-side view of sagittal ring, DSDP 341–26–3, 15–17 cm; 18, right-side view of sagittal ring, DSDP 341–29–3, 120–122 cm. 19–26, four specimens from DSDP 341–27–3, 14–16 cm; 19–20, front and back views, respectively, of paratype USNM 258899; 21–22, front and back views of atypical specimen with small lattice pores adjacent to the back of the sagittal ring. 23–24, front and back views, respectively, of paratype USNM 258900; 25–26, front and back views, respectively, of holotype USNM 258897.



Eucoronis fridtofnseni is distinguished from the latter species by its smaller overall size and well-developed primary lateral bars. The vertical spine is small and projects from the back of the sagittal ring near the juncture with the basal ring on specimens of *E. angulata* (Goll, 1969, pl. 59, fig. 7) in contrast with the large vertical spine arising high on the sagittal ring of *E. fridtofnseni* (pl. 1, fig. 9).

Specimens of *E. fridtofnseni*, consisting only of the sagittal ring and associated spines (pl. 3, figs. 16–18) are common in Site 341 sediments, particularly near the top of the *E. fridtofnseni* Range-zone. Care must be exercised to prevent misidentifying these specimens as *Zygocircus* by observing a number of individuals ranging in development from sagittal rings only to complete specimens. Sagittal rings of *E. fridtofnseni* can be distinguished from those of *Clathrospyrus sandellae* (pl. 3, figs. 9–10) by the absence of a pair of spines or lattice bars joined to the front midpoint of the sagittal ring between the apical and frontal spines.

Eucoronis fridtofnseni is distinguished from *E. circumflexa* and from the type species of *Eucoronis*, *E. perspicillum*, by the absence of large tubercles on the sagittal ring, and from *Eucoronis* sp. (pl. 1, figs. 2–3) by the absence of a sternal bar or pore.

Occurrence: The stratigraphic range of this species is confined to the *Eucoronis fridtofnseni* Range-zone (table 1 and text-fig. 1), lower Upper Miocene, and the species has been found only in 3 DSDP sites (338, 341 and 348) in the Norwegian-Greenland Sea.

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ARENACEOUS FORAMINIFERA WORKSHOP

A workshop on arenaceous foraminifera will be organized at the Institute of Earth Sciences, Free University, Amsterdam, the Netherlands in September, 1981. A date will be chosen that fits best to known micropaleontological meetings. A first circular and participation forms can be obtained from the workshop secretary: Jacob G. Verdenius, Continental Shelf Institute, P.O. Box 1883, N-7001 Trondheim NORWAY.

The organizing committee:
Amsterdam: *Jan E. van Hinte*.
Anne R. Fortuin.
Trondheim: *Jacob G. Verdenius*.