Dinoflagellate Evolution and Diversity Through Time
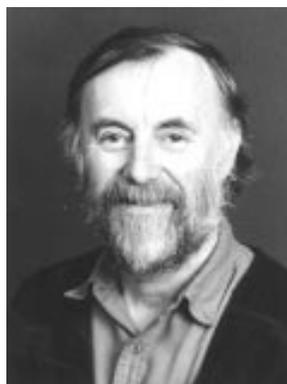
R.A. Fensome, R.A. MacRae and G.L. Williams

R.A. Fensome   *R.A. MacRae*   *G.L. Williams*

Introduction

Unlike most other groups of protists, dinoflagellates have left an extensive fossil record. This record is restricted essentially to the last 245 million years (Mesozoic and Cenozoic), though comparative anatomical and molecular phylogenetic studies of modern dinoflagellates indicate a probable Precambrian (greater than 570 million years) origin for the group. This Paleozoic (245-570 million years) gap in the dinoflagellate fossil record has been used to suggest that this record is seriously flawed and therefore cannot be used to deduce the evolutionary history of the group (Evitt 1981). However, recent studies using large datasets (Fensome *et al*. in press; MacRae *et al*. in press) and informal cladistic analyses (Fensome *et al*. 1993) demonstrate that the fossil record can indeed be used to meaningfully examine the past diversity and evolution of this major planktonic group of organisms. This work also has broader implications in helping understand the development of modern plankton biodiversity and its vital role in modern ecosystems. Aspects of this ongoing research are reviewed in the present paper.

Dinoflagellates

Dinoflagellates are primarily single-celled organisms that possess, firstly, a nucleus lacking histones and having chromosomes that remain condensed throughout the cell division cycle and, secondly, at least one life-cycle stage involving cells with two characteristic flagella (Fig. 1). As in related protists, such as ciliates, dinoflagellates possess a layer of vesicles toward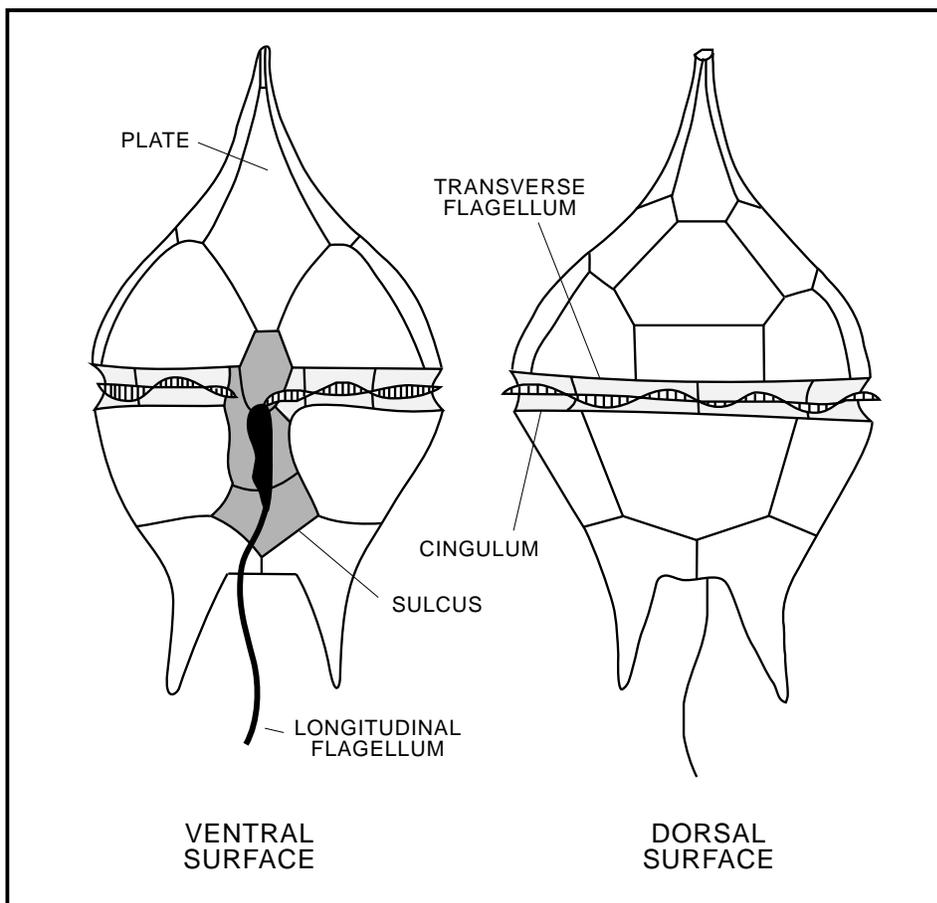s the periphery of the cell. In dinoflagellates, these vesicles commonly contain cellulosic plates arranged in consistent patterns (tabulation patterns). These patterns provide the primary basis for determining evolutionary relationships within the group.

About half of living dinoflagellate species are photosynthetic, others are heterotrophic; and some species have both nutritional modes, underlining the futility of attempting to classify these relatively simple organisms as plants or animals. Dinoflagellates are today most diverse in continental shelf environments, but also occur in oceanic and freshwater habitats. Some are parasitic and one group, popularly known as zooxanthellae, live symbiotically in the soft tissue of invertebrates such as corals, giving these animals

Figure 1: The principal morphological features of a typical modern dinoflagellate - motile stage.
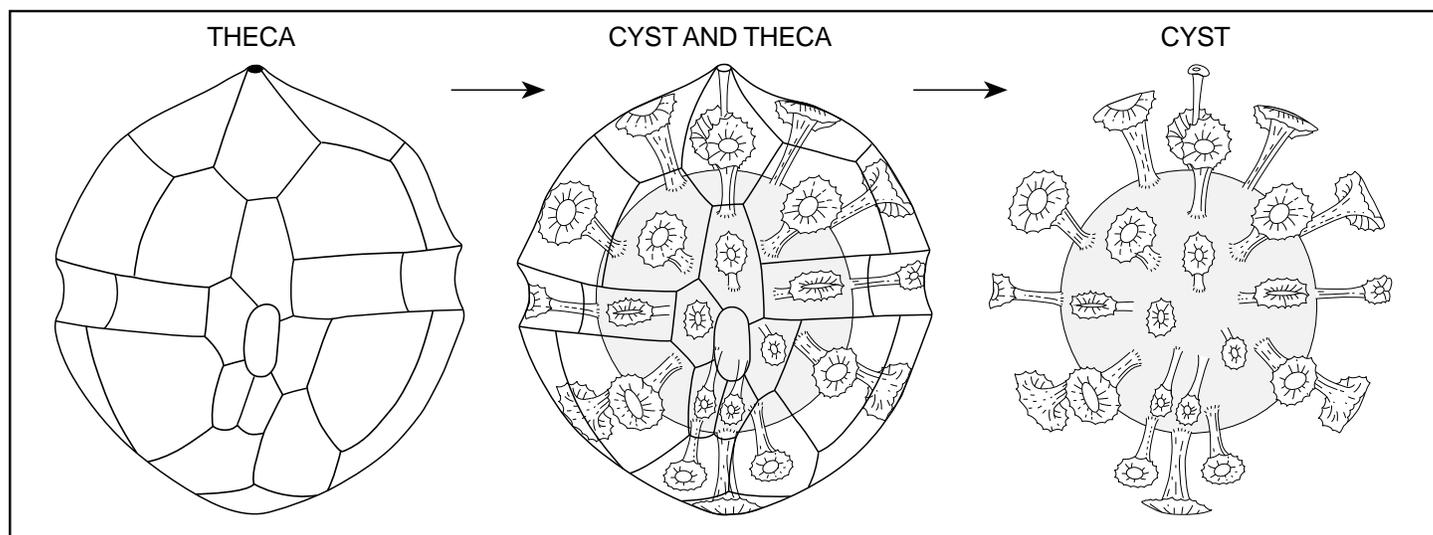
Figure 2: The relationship between a dinoflagellate motile stage (left) and the corresponding dinoflagellate cyst stage (right). Not all cysts show such a clear one process per plate relationship, but cyst affinity to the "parent" theca is usually determinable, at least to family level. Practically all dinoflagellate fossils represent the cyst stage. Figure adapted from Evitt (1985)

their bright colours. Dinoflagellates are of major economic importance, being at or near the base of the marine food-chain; they are also primary causal agents of paralytic shellfish poisoning and related toxic phenomena (red tides).

History of study

The German microscopist, Ehrenberg (1838), was the first to recognize fossil dinoflagellates, which he observed in thin sections of Cretaceous flint. Such fossils were recognized as being organic-walled as early as the mid-nineteenth century, but extraction techniques to release them from the rock matrix did not become standard procedures until the mid-twentieth century. Indeed, the real nature of most fossil dinoflagellates - that they are preservable organic-walled resting cysts - was only discovered 35 years ago (Evitt 1961). Fossil cysts can be recognized as dinoflagellates if they show direct "reflection" of the tabulation pattern on the cyst wall, or by the position and shape of processes (Fig. 2) or a type of excystment opening termed an archeopyle; archeopyles correspond to particular plates or groups of plates of the tabulation and therefore demonstrate dinoflagellate affinity, even in the absence of other diagnostic features. The presence of tabulation evidence on fossils has allowed us to develop the first detailed, integrated phylogenetic classification of fossil and living dinoflagellates (Fensome *et al*. 1993.

Fossil dinoflagellates evolved into a great diversity of morphologies from the Late Triassic to Recent. This feature and their occurrence in marine sedimentary rocks, commonly in great abundance, makes them ideal biostratigraphic index fossils, and they have been used extensively for this purpose in petroleum exploration. This has culminated, for example, in their key usage in the sequence stratigraphic methodology developed by EXXON Oil Company (Haq *et al*. 1987). One spinoff of this stratigraphic application has been an exponential increase in the amount of information on fossil dinoflagellates: for example, the number of formally described species has risen from a few dozen in 1960 to over 3,400 today (Lentin and Williams 1993). This information, if harnessed in an organized manner, has the potential to help us considerably in understanding the evolution and diversity of the group, a potential that is being realized in our present studies.

Methodology

Our investigation of dinoflagellate diversity has been made possible by the organized nature of dinoflagellate taxonomy (Lentin and Williams 1993; Fensome *et al*. 1993) and by access to a major database, PALYNODATA, compiled over the last 25 years under the auspices of several major oil companies and the Geological Survey of Canada. The PALYNODATA program

stores taxonomic, bibliographic, geographic and biostratigraphic information from all known pre-Quaternary palynological publications (palynology being the study of organic-walled microfossils such as dinoflagellates and vascular plant pollen and spores). PALYNODATA has enabled us to examine diversity patterns at the species level; the majority of previous studies for all biological groups have been restricted to analysis of diversity at higher taxonomic ranks.

From a dataset extracted from PALYNODATA, species diversity of dinoflagellates was assessed for each Mesozoic and Tertiary stage using the timescale of Harland *et al*. (1990), with slight modification. (We use the term "stage" here to refer to the time intervals sampled; they essentially correspond to geological "ages" in the Mesozoic and "subepochs" in the Tertiary.) The dataset was filtered extensively, the following data being excluded: 1) range records at greater than stage precision (e.g. those ranges recorded simply as Early Cretaceous or Jurassic rather than, say, as the Jurassic stages Bajocian-Bathonian), because such coarse records usually represent uncertainty; 2) records from catalogs and indices that do not provide original range data; 3) records with identified sampling problems, such as those involving resedimentation or other forms of contamination.
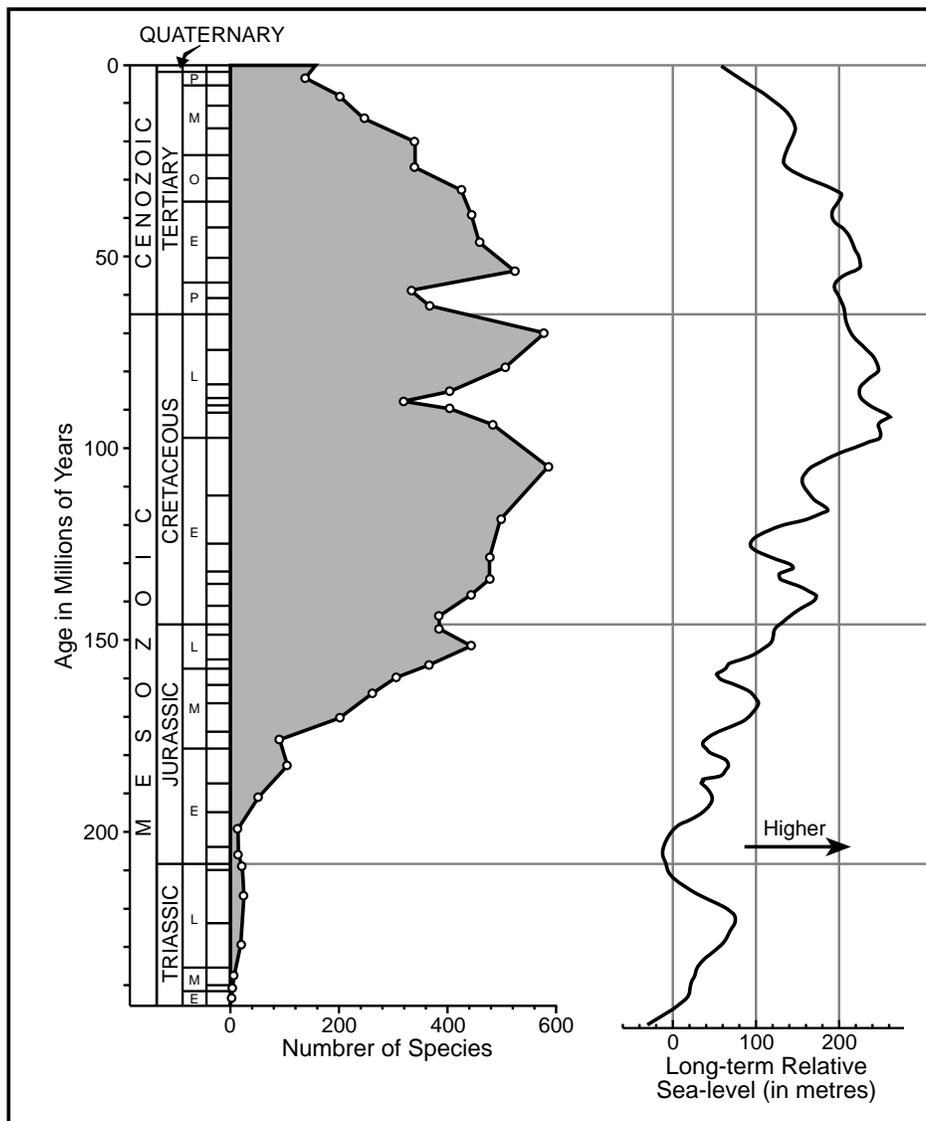
Figure 3: Left: fossil dinoflagellate species diversity (from MacRae et al. in press). Right: relative changes in long-term sea level, after Haq et al. (1987). The time scale is based on that of Harland et al. (1990); geological periods and epochs are labelled (P at base of Tertiary = Paleocene, E = Eocene, O = Oligocene, M = Miocene, P at top of Tertiary = Pliocene), stages, epochs are indicated but not labelled. Q = Quaternary; Tertiary and Quaternary together comprise the Cenozoic. Triassic, Jurassic and Cretaceous together comprise the Mesozoic.

phasize relative rates on a per-taxon basis (Sepkoski 1986); these were calculated by dividing the number of extinctions or originations by the total diversity for the interval under consideration and dividing by 100.

Dinoflagellate diversity patterns

The species diversity plot (Fig. 3) developed for dinoflagellates shows that the group first appeared in the fossil record in the Late Triassic (apart from two questionable Paleozoic species not shown). Latest Triassic extinctions caused a decline in the earliest Jurassic, but subsequently dinoflagellates generally underwent exponential growth over the next 50 million years from a low of 13 to a Late Jurassic high of 420 species. The group then maintained more or less high diversities until the Eocene, with peaks in the late Early Cretaceous (584 species), latest Cretaceous (568 species) and Early Eocene (518 species). These three peaks are punctuated by significant lows in the early Late Cretaceous (315 species) and earliest Tertiary (325 species). The early Late Cretaceous low may be in part a sampling artifact due to the presence of two short stages. The earliest Tertiary low is clearly due to the large number of extinctions (207 species) in the last Cretaceous stage, though as already noted the dataset cannot differentiate between extinctions during the stage and at the end of it.

From the Late Eocene, dinoflagellate evolutionary patterns changed dramatically. Origination rate generally declined and extinction rate generally increased, resulting in a diversity drop to a Pliocene low of 136 species.

A variety of biases can affect diversity patterns, including rock area/volume, research interests, rock type and preservational differences (see Raup 1976a, b; Sheehan 1977). For example, increased diversity commonly observed among many marine animals in younger rocks is mainly due to an increasing proportion of rock available for study (Sepkoski 1986). From our own work, it is clear that there is generally a greater number of publications from intervals with greater diversity. However, the significance of this correlation may be deceptive since, as pointed out by Raup

The filtered dataset comprises 38,000 age records from 2,129 publications. Species names are recorded in PALYNODATA directly from the literature - i.e. without regard for current taxonomy. Hence, a dictionary listing correct names and synonyms was developed and employed to convert the names in the dataset to a meaningful taxonomy. Thus, about 6,000 unique database "species" names were reduced to 2,507 names, regarded as species in the ensuing diversity analyses.

The total stratigraphic range of each species was calculated as a composite of the individual range records for each species in the filtered dataset. Diversity for each stage was then calculated by adding the number of species whose ranges pass through, begin in or terminate in each stage. A count of the number of ranges beginning in or terminating in a given stage provides data for origination and extinction plots (though the data are too coarse to make meaningful analysis of individual time horizons such as the Cretaceous-Tertiary boundary). Percentage extinction and percentage origination plots are more meaningful than simple counts, since they em-

(1977), "systematists follow the fossils".

A potential problem in the analysis of dinoflagellate evolution and diversity patterns is the cyst-based nature of the fossil record. Since most fossil dinoflagellates are organic-walled cysts and only about 13-16 percent of modern species produce fossilizable cysts (Head 1996), the question arises as to how representative the dinoflagellate record is. The vast majority of fossil dinoflagellates belong to relatively few families and there appears to be significant continuity within cyst-forming lineages. We therefore consider that, although it may not be appropriate to view fossil dinoflagellate assemblages as close proxies for past total dinoflagellate communities, the patterns observed in this and similar studies are real and their analysis will yield meaningful explanations.

What, then, are the main influences on the diversity of fossil dinoflagellates? Several hypotheses can be formulated: for example the Tertiary decline may have been the result of a cooling climate, greater seasonality, and major reorganization of ocean currents resulting from plate tectonics and the onset of glaciation. Such changes may have adversely affected lineages that developed under warmer, more uniform environments. Sea level fluctuations may also have had an effect. Indeed, there is a broad correlation between the dinoflagellate species diversity plot and the long-term sea level curve. Modern dinoflagellates are most diverse in marine shelf areas and organic-walled cyst production is also greatest in these areas (Stover *et al.* 1996). Hence, the Late Tertiary lowering of sea level and concomitant closing of continental seaways, thus decreasing shelf area, may have contributed to the dinoflagellate diversity decline. Sea levels were relatively high during the Cretaceous and continental shelves were correspondingly broad; perhaps not surprisingly dinoflagellate diversity was also generally high throughout this period.

Haq (1973) published species diversity plots for Mesozoic-Cenozoic calcareous nannoplankton, and these show some striking parallels with the dinoflagellate data. For example, maximum Mesozoic-Cenozoic levels occurred in the latest Cretaceous stage, corresponding with the second highest peak in dinoflagellates. Perhaps most significantly, the nannofossil diversity plot resembles the dinoflagellate diversity plot for the Cenozoic, peaking in the Early Eocene, then declining steadily to the present day. Knoll (1989) also found a post-Eocene decline in calcareous nannoplankton. Haq related maximum diversity to periods of maximum transgression, when more equable climatic conditions resulted in greater nannoplankton productivity.

The early Mesozoic radiation of dinoflagellates

The appearance of dinoflagellates in the early Mesozoic is intriguing: is this appearance a real evolutionary event; or is it an artifact of the fossil record, as implied by Evitt (1981)? To determine this, it was necessary to compare the evolutionary patterns shown by dinoflagellates with those of other groups undergoing evolutionary radiations. We displayed the dinoflagellate diversity data in a series of spindle plots (Fig. 4), one for each family with fossil species, the breadth of each spindle representing the number of species within the family during a given geologic stage.

The spindle plots show that by the end of the Triassic, four families were present - a small number, but including those with among the fewest and the most plates. The Early-Mid Jurassic saw the first appearance of 11 dinoflagellate families. By the end of the Jurassic all but a few families were represented in the record; those that first appeared after the Jurassic are based on minor morphological modifications in contrast to the major innovations represented in the Triassic-Mid Jurassic record. From these observations, it is clear that dinoflagellates underwent a period of "experimentation" during the late Triassic to Mid Jurassic, followed by a period of morphologic stability. This pattern of "experimentation" followed by relative stability is a classic pattern displayed by many groups of organisms (Gould *et al.* 1987) and demonstrates that the early Mesozoic expansion of dinoflagellates represents a real evolutionary radiation and is not an artifact of the fossil record. This interpretation has been independently corroborated by biogeochemical evidence (Moldowan *et al.* 1996).

Some interesting questions arise. What stimulated the early Mesozoic radiation of dinoflagellates? Assuming that the biologi-
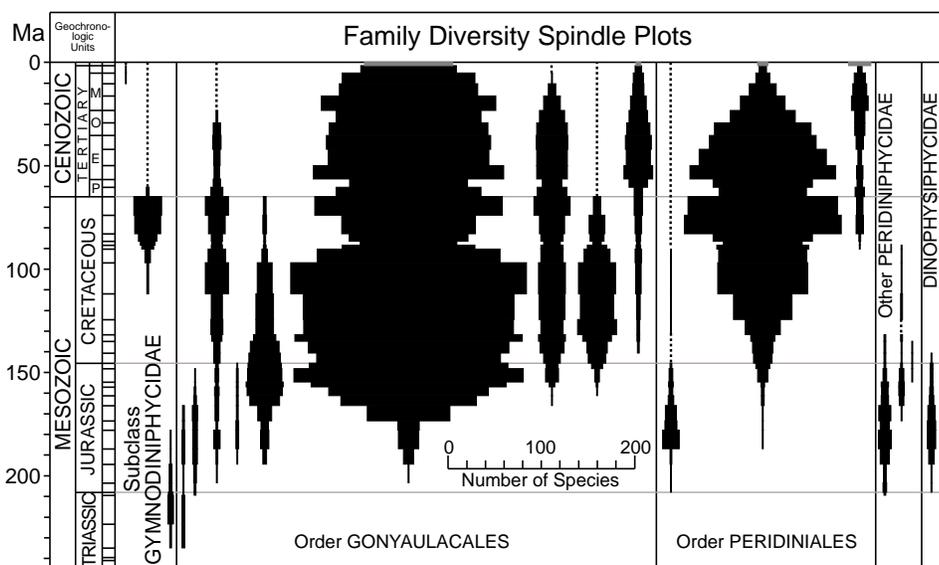

Figure 4: Spindle plots showing the number of species per family per geological stage. Timescale and geochronologic units as in Figure 3. The Quaternary is represented by the small unlabelled area above the Tertiary. Quaternary information is incomplete in PALYNODATA and therefore plots in this interval are tentative and consequently indicated in grey rather than black. Adapted from Fensome et al. *(in press).*

cal and biochemical evidence is correct in indicating a Precambrian origin for the dinoflagellate lineage, what happened to this lineage during the Paleozoic, between 245 and 570 million years ago?

The radiation was possibly stimulated by the break-up of the supercontinent Pangaea and the consequent increased number of continental shelf habitats for cyst producing organisms. Stimulation probably also came from the large amounts of ecospace available after the devastating end Permian extinctions, biotic recovery from which was gradual. Paleozoic corals, for example, were totally eradicated by the end of the Permian and their Mesozoic (probably unrelated) counterparts, the scleractinian corals, did not appear until the Mid Triassic. Geochemical evidence shows that some of these early scleractinian corals were zooxanthellate (Stanley *et al*. 1995), leading to the tantalizing possibility that corals and dinoflagellates may have co-evolved. This possibility is supported by similarities between the modern zooxanthellate dinoflagellate, *Symbiodinium*, and the Triassic fossil dinoflagellate, *Suessia*.

Moldowan *et al.* (1996) reported that triaromatic dinosteroids, which are derived almost exclusively from dinoflagellates, have not been detected in samples from the Carboniferous and Permian (362.5 to 245 million years ago), but occur sporadically in pre-Carboniferous rocks enriched in acritarchs (organic-walled microfossils of undetermined affinity). Thus at least some Paleozoic acritarchs may represent organisms from the dinoflagellate lineage. Pre-Mesozoic dinoflagellates need not have closely resembled later, known forms. For example, probably their now well-established arrangement of flagella, furrows (cingulum and sulcus) and plate patterns was an innovation of the Mesozoic radiation. If so, this would explain why Paleozoic acritarchs are not morphologically identifiable as dinoflagellates.

Future directions

Diversity studies of fossils are critical in assessing the nature and historical development of modern biodiversity. Studies of fossils and modern organisms is firmly linked through Quaternary research. Our work with fossil dinoflagellate diver-

sities has so far lacked a detailed Quaternary component, since PALYNODATA lacks a complete inventory of Quaternary data. Hence, with the aid of colleague Peta Mudie at Geological Survey of Canada (Atlantic) (GSC Atlantic), we are currently developing a database of Quaternary dinoflagellate occurrences that we can analyze for diversity patterns, thus effectively linking the past and the present.

PALYNODATA has also enabled us to make initial analyses of acritarch diversity patterns. Acritarchs are significant in that they will provide information about Paleozoic trends in organic-walled microplankton fossils and data thus developed can be added to our dinoflagellate information to give Paleozoic to Cenozoic (and even Precambrian) plots. This work has been initiated with the collaboration of Aubrey Fricker, formerly of GSC Atlantic, and Paul Strother of Boston College, Massachusetts.

The family spindle plots have provided a pilot study for another methodology that we plan to pursue. For example, spindle plots for morphological groupings may provide insights into ecological or evolutionary patterns. Finally, our data are also appropriate for analysis of diversity for particular time intervals plotted geographically - i.e. on palinospastic reconstructions, revealing clues to ancient seaways and paleoceanographic currents. And all this can be learned from fossils millions of years old and no bigger than a fraction of a millimetre.

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