

# THE FOSSIL GREEN ALGA *MIZZIA* (DASYCLADACEAE): A TOOL FOR INTERPRETATION OF PALEOENVIRONMENT IN THE UPPER PERMIAN CAPITAN REEF COMPLEX, SOUTHEASTERN NEW MEXICO<sup>1</sup>

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## ABSTRACT

A paleoenvironmental study of the dasyclad *Mizzia* Schubert, 1907 is potentially important because, unlike most of the other fossil reef-dwelling organisms found in the Guadalupe Mountains, the fossil *Mizzia* (restricted to the Permian) has a modern analog, *Cymopolia* Lamouroux, 1916 (Cretaceous to Holocene). The overall morphology of the two genera is similar: both are articulated, and observations on our specimens suggest that both were branched. The transition from the remarkably high-diversity sponge and algal assemblage in the reef into the remarkably low-diversity dasyclad-dominated assemblage in the back reef is abrupt, occurring over distances as short as 10 m. *Mizzia* is the dominant and usually the only component in grainstones, packstones, and wackestones found immediately shelfward of the Capitan reef. The low percentage of broken segments (average 10%) and the discovery of several intact sections of thallus are evidence against wave action as a possible limiting factor. Because the climate in the Guadalupe Mountains was extremely arid and because dasyclads are euryhaline, hypersalinity is considered the most likely limiting factor in this case. Our conclusion that prolific stands of dasyclads formed in shallow protected lagoons immediately behind an emergent barrier reef is not compatible with the currently accepted marginal mound hypothesis for deposition of the Capitan reef complex. We suggest that the marginal mound model must either be modified or abandoned in favor of the originally proposed barrier reef model of deposition.

**Key index words:** Chlorophyta; *Cymopolia*; *Dasycladaceae*; Guadalupe Mountains, Guadalupian; *Mizzia*; paleobotany; paleoecology; Permian

This paper explores the use of *Mizzia* as a paleoenvironmental indicator for the Capitan reef complex and perhaps for other localities. The primary objective is to define the habitat of *Mizzia* by comparing it to its modern analog, *Cymopolia*, by a review of pertinent information including the unique distribution of dasyclads in the Guadalupe Mountains, and by application of lithologic and stratigraphic information from the Guadalupe Mountains and

from European localities. The information provided by this one genus of dasyclad algae may be important to interpretation of the entire Permian reef complex.

Calcareous algae first appear in abundance in the geologic record near the Precambrian/Cambrian boundary about 570 million years ago (Palmer 1983, Riding and Voronova 1985) (Fig. 1). Few Paleozoic algae resemble modern genera and are often classified as "algae of uncertain affinities" or "alga-like problematica." Reconstruction of paleoenvironment in Paleozoic rocks containing such fossils is difficult. For example, in the Upper Permian (Guadalupian) Capitan Formation of the Guadalupe Mountains of southeastern New Mexico (Fig. 2) several examples of "algal problematica" are present (Babcock 1986). Because these organisms have no apparent modern analog, even a well-executed and thorough study (Babcock 1974) may not provide an adequate basis for paleoenvironmental interpretation.

In addition to problematic algae, a variety of sponges contribute to the framework of the Capitan reef. A better understanding of these sponges will certainly improve our understanding of this reef complex, but at this time detailed studies are unavailable (Liu and coworkers, pers. commun.). Smaller populations of other reef dwellers including foraminifera, gastropods, and tabulate and rugose corals have less potential as paleoenvironmental indicators, either because they are not abundant or because their modern analogs live in a wide variety of disparate environments.

In contrast, green algae of the family *Dasycladaceae* are abundant in the Capitan reef and associated facies. They have modern analogs and have great potential as paleoenvironmental indicators. Dasyclads, usually *Mizzia*, are present in the most shelfward zones of the massive reef and are abundant in the bedded rocks immediately shelfward of the reef. Dasyclads are the dominant fossils (commonly the only fossil) throughout tens of meters of section in the bedded backreef facies (i.e. the Tansill, Yates, and Seven Rivers formations) immediately shelfward of the Capitan Formation (Fig. 1).

The fossil genus *Mizzia* has a remarkable analog

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10 <sup>4</sup> YEARS AGO	ERA	PERIOD	AGE	FORMATION
65	CENOZOIC			
245	MESOZOIC			SHELF
				TANSILL
				YATES
				SEVEN RIVERS
570	PALEOZOIC	PERMIAN	OCHOAN	BASIN
			GUADALUPIAN	CAPITAN
			LEONARDIAN	REEF
			WOLFCAMPAN	
		PENNSYLVANIAN		
		MISSISSIPPIAN		
		DEVONIAN		
		SILURIAN		
		ORDOVICIAN		
		CAMBRIAN		
	PRECAMBRIAN			

FIG. 1. Geologic time scale showing relative age of the formations studied. Modified from Palmer (1983).

in the modern genus *Cymopolia* (Rezák 1959). Although *Mizzia* and *Cymopolia* are assigned to different tribes because of the absence of preserved sporangia in *Mizzia*, the striking morphological similarity is worthy of further consideration. The genus *Mizzia* is confined to the Permian, reached greatest generic diversity during the Middle to Late Permian (Johnson 1961), and existed for about 40 million years (Palmer 1983). The stratigraphic range for the extant genus *Cymopolia* is Cretaceous to Holocene or about 140 million years (Johnson 1961).

The general environmental factors controlling the distribution of dasyclads are well documented. Most modern dasyclads are restricted to a limited range of environments. They live in tropical to subtropical waters, on muddy, sandy, or solid substrates, and in protected low-energy environments (Flügel 1985). In addition, dasyclads can tolerate a remarkably wide range of salinities (<2 ppt to >120 ppt) and may be very abundant in waters too saline or too brackish for habitation by other marine organisms (Beadle 1988). Dasyclads generally are found at depths from just below low tide to about 30 m, and most commonly are found at depths <5 m (Flügel 1985). These general criteria for extant members of the family Dasycladaceae should not be used as the sole basis for interpretation of the paleoenvironment of fossil dasyclads. Because much habitat diversity exists among modern dasyclads and probably also existed among their fossil counterparts, each occurrence should be evaluated independently taking all evi-

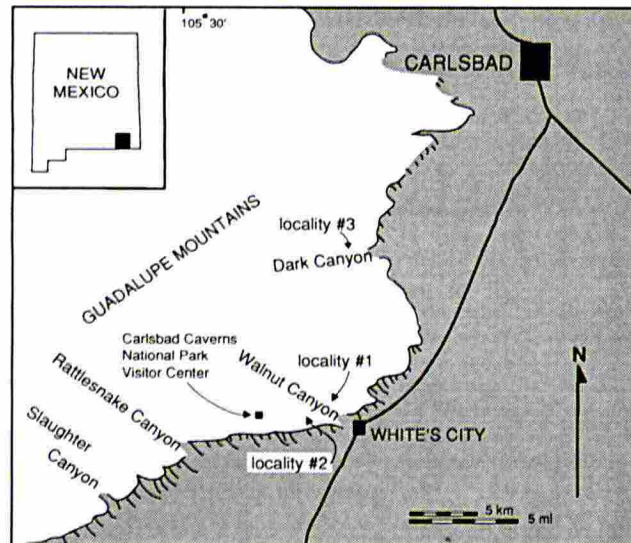


FIG. 2. Map of the study area showing configuration of the Guadalupe Mountains and sample localities. Modified from King (1948).

dence into account (Elliot 1978). With this in mind, the goal of this study is to gather all possible information in order to evaluate the habitat of the abundant *Mizzia* fossils in the sediments immediately shelfward of the Capitan Formation in the Guadalupe Mountains.

#### MATERIALS AND METHODS

**Collection of specimens.** Fossil dasyclads were collected in 1987 and 1988 from three localities in the Guadalupe Mountains of southeastern New Mexico (Figs. 2, 3). The majority of samples were collected just inside the boundary of Carlsbad Caverns National Park (with permission from the National Park Service). The first locality was 19 km southwest of Carlsbad, New Mexico on the south wall of Walnut Canyon near the mouth of the canyon. The second locality was along a recreational trail 0.5 km to the south of the first locality. The third locality was 10 km southwest of Carlsbad, New Mexico on the north wall near the mouth of Dark Canyon. Most samples were taken from outcrops at 3-m intervals along measured transects. Seven of the samples studied were selected from eroded debris where natural weathering by rain water and organic acids had revealed structural details of dasyclad fossils. The precise location of each sample was marked on enlarged photographs of the canyon wall or on a U.S. Geological Survey 7.5 minute quadrangle map.

**Section preparation.** Rock samples were cut into 45 × 25 × 10 mm blocks with masonry and trim saws. Each sample was impregnated with Ciba-Geigy Araldite 506 blue-dyed epoxy resin, and one side was polished. The polished side was then mounted onto a glass slide with Hilquist epoxy resin. The epoxy has an index of refraction equal to the reference standard, quartz. A Hilquist thin section machine was used to cut off most of the block and grind the remaining section to a workable thickness, approximately 200 μm. Final preparation was done with the Logitech Automated Thin Section Production System (Logitech LP 30 and Logitech WG2A). Although standard geologic thin sections are precisely 30 μm thick; slightly thicker sections, 35–40 μm, revealed more structural detail.

Preserved samples of *Cymopolia*, collected in Florida between 1980–1984, were obtained from the teaching collection in the Department of Botany at Louisiana State University, Baton Rouge, Louisiana. Samples were rinsed with distilled water to remove as

much preservative (FAA) as possible and then treated twice with 30% hydrogen peroxide to remove organic matter. The remaining aragonitic ( $\text{CaCO}_3$ ) skeleton was mounted in Ciba-Geigy Araldite 506, blue-dyed epoxy resin. Thin sections of the cured epoxy blocks were prepared using the same technique as described for the fossil specimens.

**Examination of samples.** Both the structure of *Mizzia* fossils in naturally weathered hand samples, i.e. small pieces of rock collected in the field (Figs. 6, 8, 10), and the calcareous skeleton of *Cymopolia* segments (Figs. 7, 9) were studied and photographed with binocular microscopes and a scanning electron microscope (SEM). Thin sections of fossil and modern specimens were studied and photographed with petrographic microscopes.

## RESULTS

### Morphology

Like all members of the family Dasycladaceae, *Mizzia* and *Cymopolia* are radially symmetrical (Figs. 4–6) with a large central axis (stem cell) and one or more whorls of branches (Wray 1977). The most obvious similarity between *Mizzia* and *Cymopolia* is the articulated thallus composed of round to barrel-shaped segments. This type of thallus, termed moniliform, is similar to a pearl necklace. Joints, i.e. uncalcified regions (Figs. 7, 8), allow for flexibility (Bassoulet et al. 1977).

*Mizzia* is most often found as disarticulated segments, and *Cymopolia* is known to quickly disarticulate into segments after death (Wray 1977). In the sections studied, *Mizzia* segments had a mean diameter of 0.84 mm ( $\text{SD} \pm 0.23$ ), and *Cymopolia* segments had a mean diameter of 1.0 mm ( $\text{SD} \pm 0.18$ ). Sampling was biased toward well preserved, articulated specimens. Of the 25 fossil samples studied, four contained articulated segments. Two of these were hand samples each containing a number of articulated sections of *Mizzia* plants. On one of these slabs the sections of articulated thallus were up to 1 cm long; the segment diameter in each section varied. At least two of these sections appeared to be branched. Preservation was poor, but a similar pattern was repeated several times in one sample (Fig. 8).

*Mizzia* and *Cymopolia* both have a euspondyle cortex; that is, the branches are arranged in regularly spaced whorls, each whorl in a preferred plane, along a central axis. The bulbous, enlarged tips of the whorls meet each other to form the cortex. Calcification is external to the cell, and the calcareous skeleton has a honeycomb pattern (Figs. 9, 10). The outer cortex of *Cymopolia* is easily abraded, and the individual segments are easily broken or crushed. In the majority of the samples studied the outer cortex of *Mizzia* showed little sign of abrasion. The percentage of broken *Mizzia* segments was consistently low (average 10%, range 0–25%).

### Habitat of Extant *Cymopolia*

Living *Cymopolia* are reported from the Caribbean, the Mediterranean, the Gulf of Mexico, the Canary Islands, and the Pacific (Britton and Millspaugh

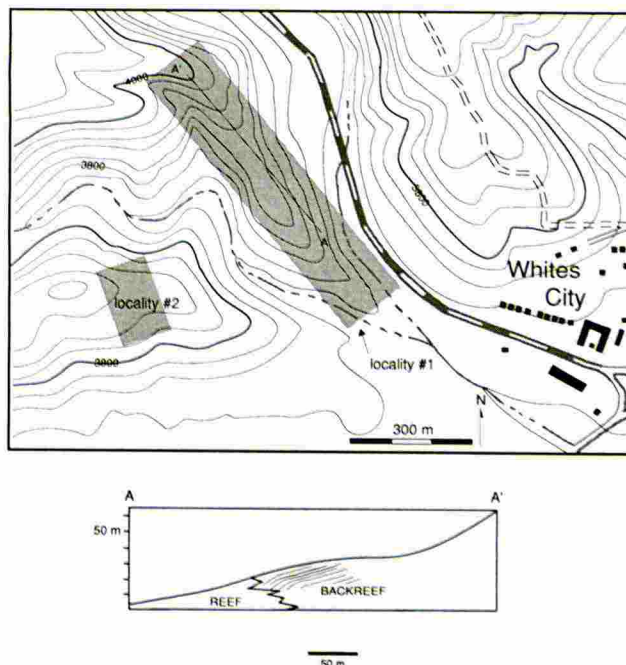


FIG. 3. Topographic map of the main study area and topographic profile of the south face of Walnut Canyon. Reef to backreef transition and backreef bedding are sketched schematically.

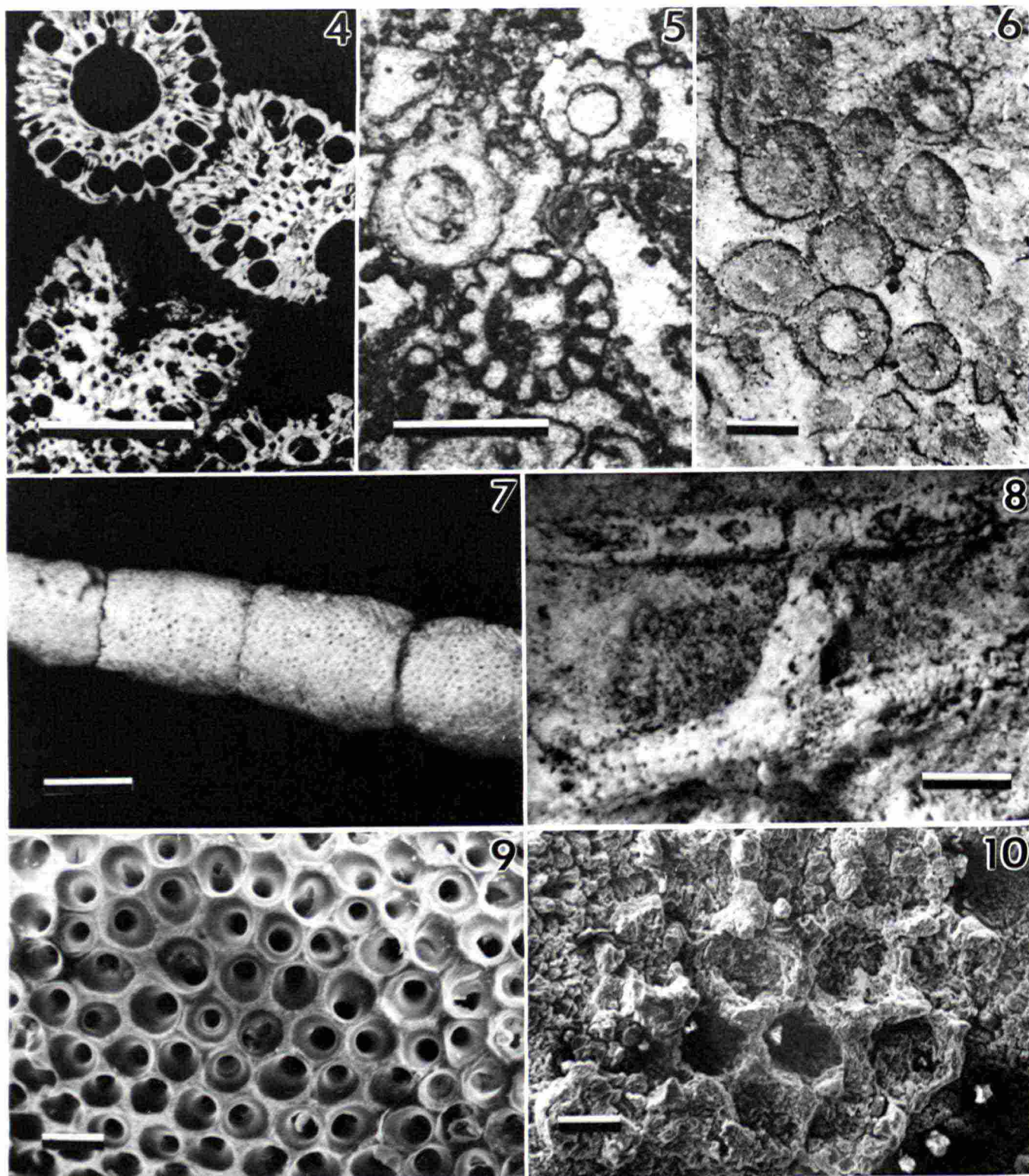
1920, Valet 1969, Hurtado-Ponce and Modelo 1983). The organism is found just below tide base in warm (20–30° C) water (Hämmerling 1944, Woelkerling 1976) and attaches itself to hard substrates in moderately agitated water (Britton and Millspaugh 1920).

### Reconstruction of Habitat

**Evidence from paleolatitude.** When occurrences of *Mizzia* are plotted on a Late Permian plate-tectonic reconstruction of the continents, they generally fall between 30° north and south latitude (Flügel 1985). Thus, *Mizzia*, like *Cymopolia* and other modern dasyclads, probably lived in warm, tropical to subtropical waters.

**Evidence from lithology.** To a geologist, lithology is usually the single most useful line of evidence for the determination of paleoenvironment. For some dasyclads lithology may be even more significant because a correlation may exist between sediment type and dasyclad species present. This correlation is related to turbulence, light intensity, and salinity (Zorn 1976). Unfortunately, in the Guadalupe Mountains such a correlation is not obvious.

In the Guadalupe Mountains, however, the variety and distribution of lithologic types among *Mizzia*-bearing rocks is significant. *Mizzia* is found in grainstones, packstones, and wackestones. A grainstone, by definition, is a rock containing no more than 1% fine (<20  $\mu\text{m}$ ) particles. A packstone contains more than 1% fine particles and is grain supported. A wackestone contains more than 10% grains



FIGS. 4–10. Photographs illustrating the morphological similarities between *Mizzia* and *Cymopolia*. FIGS. 4, 5. Petrographic microscope. Scale bars = 1 mm. FIG. 4. Calcareous portion of *Cymopolia* segments in thin section; crossed polarized light. FIG. 5. *Mizzia* fossil in this section; plane polarized light. Sample from Dark Canyon (locality 3). FIGS. 6–8. Binocular microscope. Scale bars = 1 mm. FIG. 6. Disarticulated *Mizzia* segments in naturally weathered surface. Sample from Walnut Canyon immediately shelfward of the reef (locality 1). FIG. 7. Articulated, branched portion of *Cymopolia* thallus. FIG. 8. Articulated portion of *Mizzia* thallus. Sample from Dark Canyon (locality 3). FIGS. 9, 10. Scanning electron micrographs. Scale bars = 100  $\mu$ m. FIG. 9. Calcareous portion of *Cymopolia* segment. FIG. 10. Portion of *Mizzia* segment in naturally weathered surface. Original mesh of needle-like aragonite crystals has been replaced by blocky calcite crystals.

and is mud supported (Dunham 1962). Rocks described as packstones and grainstones were deposited in conditions where fine particles were carried away by currents, or no fine particles were present. Rocks described as wackestones were deposited in conditions where current energies were too low to remove fine particles.

Grainstones and packstones composed of disarticulated dasyclad segments (Figs. 5, 6) are found at the mouth of Walnut Canyon and the mouth of Dark Canyon, immediately shelfward of the reef (localities 1, 3; Figs. 2, 3). Dasyclad wackestones were found in Walnut Canyon further shelfward of the reef (northern most portion of locality 1; Fig. 3). Perhaps the most significant lithologies are mud-rich packstones and wackestones containing articulated sections of thalli (Fig. 8). These samples were found shelfward of the mouth of Dark Canyon and also south of Walnut Canyon along the Guadalupe Mountains escarpment, shelfward of the reef (localities 2, 3; Figs. 2, 3).

Field relationships and information from other areas are useful in interpretation of the distribution of these lithologies. The Capitan and associated formations are preserved in the subsurface to the east of the Guadalupe Mountains. Paleochannels cutting through the reef are preserved in the subsurface (Silver and Todd 1969). This feature and field evidence collected as part of this study, suggest that the location of canyons in the Guadalupe Mountains may have been controlled by paleochannels. Rocks composed of disarticulated dasyclad segments are interpreted as having been deposited in grainstones and packstones in high energy conditions along paleochannels (now canyons) that cut through the reef. At locality 2 near Walnut Canyon (Figs. 2, 3), the mud-rich packstones containing articulated dasyclads were deposited in low energy, muddy environments shelfward of the reef and away from the paleochannel. Articulated dasyclads are also found shelfward of the reef in Dark Canyon. Pray (pers. commun. 1989), believes that the area around Dark Canyon was located in an embayment (Fig. 2) and energy conditions were lower there than at other places along the reef. Lower current energies along this paleochannel (now Dark Canyon) would have allowed for the preservation of articulated dasyclads.

*Evidence from population diversity.* Additional key factors in this reconstruction of paleoenvironment are the distribution and nature of the dasyclad populations in the Guadalupe Mountains, where the most striking feature of the dasyclad-dominated grainstones and packstones is their low diversity. Many samples are monospecific, dominated exclusively by *Mizzia* (*M. velebitana*?) (Schubert, 1907). The genera *Macroporella* Pia, 1912 and *Gymnocodium* (?) Pia, 1920 are also present and occasionally dominate individual samples. Associated fauna includes abundant micritic (i.e. muddy-looking) encrustations, most

of which are probably related to blue green algae, although some have structures similar to encrusting foraminifera or to the problematic organism *Tubiphytes*. Other fossils include gastropods, fragments of bivalve shells, foraminifera, sporadic ostracods, and in one section, an echinoderm fragment. Zones of intact brachiopods are found in outcrops near the reef but are not found further shelfward in the back reef. Fusulinid foraminifera are sporadically present, but not abundant, in the Tansill Formation facies studied in Walnut and Dark Canyons. Zones dominated entirely by fusulinids are present, however, in the Yates and Seven Rivers Formations. The assemblage and level of diversity present in the Tansill Formation are consistent with a hypersaline environment.

*Evidence from distribution.* The distribution of *Mizzia* fossils in the outcrops is also striking. The transition from the remarkably high-diversity sponge and algal assemblage in the reef into the remarkably low-diversity dasyclad-dominated assemblage in the back reef is abrupt (Fig. 3). In at least one locality on the south wall of Walnut Canyon this transition occurs over a distance as short as 10 m. This abrupt transition into a dasyclad-dominated assemblage seen in the Tansill Formation is repeated in the Yates Formation in Rattlesnake Canyon and in the Seven Rivers Formation in Slaughter Canyon. Abrupt facies and faunal changes are typical of reef to back reef transitions in modern settings due to an abrupt loss in energy (75–98%) as waves strike the reef and cross into the back reef (Roberts et al. 1975).

*Depth.* In attempting to reconstruct the paleoenvironment of *Mizzia* in the Guadalupe Mountains, depth is a difficult environmental parameter to deduce. Like all green algae, dasyclads are dependent on the red end of the light spectrum, which is 90% absorbed in the top 20 m of the ocean (Ginsburg et al. 1972). The deepest reported occurrence of a modern dasyclad is that of *Dasycladus* at 90 m in the Persian Gulf (Elliott 1977). Such an occurrence is rare; most dasyclads are found in much shallower water (<30 m), and virtually all prolific growths are found in shallow water. For example, *Cymopolia* grows in abundance just below low tide mark. The great abundance of *Mizzia* in the back reef facies of the Guadalupe Mountains is consistent with the suggestion that *Mizzia* also grew in shallow water. A conservative estimate based on comparison to modern analogs would be that where *Mizzia* grew in profusion, waters were less than (and probably much less than) 30 m deep.

*Wave action.* Assessing the amount of wave action in the *Mizzia* paleoenvironment is relatively straightforward. Wave action may result in low species diversity; for example, the coral *Acropora palmata* dominates the upper, high-energy zone of most Caribbean reefs and the red alga *Lithothamnium* dominates a similar zone in Pacific reefs. However, wave action is discounted as a limiting factor in the back

reef beds of the Tansill Formation of the Guadalupe Mountains because the percentage of broken *Mizzia* fragments is low (average 10%). Even fragments that showed distinct signs of abrasion are rare, and as Elliott (1978) has suggested, the degree of destruction of the outer layer of aragonite is indicative of current activity. Waves strong enough to limit diversity should result in a much higher percentage of broken and abraded fragments.

Additional evidence against wave action as a limiting factor for *Mizzia* comes from comparison with *Cymopolia*. Most dasyclads live in calm or moderately agitated water, and *Cymopolia* thrives in the latter. It is possible that the morphology of *Cymopolia*, and by comparison *Mizzia*, is an adaptation to low or moderate energy environments, not high current energies. Whether one accepts this idea or not, the fact remains that articulated sections were found in local accumulations in the Guadalupe Mountains. Thus, at least in local pockets, current energies in the Guadalupe Mountains must have been very low to permit this type of preservation. Although the dasyclad grainstones in the Guadalupe Mountains are currently considered to be a classic example of winnowed platform-edge sands (Wilson 1975), this interpretation is not consistent with the data provided by these algal fossils.

**Hypersalinity.** Hypersalinity may result in domination by one species: for example, *Acetabularia*-dominated lagoons. An ancient dasyclad-dominated environment might have resulted in the deposition of a dasyclad-dominated rock. Thus, hypersalinity has also been cited as a possible controlling factor in the formation of dasyclad grainstones from Permian and Triassic strata around the world (Beadle 1988). Modern, low diversity, dasyclad-dominated environments have associated faunas of ostracodes, foraminifera, and small mollusks, just as do many ancient dasyclad grainstones, including those from the Guadalupe Mountains (Beadle 1988).

Because reconstructions place the Permian Basin near the equator in the southern part of the northern trade-wind belt (Fischer and Sarnthein 1988), it is reasonable to assume that climatic conditions in southeastern New Mexico during the Late Permian were extremely arid. This assumption is supported by the presence of evaporites (rocks formed by chemical precipitation of sulfate and halide minerals from seawater) in the Tansill Formation preserved in the subsurface on the eastern margin of the Delaware basin (Silver and Todd 1969). These protected subsurface evaporites are equivalent to the exposed Tansill Formation outcrops in the Guadalupe Mountains. Additional evidence for hypersaline conditions comes from isotopic analyses of interstitial cements (Given and Lohmann 1985) that indicate an increase in salinity of marine waters near the end of Capitan deposition. These isotopic and subsurface data lead to the conclusion that conditions in the Guadalupe Mountains were certainly

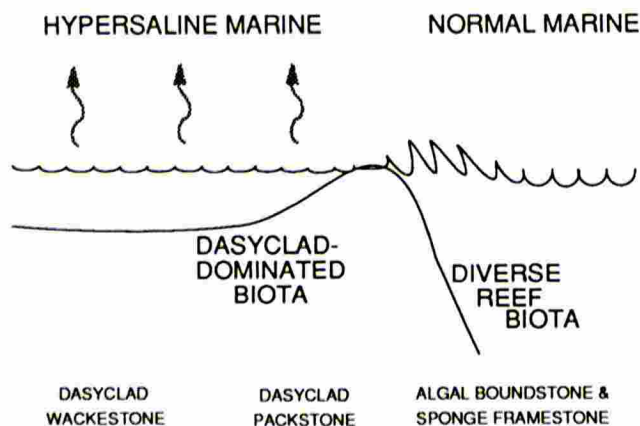


FIG. 11. Schematic cross section through reef and backreef showing relative water energies and distribution of lithologies.

arid; evaporites probably formed in inner shelf lagoons contemporaneously with the deposition of dasyclad grainstones immediately shelfward of the reef. The association of these lithologies is significant to an environmental interpretation of *Mizzia*, and it is not unique to the Guadalupe Mountains. *Mizzia* grainstones and contemporaneous evaporite deposition are also reported from the Upper Permian Zechstein Formation of Northern Europe (Clark 1980).

#### Summary of Results

We conclude that *Mizzia*, where it is found in the Guadalupe Mountains and probably at other localities throughout the world, thrived in a habitat that was warm, at most moderately agitated, sometimes restricted (i.e. protected), probably shallow, and probably hypersaline (Fig. 11). This interpretation has important implications concerning the type of reef found in the Capitan complex. We propose that the Capitan reef, which contains a striking volume of in-place, frame-building and binding organisms with abundant porosity-filling cement, grew to sea level and blocked vigorous wave action. Just as in modern reef settings, this situation created a shallow, protected lagoon immediately shelfward of the reef. Because conditions were extremely arid, these shallow waters quickly became hypersaline. This shallow, protected, hypersaline environment provided ideal conditions for prolific growth of dasyclads.

#### DISCUSSION

The comparison of the Capitan reef complex to a modern barrier reef is not a new concept. The earliest general studies of this area (Lloyd 1929, King 1948, Newell et al. 1953) came to similar conclusions. Later studies focusing on algae, lithologic types and their distribution also concluded that the Capitan reef complex is similar to modern barrier reefs (Klement 1966, Cys 1971, Cronoble, 1974) (Fig. 12A). A different model, however, has domi-

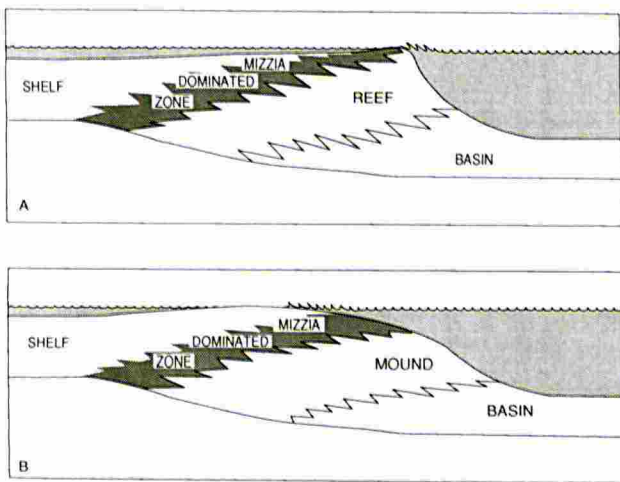


FIG. 12. Schematic diagrams. A) Original barrier reef model of deposition for the Capitan reef complex simplified from Newell et al. (1953). B) Marginal mound depositional model simplified from Dunham (1972).

nated the literature for the last 20 years (Fig. 12B). According to the marginal mound hypothesis, (Achauer 1969, Dunham 1972, Pray 1986) the Capitan reef complex is an "example of massive limestone formed at a submerged shelf edge" (Pray 1986). The terminology "marginal mound" implies not a wave-resistant reef but an accumulation of sediment forming in deep water (below wave base). This model implies that the sediments deposited shelfward of the reef were open to oceanic circulation and wave action. It does not allow for restriction of flow nor for creation of hypersaline conditions immediately shelfward of the reef. Many detailed theses and dissertations support the "marginal mound" hypothesis (Babcock 1974, Yurewicz 1976, Hurley 1978, Neese 1979, Schwartz 1981). They have all focused on specific areas, never on *Mizzia*-dominated zones, and none have fully explained the unique distribution of dasyclads in this area.

We suggest that the marginal mound hypothesis must either be modified to explain the distribution of dasyclads or it must be abandoned. We also note that many major advances in understanding carbonate rocks have come about since the marginal mound model was proposed in the late 1960's. This paper is a precursor to a much broader study which will incorporate many of these new advances including the chemistry and mechanics of cement deposition, dynamics of modern reef circulation, the relationship of reef growth to sea level change, and a better understanding of the "phyllid" algae (*Eugonophyllum* and *Archeolithoporella*). We hope that further research will show conclusively which model is correct.

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- Achauer, C. W. 1969. Origin of Capitan Formation, Guadalupe Mountains, New Mexico and Texas. *Am. Assoc. Petrol. Geol. Bull.* 53:2314-23.
- Babcock, J. A. 1974. The role of algae in the formation of the Capitan Limestone (Permian, Guadalupian) Guadalupe Mountains, West Texas-New Mexico. Ph.D. thesis, University of Wisconsin, Madison, 241 pp.
- . 1986. The puzzle of alga-like problematica, or rummaging around in the algal wastebasket. In Hoffman, A. & Nitecki, M. H. [Eds.] *Problematic Fossil Taxa*. Oxford, New York, pp. 12-26.
- Bassoulet, J. P., Bernier, P., Deloffre, R., Genot, P., Jaffrezo, M., Poignant, A. F. & Segonzac, G. 1977. Classification criteria of fossil Dasycladales. In Flügel, E. [Ed.] *Fossil Algae*. Springer, Berlin, pp. 154-66.
- Beadle, S. C. 1988. Salinity tolerance in recent and fossil dasyclads. In Danielli, H. M. C. & Cys, J. M. [Eds.] *Friends of the Algae Newsletter* 8:34.
- Britton, N. L. & Millsbaugh, C. F. 1920. *The Bahama Flora*. The Authors, New York, 695 pp.
- Clark, D. N. 1980. The sedimentology of the Zechstein 2 carbonate formation of eastern Drenthe. *Contrib. Sedimentol.* 9: 131-65.
- Cronoble, J. M. 1974. Biotic constituents and origin of facies in Capitan reef, New Mexico and Texas. *Mountain Geol.* 11:95-108.
- Cys, J. M. 1971. Origin of Capitan Formation, Guadalupe Mountains, New Mexico and Texas: discussion. *Am. Assoc. Petrol. Geol. Bull.* 55:310-5.
- Dunham, R. J. 1962. Classification of carbonate rocks according to depositional texture. *Am. Assoc. Petrol. Geol. Memoir* 1:108-21.
- . 1972. Capitan Reef, New Mexico and Texas: facts and questions to aid interpretation and group discussion. Permian Basin Section Society of Economic Paleontologists and Mineralogists Publication 72-14, 278 pp.
- Elliott, G. F. 1977. Inferred isocrynal distribution of Jurassic dasycladacean algae in Europe, North Africa and southwestern Asia. *J. Geol. Soc. London* 133:363-73.
- . 1978. Ecologic significance of post-Paleozoic, green calcareous algae. *Geol. Mag.* 115:437-42.
- Fischer, A. G. & Sarnthein, M. 1988. Airborne silts and dune-derived sands in the Permian of the Delaware Basin. *J. Sed. Petrol.* 58:637-43.
- Flügel, E. 1985. Diversity and environments of Permian and Triassic dasycladacean algae. In Toomey, D. F. & Nitecki, M. H. [Eds.] *Paleoalgology: Contemporary Research and Applications*. Springer, Berlin, pp. 345-51.
- Ginsburg, R., Rezak, R. & Wray, J. L. 1972. Geology of the Calcareous Algae (Notes for a short course). Comparative Sedimentology Laboratory, Division of Marine Geology and Geophysics, Rosenstiel School of Marine and Atmospheric Science, The University of Miami, 174 pp.
- Given, R. K. & Lohmann, K. C. 1985. Derivation of the isotopic composition of Permian marine cements. *J. Sed. Petrol.* 55: 430-9.
- Hämmerling, J. 1944. Zur Lebensweise, Fortpflanzung und Entwicklung verschiedener Dasycladaceen. *Arch. Protistenkd.* 97: 7-56.
- Hurley, N. F. 1978. Facies Mosaic of the Lower Seven Rivers Formation (Permian), North McKittrick Canyon, Guadalupe Mountains, New Mexico, M.S. thesis, University of Wisconsin, Madison, 194 pp.

- Hurtado-Ponce, A. & Modelo, R. B. 1983. Marine macrobenthic green algae of Currimao, Ilocos Norte, Luzon. *Kalayaan, Philipp. J. Biol.* 12:145-9.
- Johnson, J. H. 1961. *Limestone Building Algae and Algal Limestones*. Colorado School of Mines, Golden, 297 pp.
- King, P. B. 1948. Geology of the southern Guadalupe Mountains, Texas. U.S. Geological Survey Professional Paper 215, 183 pp.
- Klement, K. W. 1966. Studies on the ecological distribution of lime-secreting and sediment-trapping algae in reefs and associated environments. *Neues Jahrb. Geol. Paläontol. Abh.* 125: 363-81.
- Lloyd, E. R. 1929. Capitan Limestone and associated formations of New Mexico and Texas. *Am. Assoc. Petrol. Geol. Bull.* 13: 645-58.
- Neese, D. G. 1979. Facies mosaic of the upper Yates and lower Tansill Formations (Upper Permian), Walnut Canyon, Guadalupe Mountains, New Mexico. M.S. thesis, University of Wisconsin, Madison, 110 pp.
- Newell, N. D., Rigby, J. K., Fischer, A. G., Whiteman, A. J., Hickox, J. E. & Bradley, J. S. 1953. *The Permian Reef Complex of the Guadalupe Mountains Region, Texas and New Mexico*. Freeman, San Francisco, 236 pp.
- Palmer, A. R. 1983. The decade of North American Geology Geologic Time Scale. Geological Society of America, 1 p.
- Pray, L. C. 1986. Capitan Reef Complex (Permian), Guadalupe Mountains, southwestern United States: reinterpretation of deposition and diagenesis of a classic sedimentologic model. *Am. Assoc. Petrol. Geol. Bull.* 70:1762.
- Rezak, R. 1959. Permian algae from Saudi Arabia. *J. Paleontol.* 33:531-9.
- Riding, R. & Voronova, L. 1985. Morphological groups and series in Cambrian calcareous algae. In Toomey, D. F. & Nitecki, M. H. [Eds.]. *Paleoalgology*. Springer, Berlin, 376 pp.
- Roberts, H. H., Murray, S. P. & Suhayda, J. N. 1975. Physical processes in a fringing reef system. *J. Mar. Res.* 33:233-60.
- Schwartz, A. H. 1981. Facies mosaic of the upper Yates and lower Tansill Formations (Upper Permian), Rattlesnake Canyon, Guadalupe Mountains, New Mexico. M.S. thesis, University of Wisconsin, Madison, 158 pp.
- Silver, B. A. & Todd, R. G. 1969. Permian cyclic strata, northern Midland and Delaware Basins, West Texas and southeastern New Mexico. *Am. Assoc. Petrol. Geol. Bull.* 53:2223-51.
- Valet, G. 1969. Contribution à l'étude des Dasycladales, 2-3 Cytologie, reproduction, révision systématique. *Nova Hedwigia* 17:551-644.
- Wilson, J. L. 1975. *Carbonate Facies in Geologic History*. Springer, Berlin, 471 pp.
- Woelkerling, W. J. 1976. *South Florida Benthic Marine Algae*. Comparative Sedimentology Laboratory, Division of Marine Geology and Geophysics, Rosenstiel School of Marine and Atmospheric Science, The University of Miami, 148 pp.
- Wray, J. L. 1977. *Calcareous Algae*. Elsevier, Amsterdam, 185 pp.
- Yurewicz, D. A. 1976. Sedimentology, paleoecology, and diagenesis of the massive facies of the lower and middle Capitan Limestone (Permian), Guadalupe Mountains, New Mexico and West Texas. Ph.D. thesis, University of Wisconsin, Madison, 246 pp.
- Zorn, H. 1976. Über den Lebensraum fossiler Wirtelalgen in der Trias der Alpen. *Naturwissenschaften* 63:426-9.

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## DNA POLYMORPHISM WITHIN THE WH7803 SEROGROUP OF MARINE SYNECHOCOCCUS SPP. (CYANOBACTERIA)<sup>1,2</sup>

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### ABSTRACT

Genetic differences among ten strains of chroococcoid cyanobacteria (*Synechococcus* spp.) were identified by Southern blot hybridization. Data on shared number of restriction fragment length polymorphisms were used to identify the pattern and degree of genetic relatedness among the strains by two different methods of phylogenetic analysis. All the marine strains in the study contained phycoerythrin (PE) and cross-reacted with antisera directed against strain WH7803. Five contained a PE composed of phycoerythrin (PE) and phycoerythrobilin (PEB) chromophores, and three contained a PE composed of only PEB chromophores. Two freshwater strains which do not

contain PE and do not cross-react with the anti-WH7803 serum were included in the study for comparison. Dollo Parsimony analysis and cluster analysis showed that the WH7803 serogroup includes at least four widely separated genetic lineages. Strains within each lineage were closely related but the differences between lineages were as great as those between any of the marine lineages and the freshwater lineage. Strains cultured simultaneously from the same water mass were associated with different lineages. Thus, we conclude that natural assemblages of marine *Synechococcus* are, at least occasionally, composed of individuals as genetically distinct from each other as members of different species or genera in other taxa.

**Key index words:** cyanobacteria; evolution; genetics; picoplankton; restriction fragment length polymorphism; *Synechococcus*

Until this decade, cyanobacteria were believed to be poorly represented among the planktonic flora of the world's oceans (Glover 1985). This view has

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