Dasycladalean Algal Biodiversity Compared with Global Variations in Temperature and Sea Level over the Past 350 Myr

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Dasycladalean green algae show marked fluctuation in genus and species biodiversity from the Carboniferous to the Pliocene. Diversity lows (<10 species) alternate with peaks (>70 species) over periods of ~20–50 Myr. Relatively few taxa are recorded for the earliest Carboniferous, Early Triassic, Early to Mid-Jurassic, Late Cretaceous, and Pliocene. Diversity maxima occur in the Permian, Early Cretaceous, and Paleocene. With the exception of the Late Cretaceous, biodiversity broadly tracked temperature from the Carboniferous to the Pliocene. Diversity minima generally correspond with low sea level, and diversity maxima with periods of intermediate sea level. Dasycladaleans were most diverse when their main habitats—warm shallow seas—were most extensive. This observation does not preclude the influence of additional important factors on dasycladalean evolutionary history, but it suggests a strong link between long-term patterns of dasycladalean diversity and global fluctuations in temperature and sea level.

INTRODUCTION

Dasycladalean algae, informally referred to as dasyclads, are a major group of benthic marine chlorophytes in which external parts of the thallus can be heavily calcified. Although the resulting skeleton, consisting of a central stem and lateral branches, usually is separated into numerous segments and fragments, these bioclasts are locally common sediment components. Calcification can preserve branching pattern and position of reproductive structures. These details have been utilized extensively in taxonomic treatments of the group and to assess phylogenetic development (Berger and Kaever, 1992). As a result of this calcification, dasyclads have a better fossil record than any other marine green algae, and the long-term development of the group is known in considerable detail (e.g., Pia, 1920, Flügel, 1985, 1991, Barattolo, 1991, Berger and Kaever, 1992, De Castro, 1997). Strongly calcified dasyclads range from Late Ordovician (Edwards et al., 1993) to the present. The past 350 Myr of this history, or since the Mississippian, is particularly well documented, and biostratigraphic research has compiled detailed species ranges (Deloffre and Granier, 1992; Granier and Deloffre, 1993, 1994; Bucur, 1999). These taxonomic-stratigraphic abundance data reveal a secular pattern of pronounced diversity variation. From the Late Paleozoic to Cenozoic, over time scales of 20–50 Myr, recorded dasycladalean species number fluctuates from zero to ~100. Species maxima in the Permian (81 species), Early Cretaceous (72), and Paleocene (102) contrast with species minima in the Mississippian (5 species), Early Triassic (0), Early to Mid-Jurassic (2), Late Cretaceous (9), and Pliocene (<5).

These secular fluctuations could reflect a wide combination of biological and environmental factors, as well as vagaries of preservation. This paper examines the possibility that major environmental factors known to influence extant dasycladaleans—water depth and water temperature—largely may have determined their diversity through time. Elliott (1977, 1982, 1984) proposed that dasycladaleans expanded from tropical towards temperate zones during the Triassic–Jurassic, but he subsequently rejected (Elliott, 1986) this view. Present-day dasyclads are typical of warm, shallow bays and back-reef lagoons (Berger and Kaever, 1992), and paleoecologic studies indicate that this environmental predisposition has not changed substantially during the long history of the group (Flügel, 1985, 1991). Most extant species occupy habitats with minimum annual temperatures ≥20°C, and exhibit optimal growth at 25–27°C (Berger and Kaever, 1992). Although dasycladaleans are known at water depths of 90 m (Edelstein 1964), they are most common at ≤10 m (Berger and Kaever, 1992).

This study compares dasycladalean taxonomic abundance with global changes in temperature and sea level from the Carboniferous to the Pliocene. There is a broad, positive correlation between diversity and intermediate sea level, which could reflect maximum extension of shallow seas, and between diversity and temperature. In general, over the past 350 Myr, dasycladalean diversity has been greatest when warm, shallow seas were developed most extensively. It is possible, therefore, that reduced Neogene (past 23 Myr) diversity of these algae reflects the combined effects of global cooling and sea-level decline on a group that preferentially inhabits shallow, tropical-marine habitats.

DASYCLADALEAN BIODIVERSITY

Data

Dasycladalean taxonomic data are taken from compilations by Deloffre and Granier (1992), Granier and Deloffre

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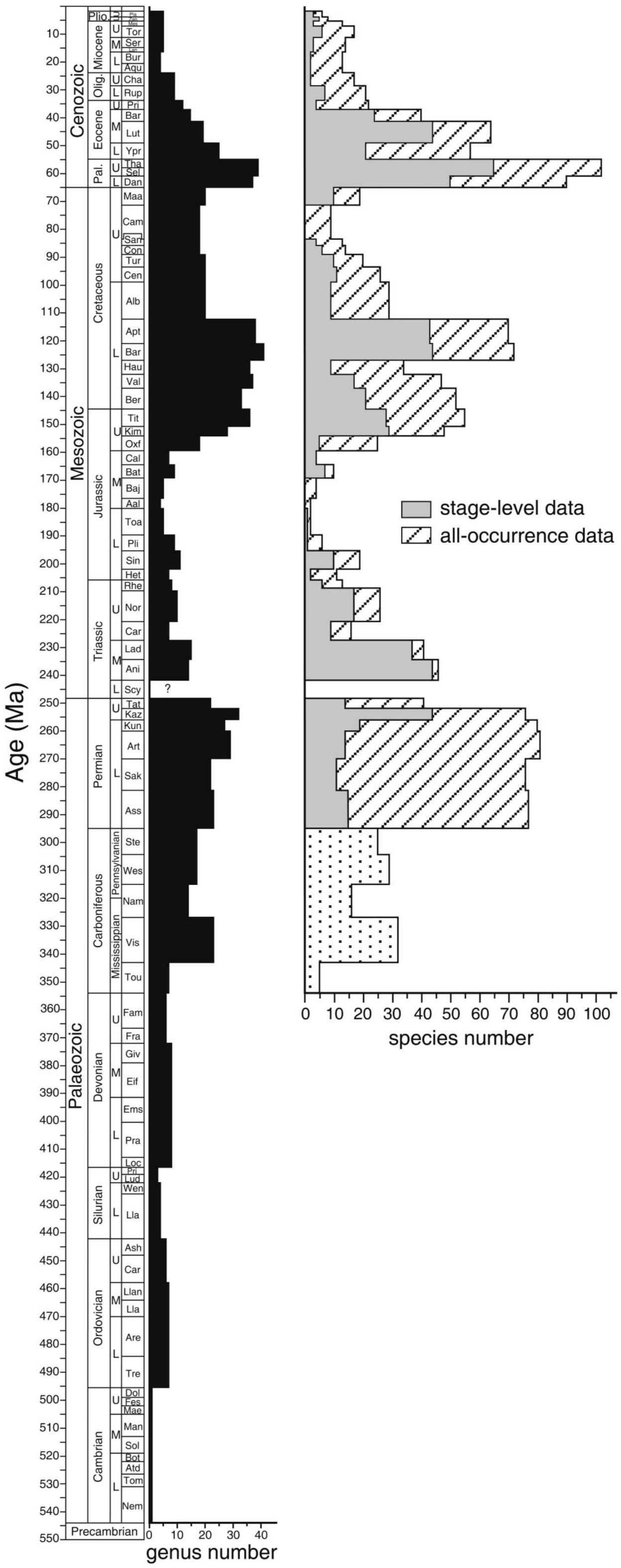

FIGURE 1—Cambrian–Pliocene generic and specific dasycladalean biodiversity data from Deloffre and Granier (1992), Granier and Deloffre (1993, 1994), and Bucur (1999) plotted against the timescale of Haq and van Eysinga (1998). Stage-level and all-occurrence species data were calculated from published certain-probable-possible species-presence assessments using the methodology of Aguirre et al. (2000a). Note that different taxonomic treatments can give rise to discrepancies where diversity is very low (e.g., in parts of the Early–Mid Jurassic where number of genera exceeds number of species). Stage-level and all-occurrence species data are not separated for the Carboniferous (stippled).

(1993, 1994), and Bucur (1999). Bucur (1999) assembled generic richness data for the Cambrian–Pliocene, inclusive, but only compiled the full inventory of species richness for the Devonian–Triassic, inclusive, and Cenozoic (excluding Pleistocene). The Jurassic–Cretaceous species gap is filled by data listed by Granier and Deloffre (1993). Previous species compilations for the Permian–Triassic (Granier and Deloffre, 1994) and Cenozoic (Deloffre and Granier, 1992) allow comparisons with Bucur's (1999) compilation. Where comparison is possible, dasycladalean species richness data of Bucur (1999) are virtually the same as those compiled by Deloffre and Granier (1992) and Granier and Deloffre (1993, 1994). Spearman rank correlation indicates no significant differences among the different databases (Table 1).

Deloffre and Granier (1992) and Granier and Deloffre (1993, 1994) record three categories of species presence: certain, probable, possible. This threefold grading is used to compile two types of datasets (stage-level and all-occurrence data), employing the methodology of Aguirre et al. (2000a, b). The stage-level data derived from Deloffre and Granier's data sets show lower diversity values due to the more limited data; however, the general trends of the curves are identical (Fig. 1, Table 1).

Numbers of species and genera in Bucur's (1999) database are resolved to stage level only for the Carboniferous–Oligocene. Species data derived from Deloffre and Granier datasets are resolved to stage level for the Permian–Pliocene, inclusive. Within the limitations of these databases, analyses here use the finest temporal resolution possible. This study focuses on the Carboniferous–Pliocene record (354–1.8 Myr) of dasycladaleans (Fig. 1) because the genus and species data are resolved to stage level for this interval. For the Carboniferous, Bucur's (1999) species data are used (Fig. 1). Genus and species richness are plotted (Fig. 1) against the time scale of Haq and van Eysinga (1998).

Generic Diversity

Generic diversity of calcified dasycladaleans for the entire Phanerozoic is shown in Fig. 1. Ordovician–Devonian dasycladalean generic diversity is low (Bucur 1999). From the Carboniferous–Pliocene, three periods of increased diversity (Viséan–Tatarian, Oxfordian–Aptian, Danian–Bartonian) are separated by periods of reduced diversity (Scythian–Callovian, Albian–Maastrichtian, Priabonian–Pliocene).

Mississippian to Late Permian High: Viséan diversification was followed by a reduction in the Namurian, and then a gradual increase to the Kazanian (Late Permian, 255 Myr), which marked the dasycladalean diversity maximum (32 genera) for the Paleozoic as a whole. Subsequently, diversity declined in the Tatarian and then abruptly collapsed at the end of the Permian.

Early Triassic to Mid-Jurassic Low: There are no re-

TABLE 1—Comparison of the shapes of the curves of dasycladalean species and generic-richness data (Deloffre and Granier, 1992, Granier and Deloffre, 1993, 1994, Bucur, 1999) using Spearman rank correlation. These results do not indicate significant differences among these different datasets; ρ-corrected for ties/*p*-values for each pair of variables.

	Bucur species	Deloffre and Granier species (Stage-level)	Deloffre and Granier species (All-occurrence)
Bucur genera	0.951/<0.0001	0.736/<0.0001	0.848/<0.0001
Bucur species		0.719/0.0017	0.980/<0.0001
Deloffre and Granier species (Stage-level)			0.892/<0.0001

cords of Scythian (earliest Triassic, 245 Myr) dasycladaleans in the data compilations used, and this is confirmed by other sources (Flügel, 1985, 1991; Barattolo, 1991). Diversity recovered to 14 genera in the Anisian and 15 in the Ladinian, decreased to 4 genera in the Aalenian (Mid-Jurassic, 180 Myr), and remained low to the Callovian.

Late Jurassic to Early Cretaceous High: Rapid Late Jurassic diversification peaked in the Tithonian (36 genera) and remained high until the Aptian, being highest (41 genera) in the Barremian (Early Cretaceous, 125 Myr), the highest level for the Mesozoic.

Mid-Late Cretaceous Reduction: An abrupt Albian diversity decline led to a plateau, with a low-point in the Coniacian–Campanian (~80 Myr) that continued until the end-Cretaceous. However, the number of genera present (18) was higher than during the Aalenian (Mid-Jurassic) decline. Late Cretaceous diversity actually was similar in magnitude to the Carboniferous–Permian average.

Paleocene to Mid-Eocene High: Rapid diversification, with a near doubling of recorded genera from the Maastrichtian (20 genera) to the Danian (37 genera), culminated in the highest level for the Cenozoic with 39 genera recorded in the Selandian–Thanetian (~55 Myr). From this peak, diversity declined progressively during the Eocene.

Oligocene to Pliocene Low: Decreased diversity continued to an Early Miocene (20 Myr) minimum (4 genera) and barely increased subsequently. This Miocene–Pliocene low (4–5 genera) is comparable to that of the Mid-Jurassic.

Present day: Present-day dasycladalean genera, such as *Acetabularia*, *Cymopolia*, and *Neomeris*, are widespread and locally abundant, with the group as a whole represented by 11 genera containing 38 species (Berger and Kaever, 1992). However, several extant genera are uncalcified, and others are so weakly calcified that they would be unlikely to create readily recognizable fossils. This situation is reflected in the Miocene–Pliocene record, which has the lowest (5) dasycladalean generic diversity since the Mid-Jurassic, 185 Myr ago.

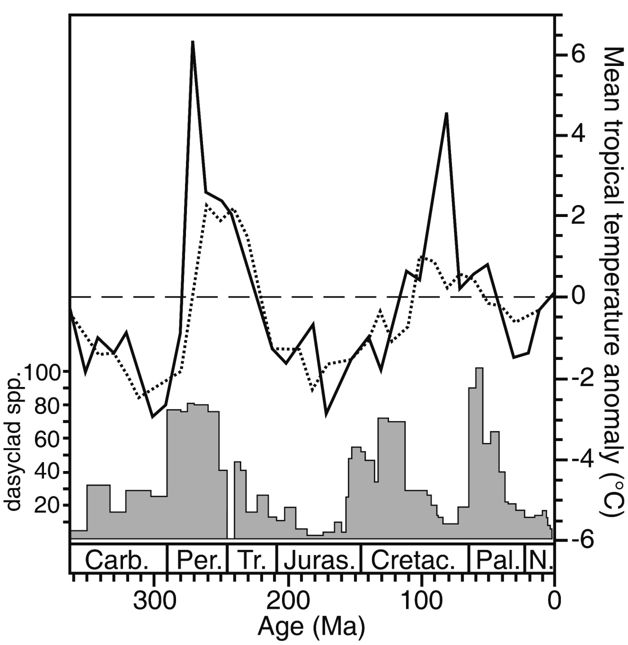

FIGURE 2—Comparative plots of Carboniferous–Pliocene dasycladalean species-richness data (combined from Deloffre and Granier 1992, Granier and Deloffre 1993, 1994, and Bucur 1999) and detrended paleotemperature anomalies derived from the $\delta^{18}O$ values of marine shells (Veizer et al., 2000, fig. 3). Veizer et al. (2000) carried out detrending by subtracting the least-squares fit from the original data. The temperature trends shown represent running means with a time step of 10 Myr and temporal windows of 20 Myr (solid line) and 50 Myr (dotted line). Time scale of Harland et al. (1990).

Species Diversity

Species richness shows a similar pattern to genus richness, although fluctuations in species diversity are more pronounced (Fig. 1). Diversity maxima are in the Artinskian (81) for the Paleozoic, Barremian (72) for the Mesozoic, and Selandian–Thanetian (102) for the Cenozoic. Minor differences in pattern are observed: (1) at the Carboniferous–Permian boundary, where species diversification is greater than genus diversification; (2) at the end-Permian, where species decline commenced in the Kungurian, ~5 Myr prior to reduction in genus diversity; (3) where species reduction in the Albian continued to a minimum in the Campanian; (4) where Paleocene diversification is greater for species than genera; and (5) a species increase in the Lutetian (Mid-Eocene), whereas genus diversity falls.

DASYCLADALEAN DIVERSITY, PALEOTEMPERATURE, AND SEA LEVEL

This study compares dasyclad diversity with published estimates of changes in global temperature and sea level. For the Carboniferous–Pliocene interval, in order to avoid uncertainties regarding absolute temperature inferences from $\delta^{18}O$ values with increasing geological time (Veizer et al., 2000), biodiversity is compared with detrended paleotemperature anomalies derived from the $\delta^{18}O$ signal of marine shells by subtracting the least-squares linear fit from the original data (Veizer et al., 2000, fig. 3) (Fig. 2). In addition, for the Cenozoic, temperature estimates derived from $\delta^{18}O$ values (Miller et al., 1987) and magnesium/calcium ratios of benthic foraminifer tests (Lear et al., 2000) are used here (Fig. 3). In Figure 4, Carboniferous–Pliocene dasycladalean diversity is compared with sea-level estimates of Haq et al. (1987) and Hallam (1992).

Diversity and Temperature

Veizer et al.'s (2000) temperature plots are based on samples from low-latitude, shallow-water environments (Veizer et al., 1999). These are, therefore, directly relevant to dasycladaleans that shared this general habitat. From the Pennsylvanian to the Early Cretaceous, dasyclad diversity tracked temperature, and the Mid-Jurassic low diversity coincides with relatively low temperature (Fig. 2). Late Jurassic–Early Cretaceous diversity rise terminated in the Aptian (115 Myr), but temperature continued to rise toward a mid-Late Cretaceous peak. Renewed Paleogene diversification occurred while temperatures were still relatively high. During the Cenozoic, there was a broad positive correspondence between species diversity and absolute temperatures estimated from $\delta^{18}O$ and magnesium/calcium values of foraminifers (Fig. 3). The Selandian–Thanetian (57 Myr) dasycladalean diversity maximum (Fig. 3) coincides with a latest Paleocene temperature peak (Zachos et al., 1993) and precedes an Ypresian (53 Myr) temperature peak (Lear et al., 2000). Subsequent diversity decline tracked rapid temperature fall to the Oligocene, and its subsequent reduced fall in the Oligocene–Mid-Miocene. Progressive Eocene diversity reduction coincided with temperature decline that culminated in onset of Southern Hemisphere glaciation in the earliest Oligocene (Zachos et al., 1993, 1996; Corfield, 1995; Lear et al., 2000). From the Oligocene–Pliocene, biodiversity was relatively static, whereas temperature shows further rapid decline after the Early Miocene.

Diversity and Sea Level

Dasycladalean diversity increased as sea level fell from the Carboniferous to Late Permian (Fig. 4). Sharp, but short-lived, Early Triassic diversity decline coincided with reduced sea level. During much of the Early–Mid Jurassic, both diversity and sea level were relatively low. They rose together during the Late Jurassic–Early Cretaceous. Early Cretaceous diversification terminated in the Aptian as sea-level rise continued. Diversity was relatively low from ~70–100 Myr ago when sea level was at its highest. Rapid Paleocene diversification, during which dasyclad diversity reached its all-time peak in the Selandian–Thanetian, coincided with falling sea level. The subsequent diversity decline broadly tracks sea-level fall that was sustained throughout the remainder of the Cenozoic.

DISCUSSION

Temperature

There is a broad positive correspondence between dasyclad diversity and paleotemperature values from the Carboniferous–Pliocene. Elevated temperatures are likely to have encouraged both growth and calcification of dasycladaleans. The principal exception to this covariation was ~70–110 Myr ago (mid-Late Cretaceous), when reduced species diversity coincided with elevated temperatures (Fig. 2). A general Late Cretaceous diversity reduction in benthic communities has been related to cooling after unusually high temperatures (Johnson et al., 1996). Alternatively, stress caused by elevated temperatures may have been responsible for dasyclad diversity decline. Temperatures of up to 32–36°C have been suggested for the Albian–Turonian (Wilson et al., 2002; Bice and Norris, 2002; Schouten et al., 2003), and are higher than those experienced by extant dasycladaleans in tropical locations that seasonally approach 30°C. However, a positive temperature anomaly of similar magnitude in the Late Permian and Early Triassic (Veizer et al., 2000, fig. 3) corresponds with substantially higher dasyclad diversity than during the Late Cretaceous (Fig. 1). Late Cretaceous discrepancy between dasyclad diversity and temperature, therefore, suggests the influence of a factor or factors other than temperature (such as exceptionally high sea level, see below). Despite this discrepancy, regression analysis of the temperature-diversity dataset for the Carboniferous–Pliocene as a whole shows a good correlation (p-value = <0.0001).

Sea Level

Dasycladalean diversity was low when sea level was low, but was not at its highest when sea level was very high. Instead, highest diversity corresponds with intermediate sea level, as in the Permian, Late Jurassic–Early Cretaceous, and Paleocene–Eocene (Fig. 4), and can be shown by plotting generic diversity against sea level (Fig. 5). This relationship suggests that very shallow-water environments (<20 m), preferentially occupied by dasycladaleans, are not only reduced when global sea level is low, but also when sea level is very high. Intermediate sea levels thus could reflect the maximum extent of shallow seas (see Riding, 1984, fig. 9). Correlation between diversity and extent of shallow seas is consistent with the positive species-area relationship suggested by Simberloff (1974). Relatively low diversity (~70–110 species) broadly coincided with carbonate-platform drowning events in the Mid-Cretaceous (~90–105 Myr; Schlager, 1981; Jenkyns, 1980, 1991; Jiménez et al., 1996), and diversity was lowest when sea level was highest, early in the Campanian. It is possible, therefore, that reduced Late Cretaceous dasyclad diversity reflects very high sea level—the highest of the past 250 Myr—that effectively drowned the very shallow (<10 m water depth) habitats preferred by dasyclad algae.

Other Factors

In examining Permian–Triassic dasycladalean diversification patterns, Flügel (1985, 1991) suggested that changes in diversity were related to substrate availability (Flügel, 1985) and salinity (Flügel, 1991), rather than temperature (Flügel, 1985), but there are no data to indicate that these factors could account for longer-term secular trends in dasyclad diversity. Berger and Kaever (1992) noted correspondence between dasycladalean diversity and reef abundance. This is consistent with an overall pos-

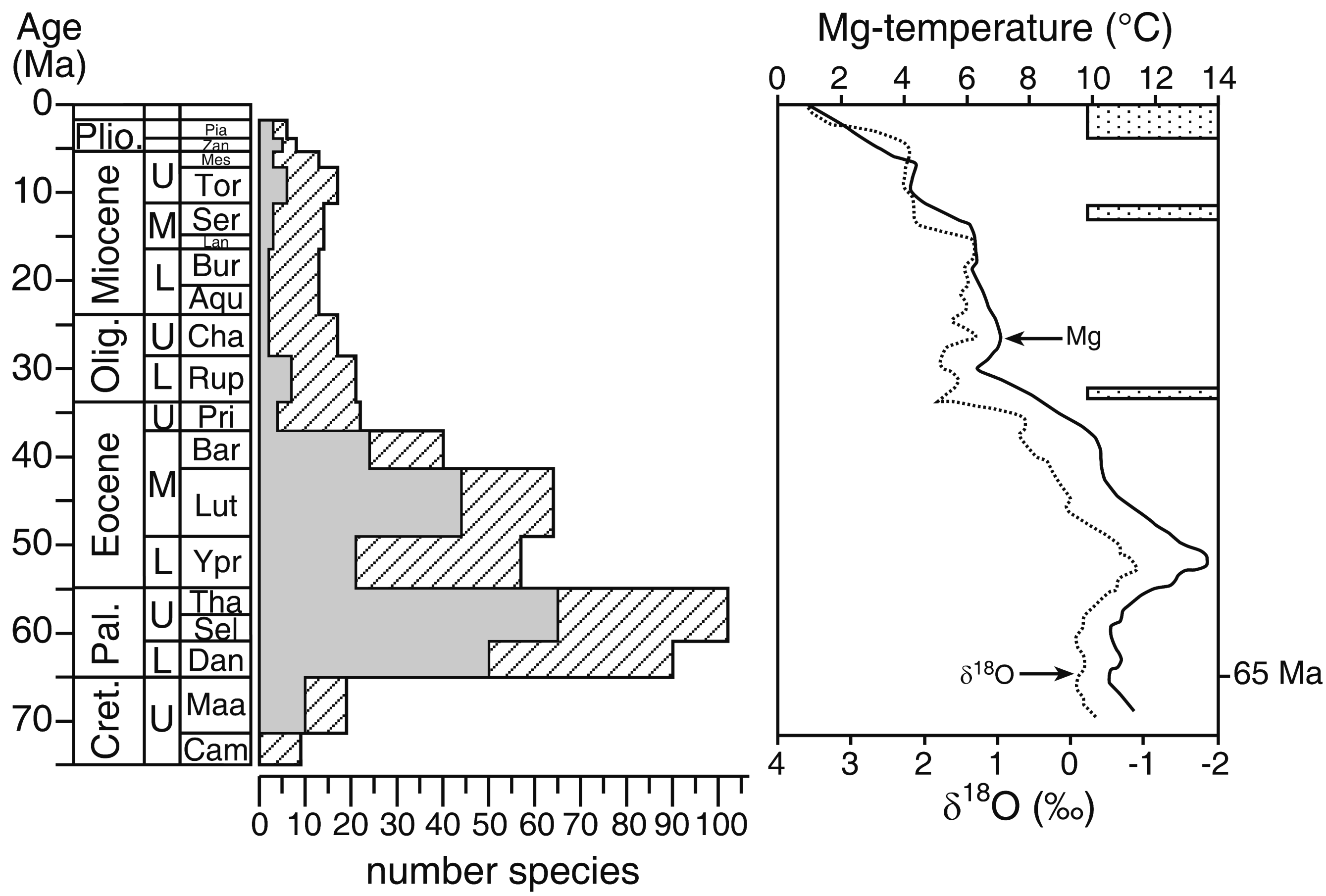

FIGURE 3—Comparative plots of dasycladalean species-richness data (combined from Deloffre and Granier, 1992, Granier and Deloffre, 1993) and paleotemperature estimates (redrawn from Lear et al. 2000, fig. 1c, d) based on $\delta^{18}O$ values (Miller et al., 1987) and magnesium/calcium ratios of benthic foraminifer tests (Lear et al., 2000). Stippled bars indicate glacial events.

itive relationship between dasycladalean diversity and extent of warm, shallow seas.

It has been suggested that the mineralogy of $CaCO_3$ shells in some marine algae and invertebrates may be affected by oscillation between calcite and aragonite seas (Stanley and Hardie, 1998). Extant dasycladaleans are aragonitic, and, with rare possible exceptions (e.g., Simmons et al., 1991), this appears to have been the principal mineralogy of the group throughout its history (Berger and Kaever, 1992). Stanley and Hardie (1998) suggested that dasycladalean abundance corresponds with aragonite sea episodes. However, both the Aragonite II (Mid-Carboniferous to Mid-Jurassic) and Calcite II (Mid-Jurassic to end-Eocene) episodes (Stanley and Hardie, 1998, fig. 1) include periods of both high and low dasycladalean diversity (see Fig. 1). Stanley and Hardie (1998, fig. 1) correctly noted that dasyclads were major sediment producers in the Permian–Triassic, during Aragonite II. However, at times, dasyclads were similarly important during Calcite II (e.g., in the Late Jurassic–Early Cretaceous and Paleocene–Eocene; Fig. 1). In fact, the peak of Calcite II (see Stanley and Hardie, 1998, fig. 1) coincides with the Barremian–Aptian (125–110 Myr) dasyclad diversification peak, which is the highest for the Mesozoic (Fig. 1). Thus, comparison of the taxonomic data compiled in Fig. 1 with the Sandberg curve shown by Stanley and Hardie (1998) does not support a straightforward relationship between dasycladalean diversity and calcite- and aragonite-sea episodes.

CONCLUSIONS

During the 350 Myr period from the Carboniferous to the Pliocene, dasycladalean algal diversity fluctuated from <10 to >70 species over periods of ~20–50 Myr. Diversification phases during the Permian–Mid-Triassic, Late Jurassic–Early Cretaceous, and Paleocene–Eocene each were succeeded by periods of reduced diversity (Fig. 1). There is a broad positive correspondence between biodiversity and paleotemperature, except for the interval ~70–110 Myr ago in the mid-Late Cretaceous (Fig. 2). The relationship between dasyclad diversity and sea level is more complicated. Diversity was low when sea level was either very high or low, and was highest when sea level was intermediate. Periods when dasyclad species number exceeded 50 (during the Permian, Late Jurassic–Early Cretaceous, and Paleocene–Eocene) generally corresponded with times of both increased temperature and intermediate sea level. Periods of intermediate sea level are inferred to reflect maximum extent of very shallow seas. Low dasyclad diversity in the mid-Late Cretaceous (~70–110 Myr ago) could reflect reduction in shallow-water hab-

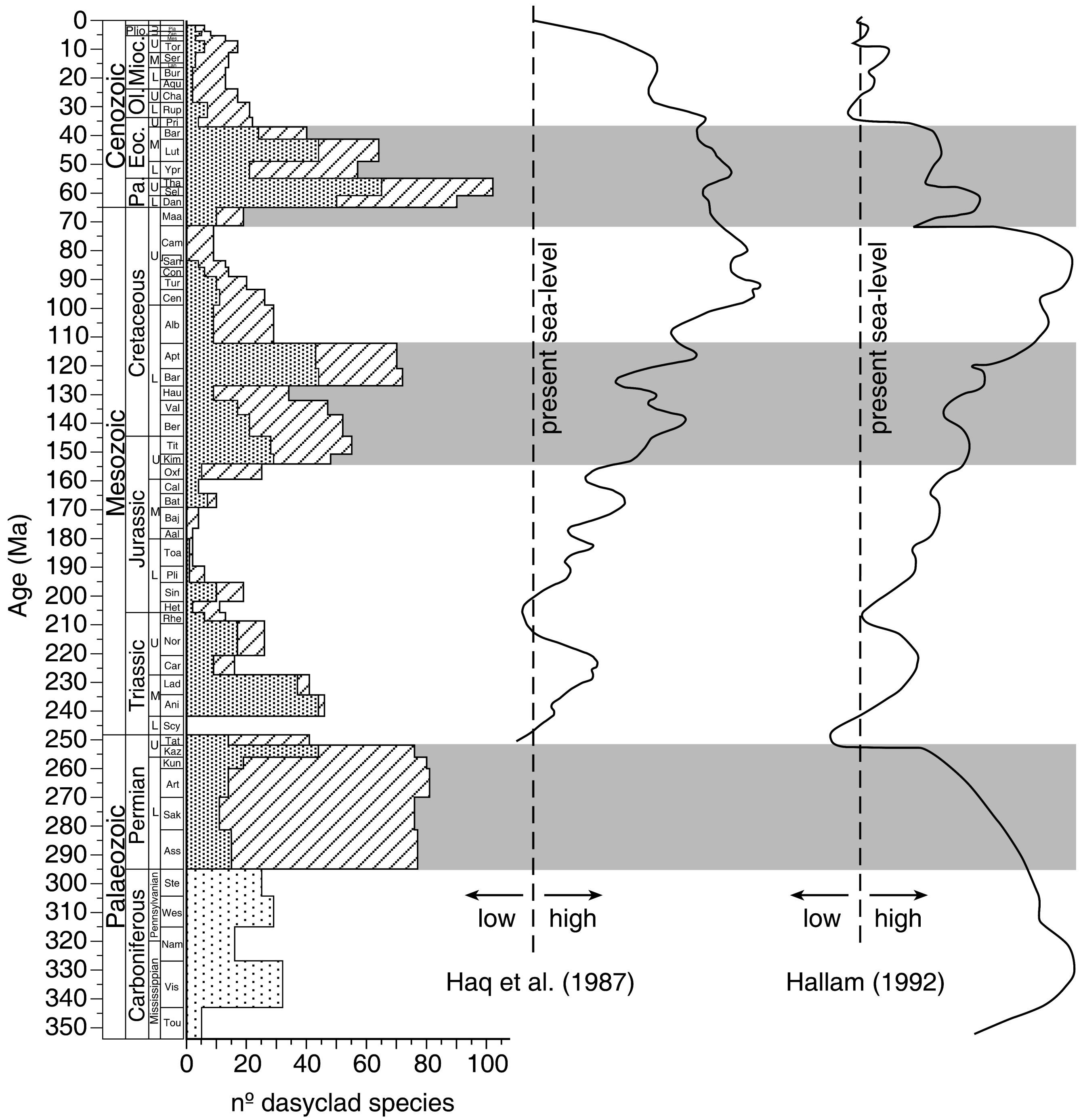

FIGURE 4—Comparative plots of Carboniferous–Pliocene dasycladalean species-richness data (combined from Deloffre and Granier, 1992, Granier and Deloffre, 1993, 1994, and Bucur, 1999; see Fig. 1) and sea-level estimates of Haq et al. (1987) and Hallam (1992). Time scale from Haq and van Eysinga (1998). These data also are compared in Fig. 5. Figure-wide gray bands indicate periods of maximum diversity (Permian, Late Jurassic–Early Cretaceous, and Paleocene–Eocene). These coincide with intermediate sea levels, possibly reflecting maximum extension of shallow seas.

itat as a consequence of platform drowning, despite temperatures favorable for dasycladalean growth and calcification.

Overall, dasycladalean algae have been most diverse when warm, shallow seas were most extensive. Therefore, long-term patterns of dasycladalean diversity are linked to global fluctuations in temperature and sea level. In general, increased temperature promoted dasycladalean growth and calcification. Extensive shallow seas provided habitats suitable for dasycladaleans, encouraging diversification through the positive relationship between diversity and habitat size (Simberloff, 1974).

Dasyclad species diversity has been in decline since the Paleocene, and currently is at its lowest level since the Ju-

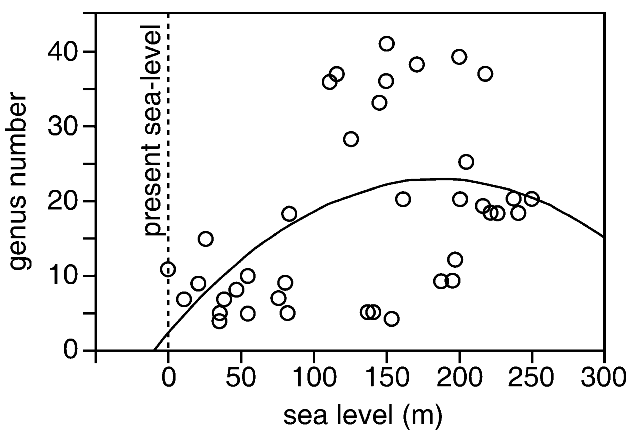

FIGURE 5—Regression plot of dasycladalean species-richness data (combined from Deloffre and Granier, 1992, Granier and Deloffre, 1993, 1994, and Bucur, 1999) against sea level (Haq et al., 1987) for the Carboniferous–Pliocene. Note that highest diversity corresponds with intermediate sea-level values (see Fig. 4).

rassic. The present study suggests that this may be attributable largely to the combined effects of Cenozoic global cooling and sea-level fall on a group adapted to inhabit warm, shallow seas. This does not exclude the influence of other factors on the history of this geologically important group of calcified green algae, but nonetheless appears to provide a striking example of the relationship between habitat size and biodiversity (see Simberloff, 1974).

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