THE NORTH AMERICAN OCCURRENCE OF THE ALGAL COENOBIUM *PLAESIODICTYON*: PALEOGEOGRAPHIC, PALEOECOLOGIC, AND BIOSTRATIGRAPHIC IMPORTANCE IN THE TRIASSIC

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Abstract

The distinctive coenobial chlorophycean alga (Chlorococcales) *Plaesiodictyon* has been recovered from Upper Triassic subsurface samples of Cass County, Texas. Specimens have been assigned to *Plaesiodictyon mosellaneum* ssp. *variable* and *Plaesiodictyon mosellaneum* ssp. *bullatum* ssp. nov. This is the first illustrated record of *Plaesiodictyon* from North America. The presence of the palynomorphs *Brodispora striata*, *Patinasporites densus, P. toralis* and *Pyramidosporites traversei* suggests a Carnian age for this occurrence.

A review of published information indicates that *Plaesiodictyon* has a wide geographic breadth in the Middle/Upper Triassic. Conjectural evidence suggests this alga lived in fresh–brackish water areas and could have been transported to marine environments via a fluvial plume. The wide, and relatively rapid, distribution of *Plaesiodictyon* may be related to aerobiological dispersal as evidenced by recent studies which have recovered viable algae (including chlorococcalean) at high altitudes and great distances from freshwater sites. Aeroalgal dissemination gives forms like *Plaesiodictyon* the capacity for wide biogeographic dispersal and colonization independent of streams and animal vectors.

INTRODUCTION

Coenobial algae are assigned to the Division Chlorophyta, Order Chlorococcales, Family Hydrodictyaceae (Batten, 1996; Batten and Lister, 1988a, 1988b). This Family exhibits an endogene vegetative reproduction and the total coenocytes (cells) in a colony are determined by the number of divisions of the mother cell (Batten, 1996; Brenner and Foster, 1994). Extant representatives are common constituents in freshwater, however, taphonomic processes can transport these algae into marine settings (Brenner and Foster, 1994; Wood and Miller, 1998; Wood and Turnau, 1998, in press). Gross characteristics, such as coenobial habit and unilayered morphology, have allowed assignment of several extinct forms to the Family Hydrodictyaceae. These include *Bijugum*, *Deflandrastrum*, *Khafia*, *Musivum*, *Paleodictyon*, *Quadrisporites* and *Petrovina* (see Batten 1996; Wood and Turnau, in press; Miller and Wood, in press). *Pediastrum*, an extant hydrodictyacean, exhibits a long fossil record (Batten 1996; Wood and Miller, 1997) and is usually the dominant recognizable alga in many Mesozoic and Cenozoic lacustrine source rock facies (Tyson, 1995; Wood and Miller, 1998). Improvements in palynological processing and microscope techniques combined with an increasing awareness of their ecologic and stratigraphic importance have resulted in algal coenobia being fairly regularly recorded in recent palynological studies (Wood and Miller, 1998).

Subsurface material from the Triassic of Texas has yielded a diverse palynological assemblage (Dunay and Fisher, 1974, 1979; Beju et al., 1986; Gawloski, 1983; Moy and Traverse, 1986; Traverse and Moy, 1986). Wood and Benson (1991), in their study of well cuttings from Texas, noted the presence of *Plaesiodictyton*; the first report from North America. The paleogeographic, paleoecologic and biostratigraphic importance this freshwater algae and possible methods for its wide, but spotty, distribution in a relatively short period of geologic time, are discussed in this paper.

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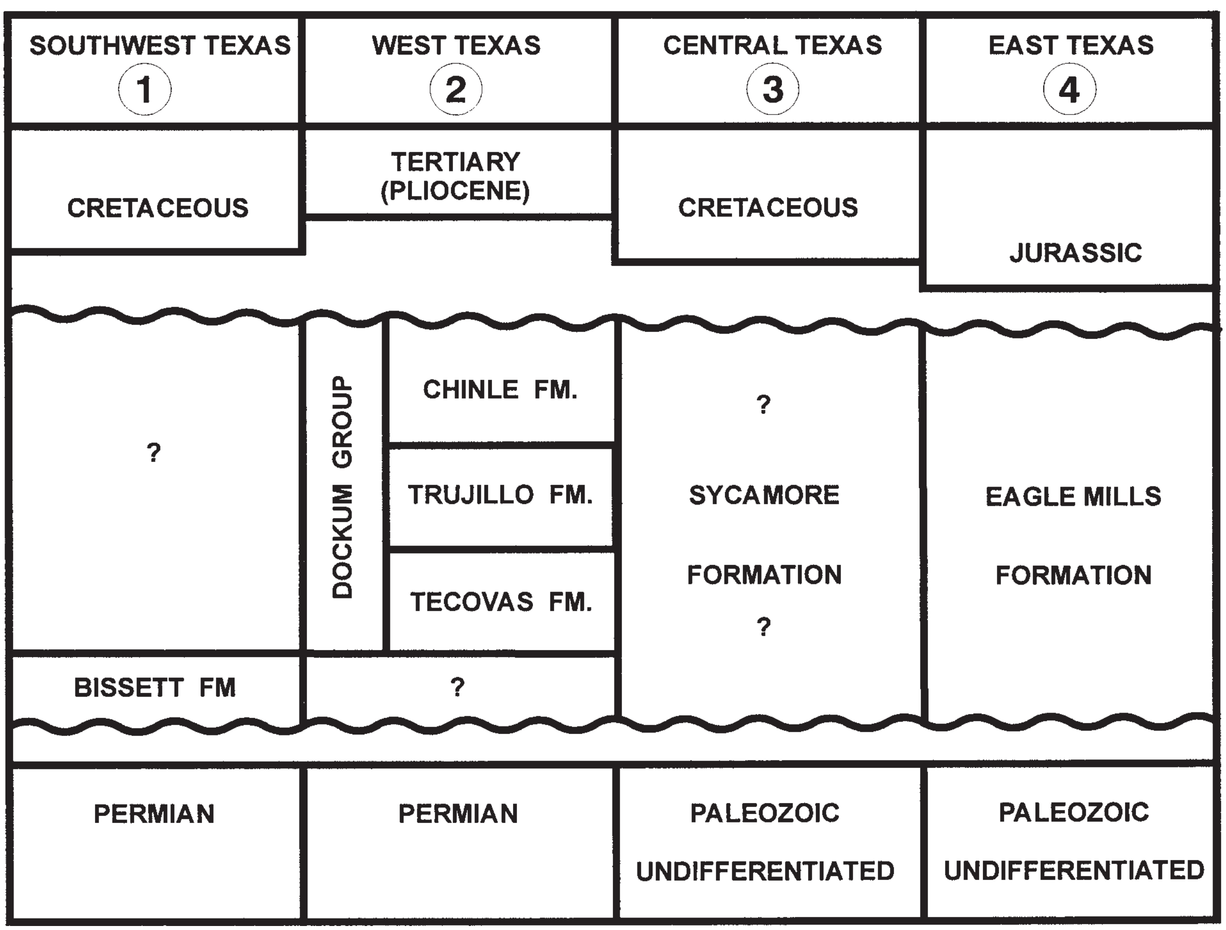
GEOLOGY

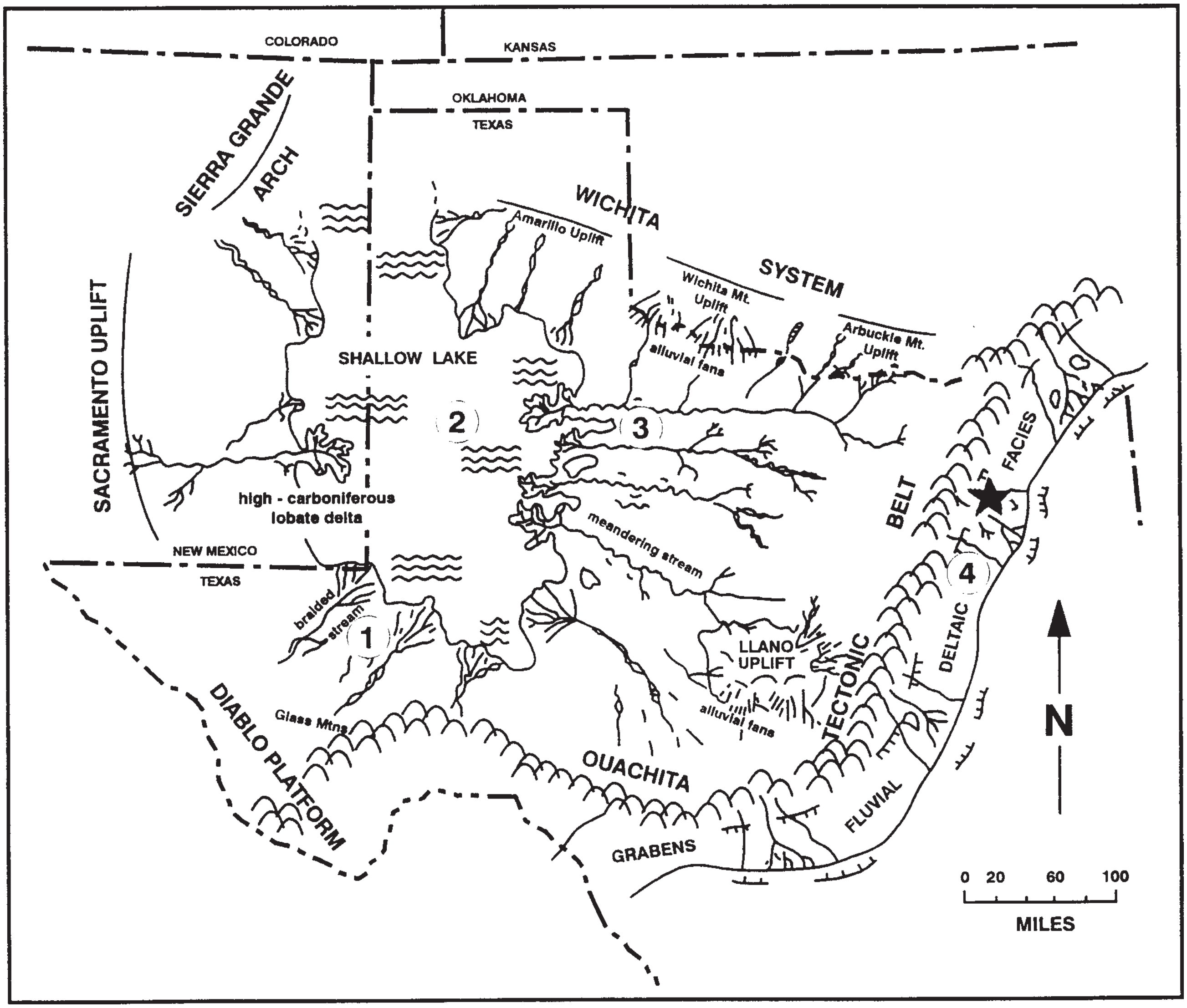
The Triassic of Texas is composed of four rock units (Gawloski, 1983; Text-Figure 1). These are the Eagle Mills Formation (south-central and northeast Texas), Sycamore Formation (central Texas), Dockum Group (west Texas) and Bissett Formation (southwest Texas). The sediments are dominated by mudstones, siltstones, sandstones, and conglomerates associated with lacustrine, alluvial fan, and braided and meandering stream depositional environments. The specimens of *Plaesiodictyon* discussed and illustrated here were recovered from the Eagle Mills Formation.

The Eagle Mills Formation (Shearer, 1938) attains a maximum thickness of approximately 1780 m (7,000 ft) and was deposited in a discontinuous arcuate pattern adjacent to the eastern edge of the Ouachita Tectonic trend (Text-Figures 2 and 3) in south-central and north-east Texas eastward into Arkansas and Mississippi (Gawloski, 1983). The Eagle Mills is a totally subsurface unit that exhibits unconformable upper and lower contacts with weathered Paleozoic rocks and Jurassic sediments, respectively (Text-Figure 1) . The discontinuous pattern of deposition is believed to be related to grabens associated with the initial rifting of the Gulf Coastal Basin (Burgess, 1976; Mason and Miles, 1986; Pindell, 1985; Salvador, 1987, 1991; Scott, 1984; Todd and Mitchum, 1975; Traverse, 1987; Van Siclen, 1983, 1984; Weeks, 1938; Woods and Addington, 1973). The sediment types are similar to the graben fill of the Newark Group and Menden Formation of the east coast of the United States (Hay et al., 1982; Mason and Miles, 1986).

Eagle Mills Formation rock types are primarily sandstone, siltstone, mudstone (often silty) and conglomerate. The dominant colors of these rocks are brick red, purple red or gray/green to dark gray for the siltstones and silty mudstones, and white–yellow sandstones. Dark gray mudstones, rare in the sequence, are believed to be lacustrine deposits (Text-Figure 2), and yield the specimens of *Plaesiodictyon* discussed and figured in this paper. Lithologic and paleogeo-



Text-Figure 1. Generalized stratigraphic column of Triassic rocks in Texas (from Gawloski, 1983). Circled numbers refer to general regions shown in Text-figure 2.



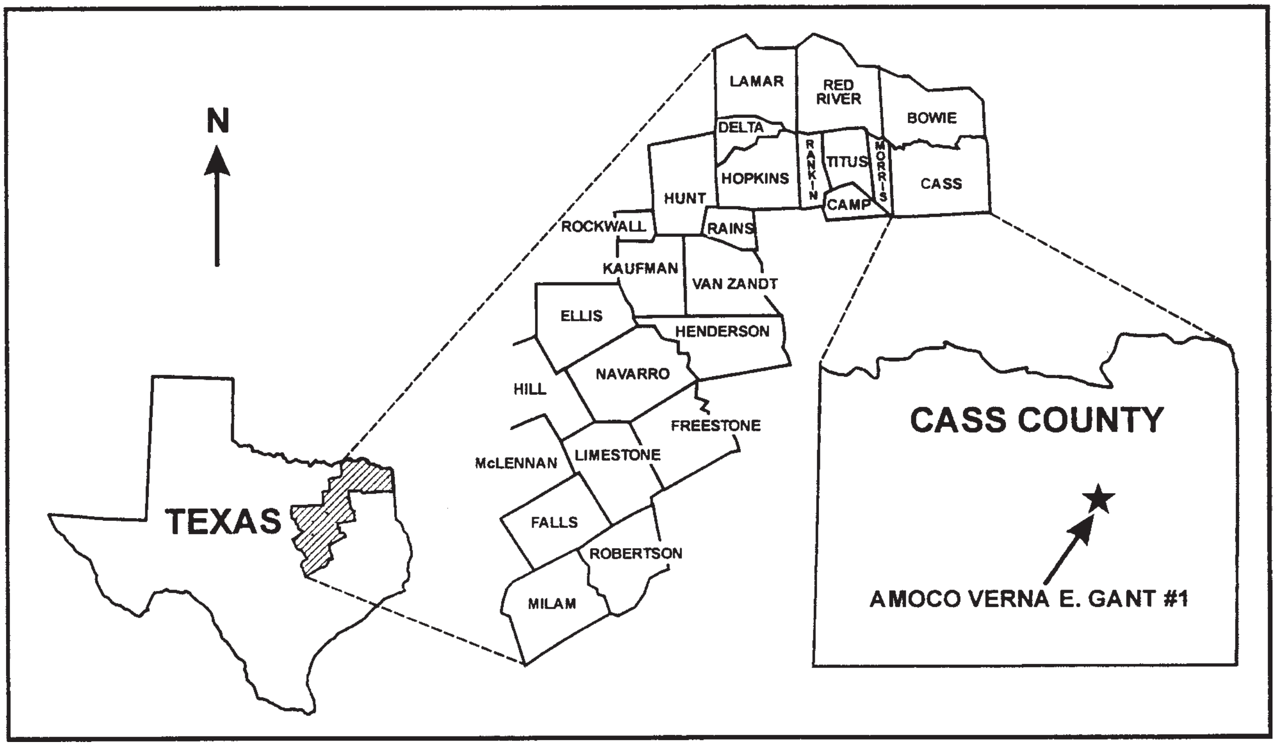
Text-Figure 2. Paleogeographic schematic of the Texas area showing rift and drainage systems in the Upper Triassic (after Gawlowski, 1983 and McGowan et al. 1979). The approximate location of the subject well is indicated with a star. Circled numbers correspond to the stratigraphic columns depicted in Text-Figure 1.

graphic information suggests deposition in a low latitude arid to semi-arid region (Gawloski, 1983; Hay et al., 1982; Salvador, 1991; Simms and Ruffell, 1989).

The Eagle Mills Formation was initially dated as Late Triassic using the presence of the fossil cycadophyte foliage *Macrotaeniopteris magnifolia* (Rogers) Schimper recovered in cores from the Humble #1 G. D. Royston well, Hempstead County, Arkansas (Scott et al., 1961; Ash, 1980). Diabasic igneous rocks in this well have been radiometrically dated as 180–200 Ma (Baldwin and Adams, 1971). Gawloski (1983; p. 29, 31) states that the Eagle Mills Formation yielded Upper Triassic palynomorphs from several wells. This has been confirmed by the palynological studies of Beju et al. (1986), Moy and Traverse (1986), Traverse and Moy (1986) and Wood and Benson (1991). Palynomorphs recovered in the samples yielding *Plaesiodictyon* indicate a probable Carnian age. The assemblage includes *Alisporites thomasii*, *Brodispora striata*, *Klausipollenites* spp., *Patinasporites densus*, *P. toralis* and *Pyramidosporites traversei*.

MATERIALS AND METHODS

Dark gray mudstone cuttings samples from the 4953.3–5007.4 m (19,500–19,660 ft) interval of the Amoco Verna



Text-Figure 3. Map showing counties where Eagle Mills sediments have been encountered and location of the Amoco Verna E. Gant #1well (after Gawloski, 1983).

E. Gant #1 well, Cass Co., Texas (Lat. 33.09236N, Long. 94.25267W) yielded the specimens of *Plaesiodictyon* discussed and illustrated in this paper (Text-Figure 3). Samples were processed using standard palynological techniques, including heavy-liquid separation ($ZnBr_2$; 2.2 s.g.) and sieving of the residue with a 20 μm sieve (Wood et al., 1996). Residues were embedded in Clearcol and cemented to a microscope slide with Elvacite for permanent palynological mounts.

Type specimens are housed at the Orton Geological Museum, The Ohio State University, 155 South Oval Mall, Columbus, Ohio, 43210. Each type specimen is assigned an Orton Geological Museum (OSU) repository number.

SYSTEMATIC PALEONTOLOGY

Division Chlorophyta Pacher 1914
Class Chlorophyceae Kützing 1843
Order Chlorococcales Marchard 1895
Family Hydrodictyaceae (Gray 1821) Dumoitier 1829
Genus *Plaesiodictyon* Wille 1970

Remarks. *Plaesiodictyon* was described and illustrated by Wille (1970) from the Triassic of Luxembourg. He recognized that coenocytes had U- or X-shaped morphologies. Variations in coenocyte size, and length and arrangement of horns/protrusions within the *Plaesiodictyon mosellanum* plexus were interpreted by Wille (1970) and Brenner and Foster (1994) as ecophenotypic expression of environmental factors (e.g., temperature, salinity, pH, etc.). Zippi (1998), in his study of the chlorococcalean *Pediastrum*, considered shape and length of processes extremely important for classification. The authors presently follow the recommendation of Brenner and Foster (1994) and consider the specimens illustrated here ecomorphs reflecting the morphologic plasticity in *Plaesiodictyon*.

Plaesiodictyon mosellanum subsp. *variable*
Brenner and Foster 1994
(Plate 1, figs. 8–12)

Discussion. Specimens from the Eagle Mills Formation are almost identical to those described and illustrated by Brenner and Foster (1994). The only exception is that unlike the illustration of Brenner and Foster (1994; fig. 9F, p. 223) the specimens recovered in this study only display intracoenobial openings down the center of the long axis.

Plaesiodictyon mosellanum ssp. *bullatum* ssp. nov. (Plate 1, figs. 1–7)

Derivation of Name. Latin (feminine), *bulla*; knob, bubble, boss, swelling.

Holotype. Plate 1, fig. 1, slide 31244-A-1,

Leitz Orthoplan coordinates 10.9/99.5; England Finder coordinates J11/1 OSU 50001.

Paratypes. Plate 1, fig. 2, slide 31244-A-2, Leitz Orthoplan coordinates 40.9/110.9; England Finder coordinates U41 OSU 50002.

Plate 1, fig. 3, slide 31244-A-2, Leitz Orthoplan coordinates 13.0/99.0; England Finder coordinates H13 OSU 50003.

Plate 1, fig. 4, slide 31244-A-2, Leitz Orthoplan coordinates 23.0/100.0; England Finder coordinates J23/4 OSU 50004.

Plate 1, fig. 5, slide 31244-A-2, Leitz Orthoplan coordinates 46.5.105.5; England Finder coordinates P47/1 OSU 50005.

Plate 1, fig. 6, slide 31244-A-2, Leitz Orthoplan coordinates 23.7/102.3; England Finder coordinates M24/1 OSU 50006.

Plate 1, fig. 7, slide 31244-A-1, Leitz Orthoplan coordinates 22.2/105.1; England Finder coordinates P22/2 OSU 50007.

Type Stratum. Subsurface cuttings sample of the Eagle Mills Formation, 4953.3–5007.4m (19,500–19,960 ft) interval, Amoco Verna E. Gant #1 well, Cass County, Texas (Lat. 33.09236 N, Long. 94.25267 W).

Diagnosis. Rectangular coenobium with U-shaped coenocytes. Intracoenobial openings are usually present only in the center of the long axis. Outer (distal) edge of peripheral coenocytes usually possess a shallow to deep concavity. At the highest (most distal) points of this invagination each coenocyte possess a rounded or knobbed area. Dehiscence slits, usually oriented diagonally within the coenocyte, are often present.

Measurements. Individual coenocyte length, 10.0(15.0)20.0 μm (Holotype 18.5 μm); individual coenocyte width, 8.0(12.5)17.0 μm (Holotype 15.5 μm); coenobium length, 51.0(64.5)78.0 μm (Holotype 71.5 μm); coenobium width 41.0(46.0)51.0 μm (Holotype 50.0 μm); rounded/knobbed area diameter, 1.0–3.0 μm. Number of specimens measured: 35.

Remarks. Peripheral coenocytes having rounded/knobbed areas distinguish *Plaesiodictyon mosellanum* ssp. *bullatum* ssp. nov. from the other subspecies.

BIOGEOGRAPHY, PALEOECOLOGY, AND BIOSTRATIGRAPHY

Plaesiodictyton mosellanum has been reported from ?Anisian–Norian–?Rhaetian age rocks and depositional environments ranging from fluvial–lacustrine, marginal marine and off-shore marine (Brenner and Foster, 1994). Table 1 depicts pertinent information concerning the occurrence of *Plaesiodictyon*. These papers vary from exhaustive, fully illustrated, studies to citations gleaned only from range charts or check-listed data. Occurrences plotted on a Carnian–Norian plate reconstruction (Text-Figure 4) exhibit a more-or-less discontinuous Tethyan distribution. This may be the result of researchers not recognizing/reporting the presence of this alga, processing techniques that were deleterious or microscopical equipment lacking pertinent instrumentation (e.g., thermally immature specimens are usually colorless and difficult to ascertain using only brightfield microscopy). However, other explanations should also be considered in interpreting how this freshwater alga can be irregularly dispersed over vast reaches of Triassic land and marine regions.

At present flying animals (e.g., water fowl) could be considered a major vector for dissemination of non-marine algae between freshwater sites. However, in the Triassic only insects, and not vertebrates, had evolved 'extended' flight. Another explanation for long distance dispersal between freshwater habitats may be via the atmosphere. A growing body of evidence has shown that viable freshwater and terrestrial algae can be present in the atmosphere. This airborne biota has long been known by aeroallergists tracking respiratory diseases and neopalynologists studying plant migration. Viable terrestrial, freshwater (including chlorococcalean forms) and marine algae, have been cultured from air samples (Benninghoff and Benninghoff, 1982; Broady, 1979; Brown, et al., 1964; Delaney et al., 1967; Drake and Farrow, 1989; Harmata and Olechi, 1991; Maynard, 1968; Melia, 1984; Prospero and Carlson, 1972; Ray-Ocotla and Carrera, 1993; Schlichting, 1961, 1969; Scott and Van Zinderen Bakker, 1985). Chlorococcalean algae, like *Pediastrum*, have been found in pollen traps (Hall, 1998) and their resting spores can survive extremely deleterious environmental conditions (Rands and Davis, 1979; Ström, 1921).

Atomization of viable freshwater algal material in the Triassic could be accomplished in four ways (Ehresmann and Hatch, 1975; Schlichting, 1961, 1969): 1, creation of aerosols by wave action in lakes and bursting of bubbles

TABLE 1. Selected information from published occurrences of *Plaesiodictyon mosellaneum*. The locations are plotted in Text-Figure 3.

LOCALITY	AUTHOR CITATION	SPECIES	STRATIGRAPHIC, AGE, AND LOCALITY INFORMATION
1	Mørk et al. (1990)	*P. mosellanum*	Skuld Formation, Kapp Toscava Group (Late Ladinian), Bjørnøya, Svalbard Archipelago outcrop, Norway.
2	Bakken (1990)	*P. mosellanum*	Fruholmen Formation, Saga Petroleum 7124/3-1 well (lower Late Norian), Barents Sea, Norway.
3	Hochuli et al. (1989)	*P. mosellanum*	Spitsbergen, Bjørnøya, and Barents Sea boreholes, (?Anisian–Norian), Norway.
4	Vigran et al. (1998)	*P. mosellanum*	Steinkobbe (late Anisian) and Snadd (Ladinian) formations of IKU coreholes 7323/07-U-02, -05, -09, -10, Svalis Dome, central Barents Sea, Norway.
5	Eide (1989)	*P. mosellanum*	Snorre and Lunde formations (Norian–?Early Rhaetian), wells in offshore blocks 33/9, 34/4, 34/7 and 34/10, Norway.
6	Old et al. (1991)	*P. mosellanum*	Arden Sandstone Member, Mercia Mudstone Group (late Carnian), United Kingdom.
7	Ruffell and Warrington (1988)	*P. mosellanum*	Mercia Mudstone Group (?Carnian–?late Carnian), Norton Manor Camp grounds, near Tauton, Somerset, United Kingdom.
8	Warrington and Williams (1984)	*P. mosellanum*	North Curry Sandstone Member, Mercia Mudstone Group (?Carnian), Gainsload Drive Section, Taunton, Somerset, United Kingdom.
9	Adloff et al. (1984)	*P. mosellanum*	Briod 2 well, Faramans 1 well, Bizonnes 1 well, Paladru 1 well, Brezins 1 well, Saint-Lattier 1 & 2 wells (upper Ladinian), Bas Dauphone, France.
10	Wille (1970)	*P. mosellanum* ssp. *divergens* *P. mosellanum* ssp. *perforatum* *P. mosellanum* ssp. *sinuosum* *P. mosellanum* ssp. *mosellanum*	Lower part of the Lower Keuper, section exposed along a street in Syrberg, Luxembourg.
11	Heunisch (1986)	*P. mosellanum*	Upper Muschelkalk–Lower Keuper (Ladinian) outcrop section, Lower and Middle Fraconia, and Lower Keuper (Ladinian) outcrop sections, northern Baden-Württemberg, Germany.
12	Hauschke and Heunisch, 1989	*P. mosellanum*	Lower Gipskeuper (Carnian), Vahlhausen outcrop section, Germany.
13	Hauschke and Heunisch, 1990	*P. mosellanum* ssp. *sinuosum*	Upper Keuper–Lower Gipskeuper (Ladinian–Carnian), USB-3 well, eastern North-Rhine Westphalia, Germany.

at the water–air interface; 2, formation of scums, windrows or weed-lines that could become airborne via wind gusts; 3, generation of aerosols by turbulent streams and rivers; and 4, catastrophic causes (tornadoes, water spouts, volcanic eruptions; see also Sohn, 1996). Unlike anemophilous plants which have evolved aerial diffusion of reproductive entities, this mode of dissemination has not really been considered to explain the fossil distribution of freshwater algae. Evidence from neopalynology/aeroallergy studies indicate atmospheric dispersal of freshwater algae in the Triassic is a credible propagation mechanism.

TABLE 1 (continued). Selected information from published occurrences of *Plaesiodictyon mosellaneum*. The locations are plotted in Text-Figure 3.

LOCALITY	AUTHOR CITATION	SPECIES	STRATIGRAPHIC, AGE, AND LOCALITY INFORMATION
14	Heunisch (1990)	*P. mosellanum*	Upper Muschelkalk–Lower Keuper (upper Ladinian), “Natzungen 1979” corehole, Germany.
15	van Bergen and Kerp (1990); Brugman et al. (1994)	*P. mosellanum*	Lower Keuper (upper Ladinian; *Heliosaccus dimorphous – Corditina minor* through *Heliosaccus dimorphous Illinites chitinoides* ecophase), Obemees well 1983, Franconia, Bavaria, Germany.
16	Adloff et al. (1986)	*P. mosellanum*	Ras-Hamia Unit (“Zone A:” Myophories subunit), Well A-23 & D3-23 (Ladinian), Tripoli, Libya.
17	Geleta and Wille (1998)	*Plaesiodictyon mosellanum*	Fincha-a River valley section (late Ladinian; *Staurosaccites quadrifidus* zone of Helby et al. (1987)), Horo Guduru (Lat. 9° 44' 48" N, Long. 37° 22' 48" E) western central Ethiopia.
18	Brenner (1992); Brenner and Foster (1994)	*P. mosellanum* ssp. *sinuosum*	Wombat Plateau, Australia
		P. mosellanum ssp. *mosellanum*	DSDP Site 759, Wombat Plateau (Norian), northwestern Australia.
		P. mosellanum cf. ssp. *divergens*	Sahul Platform, BOC Sahul Shoals No. 1, northwestern Australia (late Anisian/Ladinian) DSDP Site 760, Wombat Plateau (Norian), northwestern Australia.
		P. mosellanum ssp. *perforatum*	DSDP Sites 759 and 760, Wombat Plateau (Norian), northwestern Australia.
		P. mosellanum ssp. *symmetricum*	Sahul Platform, BOC Sahul Shoals No. 1, northwestern Australia (late Anisian/Ladinian) DSDP Site 760, Wombat Plateau (Norian), northwestern Australia.
		P. mosellanum ssp. *variable*	DSDP Sites 759 and 760, Wombat Plateau (Norian), northwestern Australia.
		P. decussatus ssp. *decussatus*	Sahul Platform, BOC Sahul Shoals No. 1, northwestern Australia (late Anisian/Ladinian) DSDP Site 760, Wombat Plateau (Norian), northwestern Australia.
		P. decussatus spp. *tetracornuta*	Sahul Platform, BOC Sahul Shoals No. 1, northwestern Australia (late Anisian/Ladinian) DSDP Site 760, Wombat Plateau (Norian), northwestern Australia.

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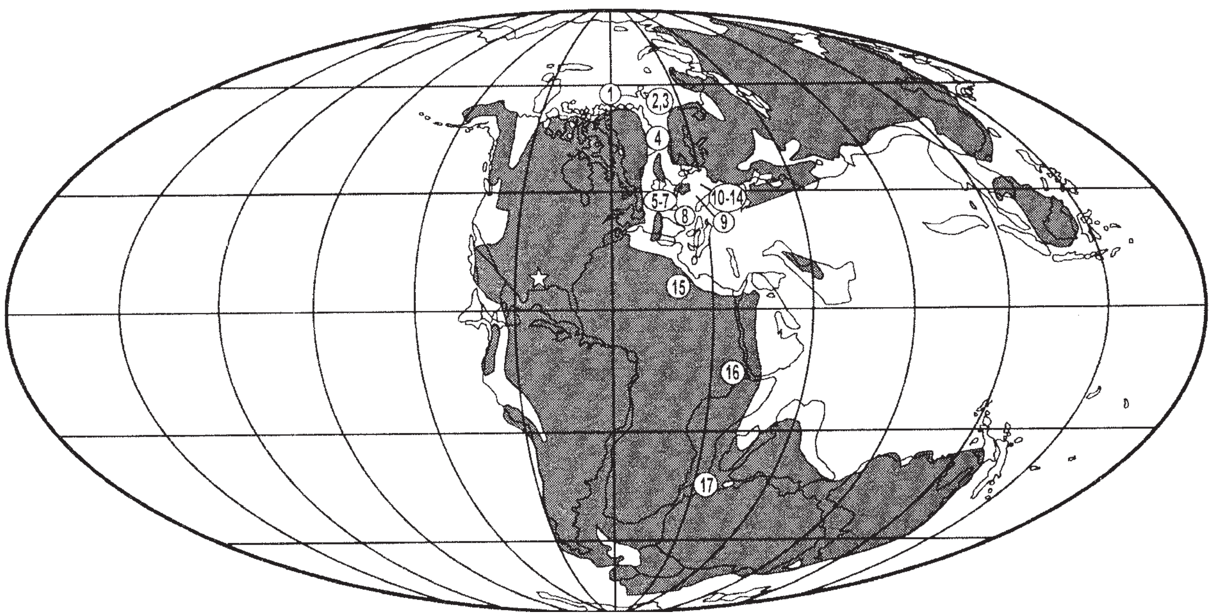

Text-Figure 4. *Plaesiodictyon* occurrences plotted on a Carnian/Norian plate reconstruction (after Smith et al. 1994). Locality numbers are keyed to Table 1. The star indicates the geographic position of the specimens discussed in this paper.

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PLATE 1

All figures x625. In all cases maceration and slide numbers are followed by microscope (Leitz Orthoplan No. 986086) vernier and England Finder coordinates (the latter for type specimens).

1 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Holotype); note dehiscence slits; 31244-A-1; 10.9/99.5, J11/1.

2 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Paratype); 31244-A-2, 40.9/110.9, U41.

3 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Paratype) with dehisence slits; 31244-A-2, 13.0/99.0, H13.

4 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Paratype); 31244-A-2, 23.0/100.0, J23/4.

5 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Paratype); 31244-A-2, 46.5/105.5, P47/1.

6 *Plaesiodictyon mosellanum* spp. *bullatum* n. ssp.(Paratype); 31244-A-2, 23.7/102.3, M24/1.

7 *Plaesiodictyon mosellanum* spp. *bullatum* n. spp. (Paratype); 31244-A-1, 22.2/105.1, P22/2.

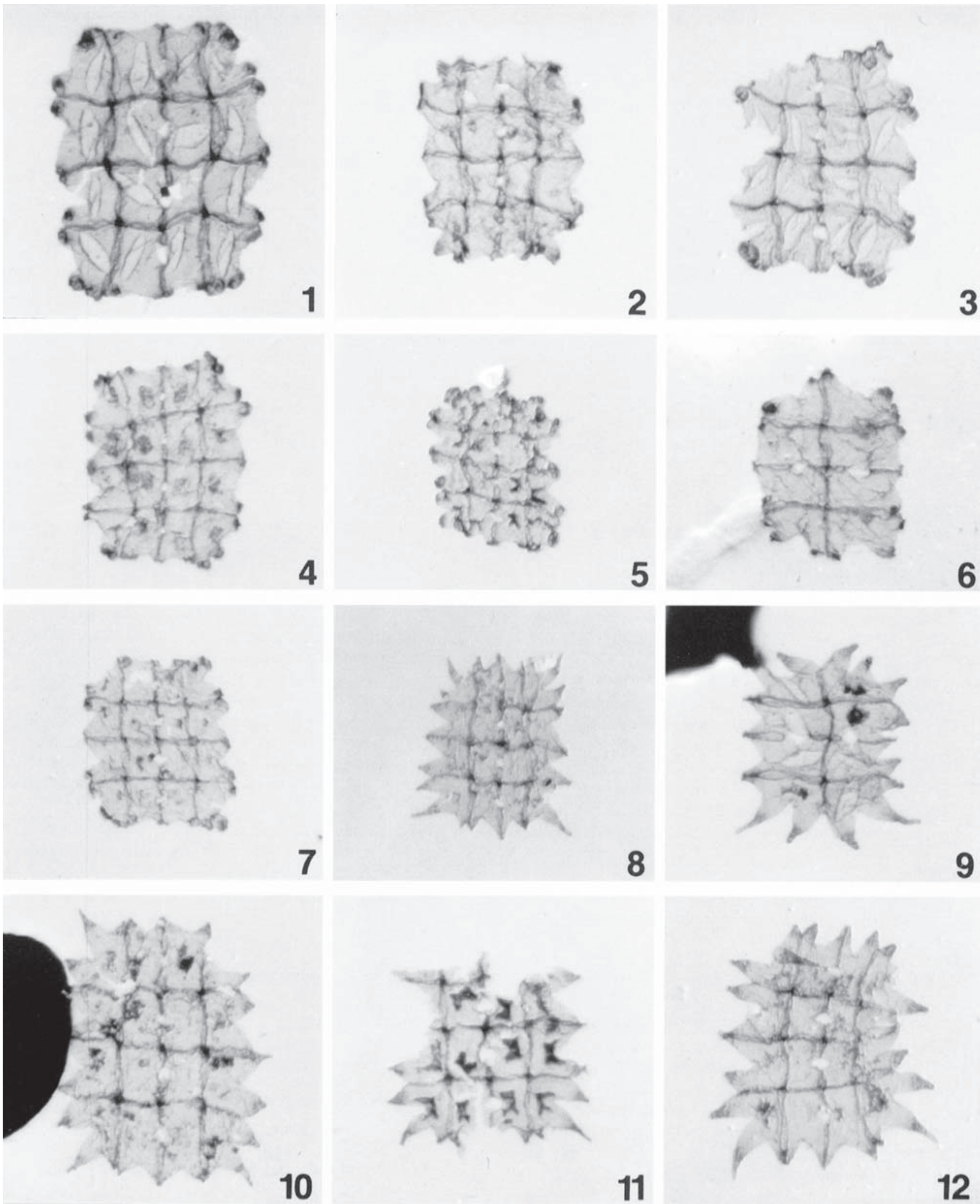
8 *Plaesiodictyon mosellanum* spp. *variable*; 31244-A-2, 44.7/96.5.

9 *Plaesiodictyon mosellanum* spp. *variable*; note dehisence slits; 31244-A-2, 16.8/102.8.

10 *Plaesiodictyon mosellanum* spp. *variable*; 31244-A-1, 27.7/99.3.

11 *Plaesiodictyon mosellanum* spp. *variable*; 31244-A-2, 36.3/104.5.

12 *Plaesiodictyon mosellanum* spp. *variable*; 31244-A-2, 18.6/109.7.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