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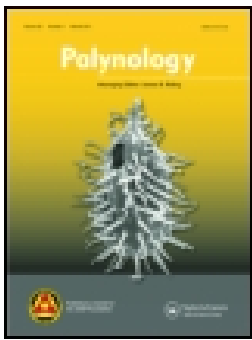
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Early Cretaceous (Albian) spores and pollen from the Glen Rose Formation of Texas and their significance for correlation of the Potomac Group

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ABSTRACT

Because the Gulf Coast Lower Cretaceous is dated by ammonites, it has great potential as a reference section for correlating continental sequences such as the Potomac Group and dating events in the rise of angiosperms. Middle Albian terrestrial palynofloras from Oklahoma have been described in detail, but the early Albian interval, represented in the Glen Rose Formation of Texas, is less well known. Samples from two localities on the Paluxy River, which correlate with horizons containing late early Albian ammonites, are dominated by *Classopollis* and *Exesipollenites*, but angiosperm pollen is the next most common terrestrial element, and there are several index spore species for Zone II in the Potomac Group. Among the angiosperms, reticulate monosulcates are most common and diverse, but there are also several tricolpate species. Stratigraphically important angiosperms include the *Clavatipollenites rotundus* group and reticulate tricolpates, which appear in the upper part of Potomac Zone I and the dated earliest Albian of England and Portugal. However, there are also tricolpates with striate-reticulate sculpture, a pollen type that is not known from upper Zone I but appears in the late early Albian of Portugal. This assemblage contrasts with floras from Potomac Zone II and the middle Albian (lower Fredericksburg Group) of Oklahoma, where tricolpates overtook monosulcate angiosperms in species diversity. These results confirm arguments based on the Portuguese section that there is a significant hiatus between Potomac Zones I and II, and that this gap is at least partly late early Albian. The dominance of *Classopollis* and *Exesipollenites* and the occurrence of isolated Northern Gondwanan elements (*Sergipea*, *Tucanopollis*) suggest that Texas lay in a transition zone between Southern Laurasia and the hotter and drier Northern Gondwana province, but regional studies are needed to disentangle geographic and climatic factors from effects of the lagoonal local environment.

KEYWORDS

Cretaceous; Albian; Texas; palynology; angiosperms; stratigraphy; Potomac

1. Introduction

A major problem in documenting the rise of angiosperms and other changes in land vegetation during the Early Cretaceous is the fact that the sediments that are best known paleobotanically are largely or entirely continental and therefore poorly dated by marine fossils. A classic example is the Potomac Group of the US Atlantic Coastal Plain (Virginia, Maryland, Delaware: Fontaine 1889; Berry 1911; Brenner 1963; Doyle 1969, 1992; Doyle & Hickey 1976; Doyle & Robbins 1977; Upchurch 1984; Crane et al. 1986, 1993, 1994; Friis et al. 1986, 2011; Upchurch et al. 1994; Jud & Hickey 2013; Doyle & Upchurch 2014; Jud 2015). Early studies of leaves and vertebrate remains allowed some crude correlations, but present dating of the Potomac sequence is based mainly on palynological correlations with faunally dated marine sequences elsewhere, for example in England (Kemp 1968, 1970; Laing 1975; Hughes et al. 1979; Hughes & McDougall 1987, 1990; Hughes 1994). Both regions belonged to the same Southern Laurasian province, which is an important consideration in view of significant geographic differences among floras and diachronous appearances of angiosperm taxa at this time (Brenner 1976, 1996; Doyle et al. 1977,

1982; Hickey & Doyle 1977; Crane & Lidgard 1989; Doyle 1992; Heimhofer et al. 2005; Heimhofer & Hochuli 2010; Coiffard & Gomez 2012; Coiffard et al. 2012; Horikx et al. 2016).

Sediments with potential for more complete characterization and dating of the Early Cretaceous palynological succession in Southern Laurasia occur in the US Gulf Coastal Plain, best exposed in Texas and Oklahoma, where alternating continental and marine sediments were deposited on the continental shelf. The Lower Cretaceous or Comanchean Series here is represented by the Trinity, Fredericksburg and Washita Groups (Figure 1). Terrestrial palynofloras have been described in detail from two units in this sequence in Oklahoma: the middle Albian 'Walnut' facies of the Fredericksburg Group (Hedlund & Norris 1968; Srivastava 1975, 1981), and the upper Albian Denton Shale Member of the Bokchito Formation of the Washita Group (Wingate 1980). However, the Aptian and lower Albian Trinity Group has been less studied. The goal of the present work is to shed light on this interval by describing the terrestrial palynoflora from the Glen Rose Formation of the Trinity Group, and to compare the results with palynological sequences described from the Potomac Group and near-shore marine sediments in

Washita Group	Georgetown Limestone (Kiamichi Formation)	Cenomanian
		Upper Albian
Fredericksburg Group	Edwards Limestone / Goodland Limestone	Middle Albian
	Walnut Formation	
Trinity Group	Paluxy Formation	Lower or middle Albian
	Ammonite zones: <i>comalensis</i>	Thorp Spring Member
	<i>mammillatum</i> ----- GLEN ROSE FORMATION ----- <i>Corbula</i> bed -----	Lower Albian
	<i>cragini</i>	
	<i>spathi</i>	
	Hensel Sandstone / Bluff Dale Sandstone	Aptian

Figure 1. Generalized stratigraphic units for the upper Aptian through lower Cenomanian in central Texas.

coastal sections in Portugal (Heimhofer et al. 2005, 2007, 2012; Horikx et al. 2016). Studies of the Portuguese sections have challenged previous correlations of both the Potomac sequence and mesofossil floras described from continental beds in Portugal (Friis et al. 1994, 2006, 2010, 2011), notably in the part of the Albian represented in the Glen Rose Formation (Hochuli et al. 2006). Palynological investigations of the Glen Rose could therefore provide independent tests of competing stratigraphic interpretations.

1.1. Geological background

The Glen Rose Formation was first described by Shumard (1860) as the *Caprotina* Limestone, and was given its present name by Hill (1891). Together, the Glen Rose and the underlying Hensel Sandstone form the last of two or three major transgressive–regressive cycles in the Trinity Group (Hayward & Brown 1967; Hendricks 1967; Stricklin et al. 1971; Mancini & Scott 2006). Older Trinity units occur mainly in the subsurface, reflecting the broadly transgressive spread of Cretaceous sedimentation onto the Paleozoic basement. Trinity deposition was affected by a positive area in central Texas called the Llano Uplift, resulting in a rough division into north central and south central Texas outcrop areas (Forgotson 1963; Stricklin et al. 1971).

The type area of the Glen Rose Formation is in north central Texas, along the Paluxy River above the town of Glen Rose in Somervell County, where it includes lagoonal limestones that are famous for containing abundant dinosaur tracks, as well as xeromorphic and presumably halophytic conifers of the extinct family Cheirolepidiaceae (Fontaine 1893; Watson 1977). Sections in this area were described in detail by Rodgers (1967), analyzed sedimentologically by Nagle (1968), Perkins (1979) and Bergan (1987, 1991), and integrated with subsurface stratigraphy by Pittman (1989). Here the Glen Rose Formation is divided into a lower and an upper member separated by a massive limestone unit called the Thorp Spring Member (Hill 1891). It reaches a total thickness of ca. 240 ft (73 m) near Glen Rose

(Hayward & Brown 1967). It becomes sandier and more continental to the west (updip), with the lower member grading laterally into the Hensel Sandstone (Rodgers 1967) and the upper member grading into the overlying Paluxy Formation. The Paluxy Formation has been assigned to the Trinity Group by some authors (e.g. Hendricks 1967) and to the Fredericksburg Group by others (e.g. Young 1967a; Scott et al. 2003).

The best-dated sections of the Glen Rose Formation, based on a monographic study of ammonites by Young (1974), are in Comal County in south central Texas, where the formation is thicker (ca. 700 ft, 213 m) and more marine (Stricklin et al. 1971; Ward & Ward 2007). It is underlain by the Hensel Sandstone but directly overlain by the Walnut Formation of the Fredericksburg Group, with no intervening Paluxy Formation. Here the Glen Rose Formation is divided into two members, separated by the so-called *Corbula* bed, a 0.3–1 m unit of one to three limestone beds packed with small, articulated clams formerly called *Corbula martinae* (*Eoursivivas harveyi*; Ward & Ward 2007), which can be traced over ca. 5000 sq mi (13,000 km²) of outcrop (Whitney 1952; Stricklin et al. 1971; Scott et al. 2007). This bed overlies a highly fossiliferous 3–6 m interval called the *Salenia texana* Zone. Young (1974) recognized four ammonite zones in the Glen Rose: the *Kasanskyella spathi* Zone (late Aptian), the *Hypacanthoplites cragini* Zone (earliest Albian), the *Douvilleiceras mammillatum* Zone and the *Hypacanthoplites comalensis* Zone. The *Salenia texana* Zone and the *Corbula* bed fall in the *mammillatum* Zone. Except in its lower part (which contains *H. comalensis*), the upper member has yielded no stratigraphically useful ammonites, only endemic egonocerids. Young (1974) correlated the *mammillatum* and *comalensis* Zones in Texas with the *mammillatum* Zone in England, which is the second of two zones in the early Albian, after the *Leymeriella tardefurcata* Zone (Casey 1961). He presumed that the part of the Glen Rose Formation above the *comalensis* Zone was of early and/or middle Albian age, but in Young (1986) he favored an early middle Albian age. Another age indicator is the latest Aptian through early Albian benthic foraminifer *Orbitolina texana*, which ranges

from the basal Glen Rose into the upper member (Stricklin et al. 1971; Mancini & Scott 2006; Scott et al. 2007).

Mancini & Scott (2006) and Scott et al. (2007) integrated the south central Texas section into a sequence-stratigraphic framework, building on studies that correlated eustatic cycles in the Middle East and the Gulf Coast (Scott et al. 2000). They recognized the Hensel Sandstone and Glen Rose Formation as a major transgressive–regressive sequence (T-R K2), bounded by lower (Ap SB PR2) and upper (Al SB FR1) unconformities, which contains five medium-scale cycles separated by transgressional disconformities. The disconformity between the second and third cycles, below the *Salenia texana* Zone, is a regionally recognizable sequence boundary (Al SB GR2). This further supports the view that the *Corbula* bed represents a time horizon, although Ward & Ward (2007) suggested that it may be diachronous at a finer temporal scale. The upper unconformity occurs between the Glen Rose Formation and the Walnut Formation in south central Texas but within the Paluxy Formation to the north (Scott et al. 2003, 2007; Mancini & Scott 2006). Using the absolute time scale of Gradstein et al. (2004), Scott et al. (2007) estimated that the age of the Glen Rose Formation ranges from 113.3 to 108.0 Ma.

The Paluxy River section has not been compared in detail with the current scheme for south central Texas, but some inferences seem clear. In the lower member as defined in north central Texas (i.e. below the Thorp Spring Member), Nagle (1968) recognized seven subtidal to supratidal cycles, of which the lowest (his '*Corbula* cycle') contains what he identified as the *Corbula* bed. He noted that there are at least three other beds with *Corbula* in the lower Glen Rose Formation, but this is the only bed with articulated detrital *Corbula* in a shell hash. In comparing the Paluxy River section with extensive subsurface data, Pittman (1989) reaffirmed the continuity of the *Corbula* bed between this area and south central Texas. He noted that Bergan's (1987, p. 83) description of beds 2 and 3 at Dinosaur Valley State Park on the Paluxy River would apply to the *Salenia texana* Zone and the *Corbula* bed in south central Texas. In addition, he correlated the Thorp Spring Member with a massive limestone that lies between two main evaporite intervals in

the upper Glen Rose Formation in the south central Texas subsurface. Thus, the upper part of the lower member as defined in north central Texas corresponds to the lower part of the upper member as defined in south central Texas.

1.2. Previous palynological studies

The main previous palynological studies of the Glen Rose Formation are an unpublished thesis and a published article by Kessler (1968a, 1968b) and an unpublished thesis by Beach (1981a), both focused on north central Texas. Kessler (1968a) provided figures and identifications of pollen, but most taxa are poorly illustrated and many appear to be misinterpreted. Kessler (1968b) focused on an analysis of the relation of palynomorph groups to depositional environments, rather than systematic or stratigraphic problems. Beach (1981a) emphasized younger Lower Cretaceous units; his only productive samples of the Glen Rose Formation were from the upper member, and although he presented a talk on the angiosperm pollen from this unit at the 1979 American Association of Stratigraphic Palynologists (AASP) meeting, only an abstract was published (Beach 1981b). Bond (1972) reported briefly on the palynology of the DeQueen Formation of Arkansas, which is thought to be equivalent to the Glen Rose. Phillips & Felix (1971a, 1971b) described spores and pollen from the Paluxy Formation of Louisiana, which could be in part equivalent to the Glen Rose (Mancini et al. 2008). Counts of terrestrial palynomorph groups in one of the samples treated in the present study (sample 79-26) were included in a paper on frenalopsid conifers in the Potomac Group, by Upchurch & Doyle (1981).

2. Material and methods

The 11 samples included in this study were collected during the 1979 post-meeting field trip of the AASP at three localities on the Paluxy River (Figure 2): Paluxy Townsite, Cedar Brake Camp and Barker Branch (Rodgers 1967; Nagle 1968; Perkins 1979; Bergan 1987, 1991). At Paluxy Townsite, the Thorp Spring Member occurs about a quarter of the way up in the section. At this

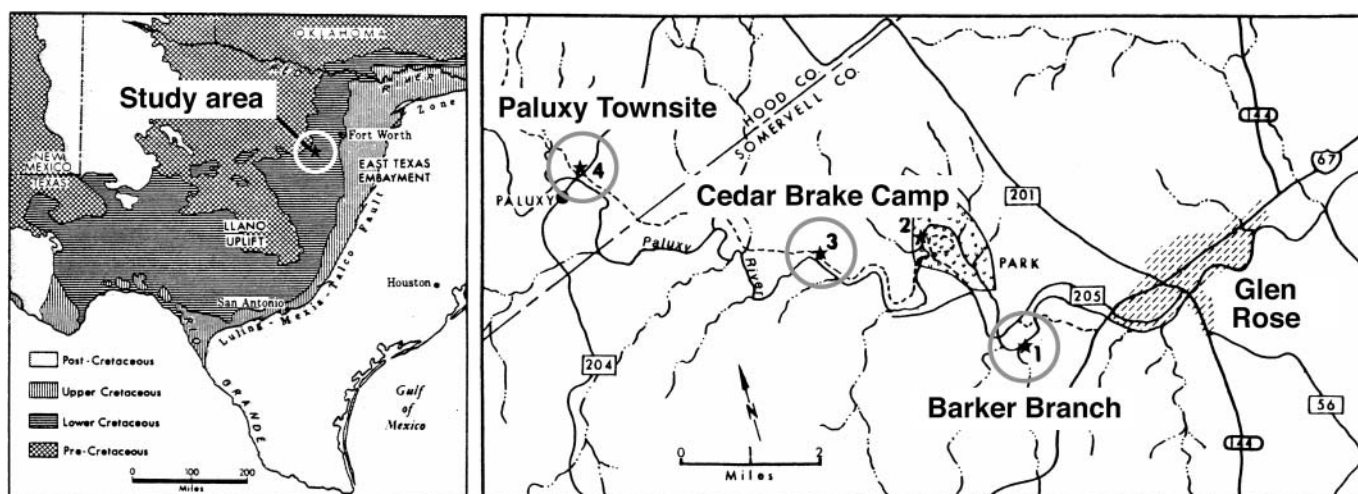


Figure 2. Left, location of the study area in Texas; right, map of the Paluxy River Valley showing sample localities (modified after Perkins 1979).

locality the sediments below the Thorp Spring are sandier, illustrating the trend to more continental conditions to the west. Unfortunately, the single sample collected (79-30), and the only one from the upper member (above the Thorp Spring), did not yield usable pollen.

The Thorp Spring Member is exposed at the top of the sections at Cedar Brake Camp and Barker Branch. Nagle (1968) described the lower member at Cedar Brake Camp in greatest detail; as noted above, he interpreted this interval as consisting of seven subtidal to supratidal regressional cycles (with no clear transgressional phase at the base), with more sandy terrigenous input in the upper cycles. The *Corbula* bed (his bed 2), in the first cycle, which includes a subtidal mudstone with a mollusk-serpulid fauna below (bed 1) and a marsh deposit above (beds 3-4), occurs ca. 19 ft (6 m) below the Thorp Spring Member. He identified the same cycle, with units becoming more marine to the east, at other localities on the Paluxy River, including Barker Branch. At Barker Branch, Nagle (1968, fig. 3) illustrated only the *Corbula* cycle part of the section, but this can be fitted into the 56 ft (17 m) composite section of Perkins (1979, fig. 8). Nagle's *Corbula* bed corresponds to bed 4 of Perkins, which he described as 1 ft (0.3 m) of lime mudstone with abundant articulated detrital shells of *Corbula*, ca. 22 ft (6.7 m) below the Thorp Spring Member. Bergan (1991) also concentrated on Barker Branch, but her section at this locality began above the *Corbula* bed. Contrary to Nagle (1968), she (Bergan 1987, p. 71-72) interpreted the saltmarsh marls as intertidal rather than supratidal.

All our productive samples (Figure 3) are from between the *Corbula* bed and the Thorp Spring Member. Most are from marly saltmarsh shales, namely beds 7-8 (79-21, 79-22, 79-23, 79-24) and 11 (79-20) of Perkins (1979) at Barker Branch, and beds 4 (79-25) and 8 (79-26, 79-27, 79-28) of Nagle (1968) at Cedar Brake Camp. Nagle's bed 4 represents the saltmarsh phase in the upper part of his *Corbula* cycle. Sample 79-29 from Cedar Brake Camp is from Nagle's bed 14, which has more sandy clastic input. All samples are therefore from the upper part of the lower member of the Glen Rose Formation as defined in north central Texas. This interval corresponds to the base of the upper member as recognized in south central Texas, which is defined as beginning above the *Corbula* bed. This implies that the samples are from the *mammillatum* Zone or the *comalensis* Zone, in either case from the latter part of the early Albian, postdating the earliest Albian *craigini* Zone in Texas and the *tardefurcata* Zone in Europe.

Most observations are based on slides prepared soon after the 1979 AASP meeting (79-21, 79-25, 79-26, 79-29). These were supplemented by preparations of previously unprepared samples (79-20, 79-22, 79-23, 79-24, 79-27, 79-28, 79-30), which were generally less fossiliferous. The older preparations involved maceration with HCl and HF, heavy liquid separation with zinc chloride at s.g. 2.0, usually brief bleaching followed by acetolysis, and mounting on slides in glycerine jelly. The new preparations included sieving with a 5- μ m sieve. Slides were scanned under the 40 \times objective of a Zeiss RA microscope and photographed with an AmScope MT Series digital microscope camera, generally using a 100 \times oil immersion objective. Specimens are located with an England Finder slide.

3. Results

Our samples contain numerous dinoflagellates, but because the Glen Rose Formation is already well dated with ammonites and our emphasis is on correlation with the Potomac Group, which is almost entirely continental, we have concentrated on the terrestrial flora. This is overwhelmingly dominated by *Classopollis* (often > 75%), representing the xeromorphic conifer family Cheirolepidiaceae, which is also dominant in the megafossil flora of the Glen Rose in its type area (Fontaine 1893; Watson 1977) and elsewhere (Daghlian & Person 1977); most common is *Pseudofrenelopsis varians*, which superficially resembles the saltmarsh angiosperm *Salicornia* (Amaranthaceae). Cheirolepidiaceae are associated with hot and dry climates at a global scale and often with marine-influenced facies at a local scale (Vakhrameev 1970, 1981; Upchurch & Doyle 1981; Heimhofer et al. 2008, 2012). Next most common is *Exesipollenites*, a monoporate pollen type that is often associated with *Classopollis*. *Exesipollenites* is strikingly more abundant in sample 79-25 than in other samples. It has been compared with both cupressaceous conifers and Bennettitales (van Konijnenburg-van Cittert 1971; Harris 1974; Peñalver et al. 2015), but the most similar *in situ* pollen is that of the Jurassic bennettitalean flower *Williamsoniella lignieri* (Harris 1974), consistent with the presence of bennettitalean foliage in the Glen Rose and Potomac beds that are rich in *Exesipollenites* (Fontaine 1893; Upchurch & Doyle 1981).

Despite the dominance of *Classopollis* and *Exesipollenites*, persistent searching reveals a large number of other taxa. These include many typical Southern Laurasian Early Cretaceous spore and gymnosperm pollen groups, although not as many as in the Potomac Group, whether due to less favorable climate or less suitable local habitats. Angiosperm pollen, which includes both monosulcate and tricolpate types, makes up about 2% of the terrestrial palynoflora. No angiosperm leaves are known from the Glen Rose Formation, but three species were reported by Ball (1937) from the Paluxy Formation in Erath County, immediately to the west, which may be either laterally equivalent to the upper Glen Rose or younger.

The following section lists all taxa identified, in alphabetical order within major morphological categories, with brief notes on sample occurrence, diagnostic characters, taxonomic problems, and any restriction to palynostratigraphic units of Brenner (1963) and Doyle & Robbins (1977) in the Potomac Group. Several taxa show similarities to particular Potomac species but also substantial differences from them, suggesting that they may be related but are not identical; these are indicated with the qualifier 'aff.'

3.1. Spores

3.1.1. *Triletes*

Achradosporis vitellinus Srivastava (Plate 1, figure 1; 79-21, 79-26). Trilete spore with detached thick outer layer and foveolate sculpture. Not reported from the Potomac Group, but described by Srivastava (1975) from the Goodland Formation of the Fredericksburg Group of Texas.

Alsophilidites cf. *pannucis* Brenner (Plate 1, figure 2; 79-21, 79-25).

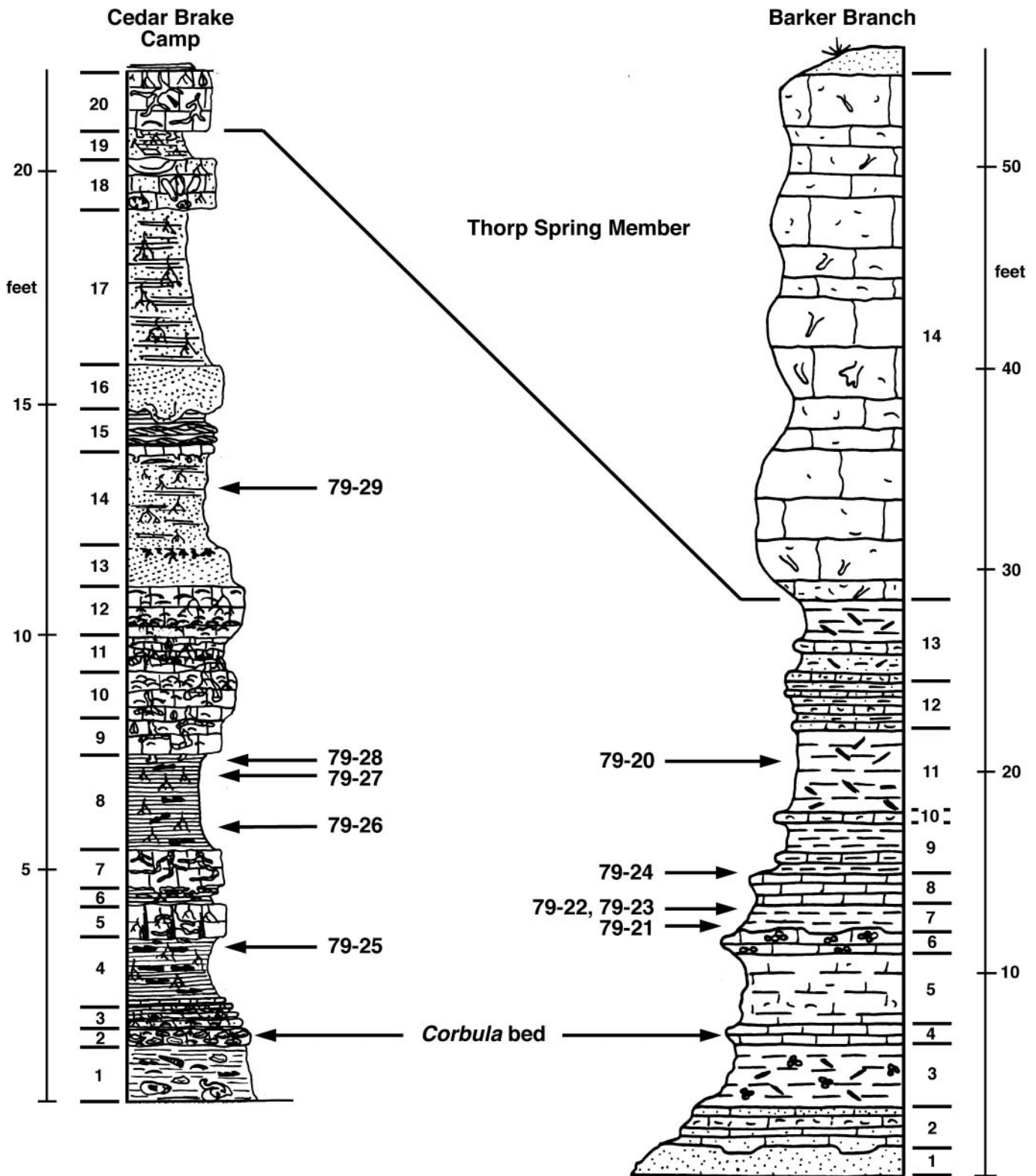


Figure 3. Graphic sections of the Glen Rose Formation, including the *Corbula* bed and the basal part of the Thorp Spring Member, exposed at Cedar Brake Camp (modified after Nagle 1968) and Barker Branch (modified after Perkins 1979), with numbers indicating beds of Nagle (1968) and Perkins (1979) and sample horizons in this study. 1 foot = 30.48 cm.

Apiculatisporis sp. (Plate 1, figure 3; 79-21). Similar in sculpture to the Subzone II-B index species *Apiculatisporis babsae* Brenner, but much smaller (28 μm vs. 32–45 μm) and not clearly related.

Appendicisporites potomacensis Brenner (Plate 1, figure 8; 79-21, 79-26).

Appendicisporites tricornitatus Weyland & Greifeld (Plate 1, figure 9; 79-26).

Ceratosporites parvus Brenner (Plate 1, figures 5, 6; 79-26, 79-29). Some specimens (e.g. Plate 1, figure 6) are larger than Brenner's material. Zone II index species.

Cicatricosisporites sp. (Plate 1, figure 10; 79-21, 79-26). In its size and reduced number of muri, this spore is suggestive of the Subzone II-B index species *C. patapscoensis* Brenner, but the muri are very different in being narrow and peaked rather than wide and flat topped.

Cingulatisporites cf. *reticingulus* Brenner (Plate 1, figures 11, 12; 79-25, 79-26, 79-29). Some specimens are larger than Brenner's material (e.g. Plate 1, figure 11).

Cingulatisporites sp. (Plate 1, figure 13; 79-26). Similar to *C. cf. reticingulus* but lacking spines.

Concavissimisporites punctatus (Delcourt & Sprumont) Brenner (Plate 1, figure 14; 79-26, 79-29).

Cyathidites minor Couper (Plate 2, figure 9; 79-29). Much less common than in the Potomac Group, where it is one of the most abundant taxa.

Densoisporites cf. *circumundulatus* (Brenner) Playford (Plate 2, figure 3; 79-29). More sculptured than Brenner's (1963) material, which he assigned to *Psilatrilletes*.

Dictyophyllidites sp. (Plate 2, figure 4; 79-25, 79-26).

Echinatisporis varispinosus (Pocock) Srivastava (Plate 2, figure 5; 79-21, 79-25, 79-26, 79-29). Spines narrower than in *Ceratosporites parvus*, sometimes bifurcate. Essentially identical to material of Srivastava (1975, especially pl. 17, figs 8-9), but also very similar to *Ceratosporites* sp. cf. *C. parvus* of Kemp (1970).

Foraminisporis asymmetricus (Cookson & Dettmann) Dettmann (Plate 1, figure 4; 79-26).

Foraminisporis dailyi (Cookson & Dettmann) Dettmann (Plate 2, figure 6; 79-26).

Gleicheniidites circinidites (Cookson) Brenner (79-21).

Leptolepidites proxigranulatus (Brenner) Wingate (Plate 2, figures 1, 2, 7, 8; 79-21, 79-25, 79-26, 79-28). Some specimens (Plate 2, figures 2, 8) resemble British spores that Kemp (1970) identified as *Patellasporites* sp. cf. *P. distaverrucosus* (Brenner) Kemp in showing varying degrees of fusion of verrucae in the equatorial area (with the specimen in Plate 2, figure 8 possibly representing an extreme case), but they are more similar to *L. proxigranulatus* than *P. distaverrucosus* of Brenner (1963) in having a rounder equatorial outline and larger, more prominently rounded verrucae.

Patellasporites distaverrucosus (Brenner) Kemp (Plate 2, figure 7; 79-21, 79-26). Kemp (1970) transferred Brenner's species from *Cingulatisporites* to *Patellasporites* because it has a thick distal patina extending beyond the equator and lacks a true cingulum. However, her British material differs from Brenner's Potomac species and the Glen Rose spore figured here, both of which have a subtriangular equatorial outline and smaller, less rounded verrucae (see discussion of *Leptolepidites proxigranulatus*).

Pilosisporites trichopapillosus (Thiergart) Delcourt & Sprumont (79-26).

Reticulatisporites arcuatus Brenner (Plate 2, figure 10; 79-26). Reticulate trilete spore with tall muri of highly irregular thickness (width). Zone II index species.

Staplinisporites caminus (Balme) Pocock (Plate 1, figure 7; 79-21). Zone II index species (*Cingulatisporites caminus* in Brenner 1963).

Taurocusporites segmentatus Stover (Plate 2, figure 11; 79-25, 79-29). May include spores with similar sculpture but no distinct trilete scar (Plate 2, figure 12; 79-29, 79-26).

Trilobosporites sp. (Plate 2, figure 13; 79-21, 79-25, 79-26). Apical sculpture elements smaller and less closely spaced than in *Trilobosporites marylandensis* Brenner.

Undulatisporites sp. (Plate 2, figure 14; all samples). Similar to *U. undulapulus* Brenner but smaller.

3.1.2. Monoletes

Laevigatosporites gracilis Wilson & Webster (79-26).

Peromonolites allensis Brenner (Plate 2, figure 15; 79-21, 79-26). Monolete spore with wrinkled perispore.

3.2. Gymnosperm pollen

Bisaccates (various types, low frequencies in all samples).

Cerebropollenites mesozoicus (Couper) Nilsson (Plate 2, figure 16; 79-21).

Classopollis sp. (Plate 2, figure 17; dominant in all samples). Often preserved in tetrads. Some smaller grains are of the type sometimes assigned to *Circulina* Malyavkina ex Klaus.

Ephedripites spp. (all samples). Monosulcate or inaperturate pollen with striations parallel to the long axis.

Eucommiidites sp. (Plate 2, figure 19; 79-21, 79-29).

Exesipollenites tumulus Balme (Plate 2, figure 18; all samples, notably abundant in 79-25).

Inaperturopollenites dubius (Potonié & Venitz) Thomson & Pflug (Plate 2, figure 20; 79-26).

Sergipea sp. (Plate 3, figure 1; 79-25). Inaperturate pollen with bilateral symmetry and three belts of thicker exine. First described from the Aptian and Albian of Brazil (Regali et al. 1974).

3.3. Angiosperm pollen

3.3.1. Monosulcates

Clavatipollenites hughesii Couper (Plate 3, figure 2; 79-21, 79-26). Small with fine columellae, reticulum not readily visible under light microscopy.

Clavatipollenites minutus Brenner (Plate 3, figures 3-6; 79-21). Smaller and more distinctly reticulate than *C. hughesii*. Trichotomosulcate grains with similar size and sculpture (Plate 3, figures 7, 8; 79-26) may be variants of this species.

Clavatipollenites rotundus Kemp (Plate 3, figures 9-12; all samples). Similar to pollen reported from Zone II by Brenner (1963) as *Liliacidites dividius* (Pierce) Brenner in having a distinct reticulum supported by sparse columellae that tend to detach from the nexine, and a narrow sulcus with thickened margins, but more coarsely reticulate, as in *C. rotundus* from the lower Albian of England (Kemp 1968) and upper Zone I (Doyle & Robbins 1977). Pierce (1961) described the sulcus in the type *Retimonocolpites dividius* from the Cenomanian of Minnesota as extending more than halfway around the grain, unlike the Zone II grains or *C. rotundus*. Sulcus margins less thickened in some specimens (Plate 3, figures 11, 12).

Clavatipollenites aff. *rotundus* (Plate 3, figures 13, 14; 79-21). Coarser muri and thicker nexine than in typical *C. rotundus*.

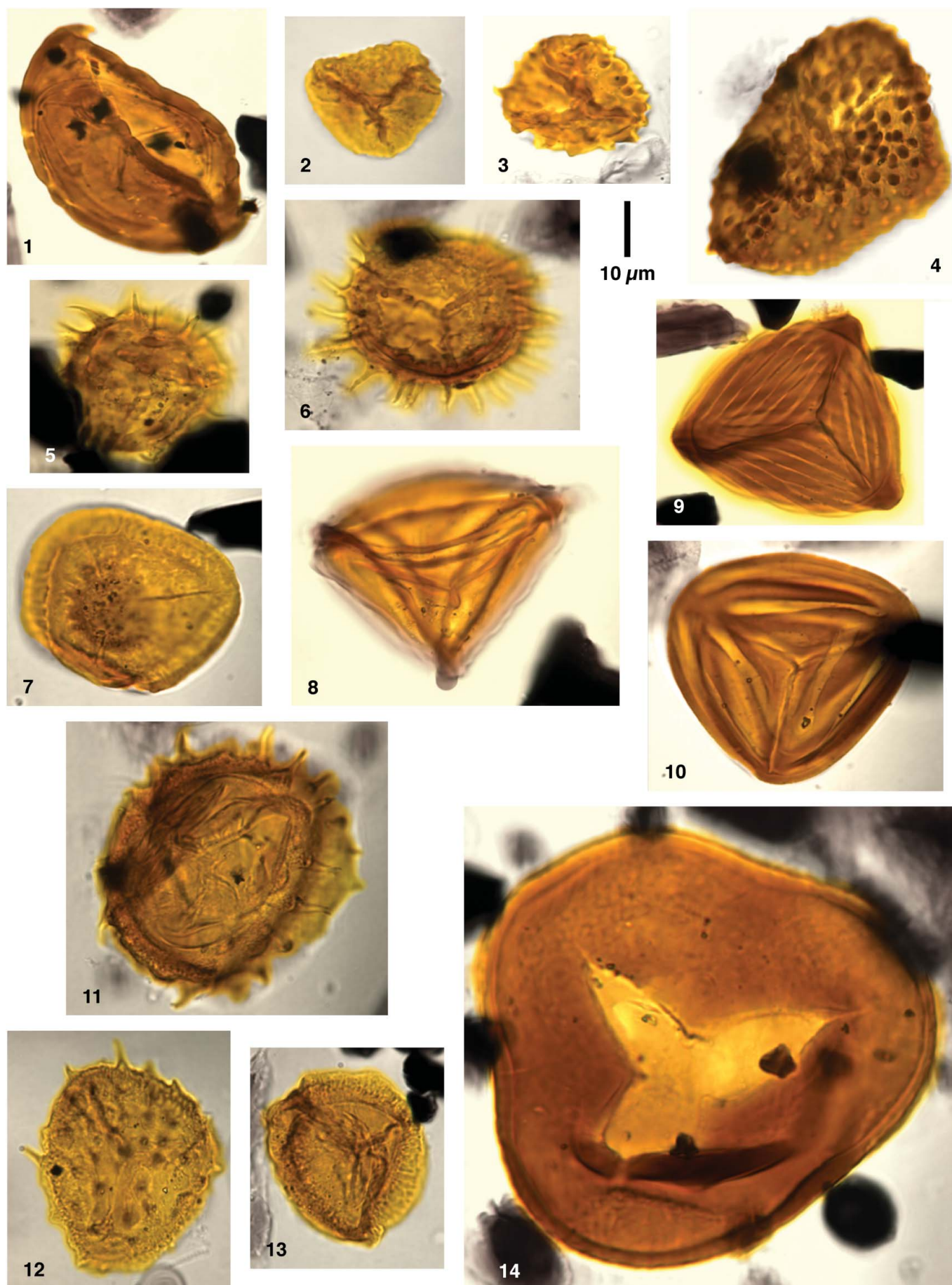
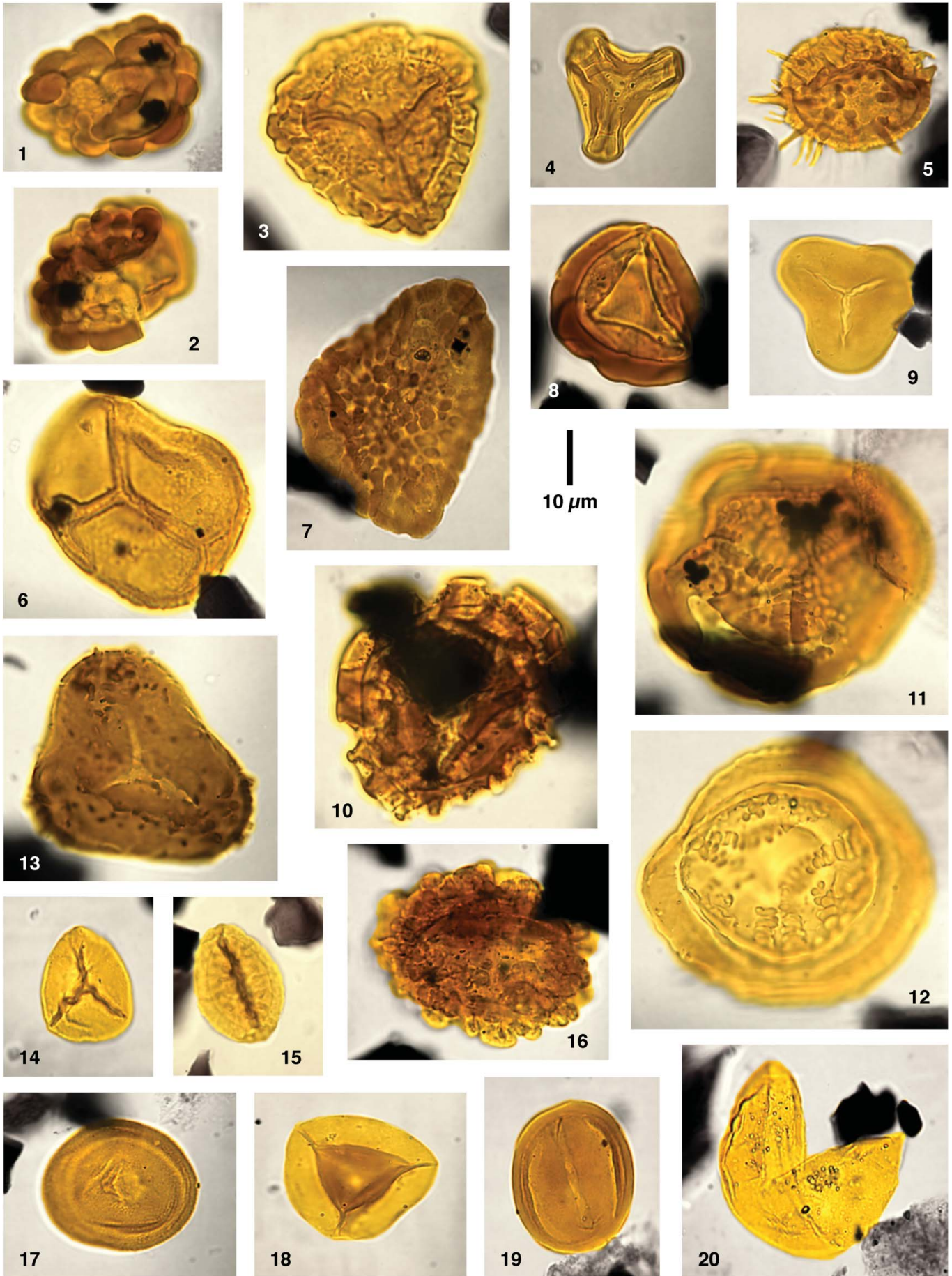


Plate 1. Spores from the Glen Rose Formation. 1. *Achradosporis vitellinus* (79-26 1.2, G38.3). 2. *Alsophilidites* cf. *pannucous* (79-25, O53.2). 3. *Apiculatisporis* sp. (79-21, F41.4). 4. *Foraminisporis asymmetricus* (79-26 1.2, M56.0). 5, 6. *Ceratosporites parvus* (5: 79-26 1.1, H28.0; 6: 79-26 1.2, U45.1). 7. *Staplinisporites caminus* (79-21, S45.0). 8. *Appendicisporites potomacensis* (79-21, Y48.0). 9. *Appendicisporites tricornitatus* (79-26 1.3, H33.0). 10. *Cicatricosisporites* sp. (79-21, U39.2). 11, 12. *Cingulatisporites* cf. *reticlingulus* (11: 79-29, S52.3; 12: 79-25, G45.0). 13. *Cingulatisporites* sp. (79-26 1.3, J53.0). 14. *Concavissimisporites punctatus* (79-29, U45.0).



Similar to *Retimonocolpites* sp. 7 of Heimhofer et al. (2007), which was assigned to *R. dividuus* by Horikx et al. (2016).

Clavatipollenites tenellis Phillips & Felix (Plate 3, figures 15, 16; 79-21, 79-26). Similar to *C. hughesii* but larger and with coarser columellae. Appears in upper Zone I.

Clavatipollenites sp. 1 (Plate 3, figures 17, 18; all samples). Similar to *C. hughesii* but larger, with finer sculpture than in *C. tenellis*. Similar to *Clavatipollenites* sp. 2 of Heimhofer et al. (2007). The most common species after *Classopollis* and *Exesipollenites*.

Clavatipollenites sp. 2 (Plate 3, figures 19, 20; 79-21, 79-26). Intermediate between *C. tenellis* and *C. hughesii* in size and sculpture.

Clavatipollenites sp. 3 (Plate 3, figures 24, 25; all samples in low frequency). Reticulate monosulcate resembling *C. rotundus* in tendency for the columellae to detach from the nexine, but with a coarser reticulum made up of finer muri and no thickening of the sulcus margins.

Clavatipollenites sp. 4 (Plate 3, figures 26, 27; 79-26). Similar to *C. rotundus* in having thickened sulcus margins, but smaller and with lumina of the reticulum of two sizes, like '*Liliacidites* sp.' of Doyle (1969, fig. 1f, g).

Crassipollis aff. *chaloneri* (Brenner) Gózcán & Juhász (Plate 3, figures 28, 29; 79-26). Similar to pollen with large, low verrucae and a circular amb that Brenner (1963) described as the Zone II index species *Monosulcites chaloneri* and that Gózcán & Juhász (1985) transferred to *Crassipollis*, but with thinner exine and smaller verrucae.

Dichastopollenites sp. (Plate 3, figures 21-23; 79-29). Coarsely reticulate pollen with sulcus running more than halfway around the grain.

Pennipollis peroreticulatus (Brenner) Friis, Pedersen & Crane (Plate 3, figures 30, 31; 79-21, 79-26). Very coarsely reticulate pollen without columellae. Originally placed by Brenner (1963) in the monoete spore genus *Peromonolites* but subsequently recognized as monosulcate pollen and transferred to *Liliacidites* (Singh 1971), *Retimonocolpites* (Doyle et al. 1975), *Brenneripollis* (Juhász & Gózcán 1985) and *Pennipollis* (Friis et al. 2000), which is the most appropriate genus because it is defined as lacking columellae. A few Glen Rose grains may represent other *Pennipollis* species, but it is unclear whether or not they lack columellae.

Racemonocolpites cf. *exoticus* Ward (Plate 4, figures 1, 2; present in low frequency in most samples). Large monosulcate pollen with gemmate to clavate sculpture, similar to *R. cf. exoticus* of Heimhofer et al. (2007, pl. VI, fig. 5) from the lower Albian of Portugal.

Stellatopollis sp. (Plate 4, figure 3; 79-28). In size of the grain and the triangular suprategal elements, this specimen falls in the range of the Zone II type species *S. barghoornii* Doyle, Van Campo & Lugardon, but because of crushing its shape and aperture condition are unclear.

Tucanopollis spp. (Plate 4, figures 4, 5; 79-25, 79-26). *Tucanopollis* differs from *Clavatipollenites* in having a continuous tectum. Similar pollen was described from the Barremian–Aptian of Brazil as *Inaperturopollenites crisopolensis* by Regali et al. (1974) but transferred to *Tucanopollis* by Regali (1989) because of its sulcate aperture condition. *Transitoripollis* from the Albian of Hungary (Gózcán & Juhász 1984) may differ in having less suprategal sculpture, but the distinctness of the two genera is uncertain.

3.3.2. *Tricolpates*

Rousea cf. *georgensis* (Brenner) Dettmann (Plate 4, figures 6, 7; 79-21, 79-26, 79-29). Brenner's (1963) Potomac species was transferred by Dettmann (1973) from *Retitricolpites* to *Rousea* Srivastava because of its graded reticulate sculpture (coarser at the equator, finer at the poles).

Rousea sp. (Plate 4, figures 8, 9; 79-26). Somewhat larger graded-reticulate tricolpate pollen with thicker exine and more robust muri.

Striatopollis aff. *paraneus* (Norris) Singh (Plate 4, figures 10–13; 79-26). Differs from *S. paraneus* in being striate-reticulate rather than prominently striate.

Striatopollis sp. (Plate 4, figures 14, 15; 79-26). Suggestive of *Tricolpites sagax* Norris from Zone II and the Albian of Alberta (Norris 1967) and Oklahoma (Hedlund & Norris 1968) in its relatively fused (foveolate?) tectum, but with a tendency for striation.

Tricolpites aff. *crassimurus* (Groot & Penny) Singh (Plate 4, figures 18, 19; 79-21). The most consistently occurring tricolpate pollen group in upper Zone I, characterized by finely reticulate-foveolate sculpture and thicker exine at the poles.

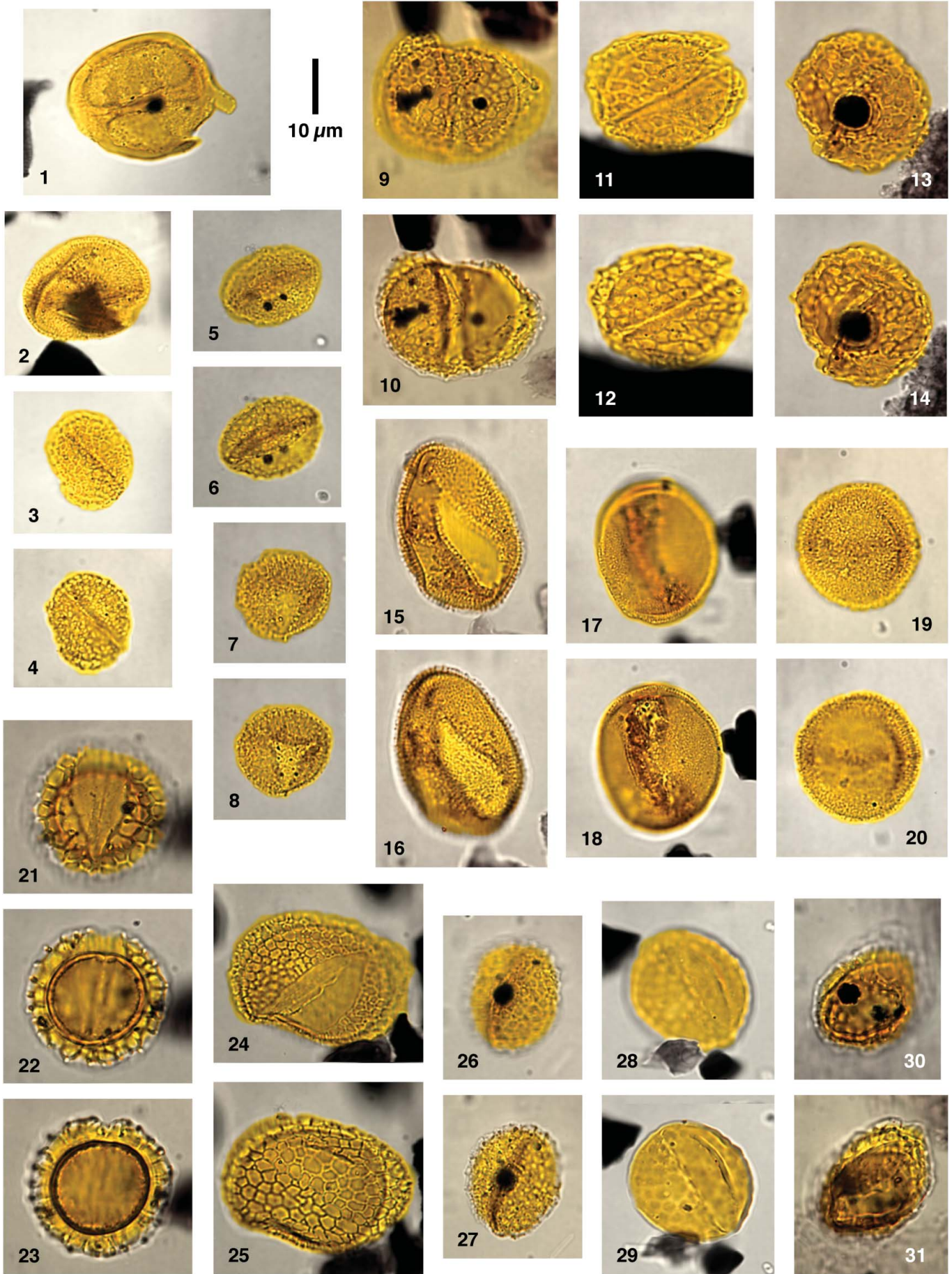
Tricolpites aff. *fragosus* Hedlund & Norris (Plate 4, figures 16, 17; 79-21). Like the Subzone II-B species *T. fragosus* in having coarser sculpture at the poles, but more reticulate than foveolate.

4. Discussion

4.1. Background on the Potomac and Portuguese sequences

Our observations provide important new data for correlation of the Potomac Group. The first palynological zonation of the Potomac was by Brenner (1963), based on two wells just down-dip from the outcrop belt in Maryland and numerous outcrop samples. He recognized two zones, Zone I and Zone II, with Zone II divided into Subzones II-A and II-B. The boundary between Zones I and II was based primarily on the appearance of new species of spores and the first tricolpate angiosperm (eudicot) pollen. In Zone I Brenner reported reticulate-columellar monosulcates, including *Clavatipollenites*, which was first described from the Barremian of England (Couper 1958). He

Plate 2. Spores and gymnosperm pollen from the Glen Rose Formation. 1, 2. *Leptolepidites proxigranulatus* (1: 79-21, T48.0; 2: 79-21, Q55.3). 3. *Densoisporites* cf. *circumundulatus* (79-29, O39.1). 4. *Dictyophyllidites* sp. (79-25, E38.4). 5. *Echinatisporis varispinosus* (79-21, H57.0). 6. *Foraminisporis dailyi* (79-26 1.3, Q33.4). 7. *Patellasporites distaverrucosus* (79-21, N35.2). 8. Cf. *Leptolepidites proxigranulatus?* (79-21, N57.4). 9. *Cyathidites minor* (79-29, X48.3). 10. *Reticulatisporites arcuatus* (79-26 1.1, N29.2). 11. *Taurocusporites segmentatus* (79-29, Q52.3). 12. *Taurocusporites segmentatus?* (79-29, U31.1). 13. *Trilobosporites* sp. (79-25, P45.2). 14. *Undulatisporites* sp. (79-25, G32.3). 15. *Peromonolites allensis* (79-26 1.2, S39.3). 16. *Cerebropollenites mesozoicus* (79-21, W46.0). 17. *Classopollis* sp. (79-25, K33.2). 18. *Exesipollenites tumulus* (79-25, L32.0). 19. *Eucommiidites* sp. (79-21, K55.0). 20. *Inaperturopollenites dubius* (79-26 1.3, V59.2).



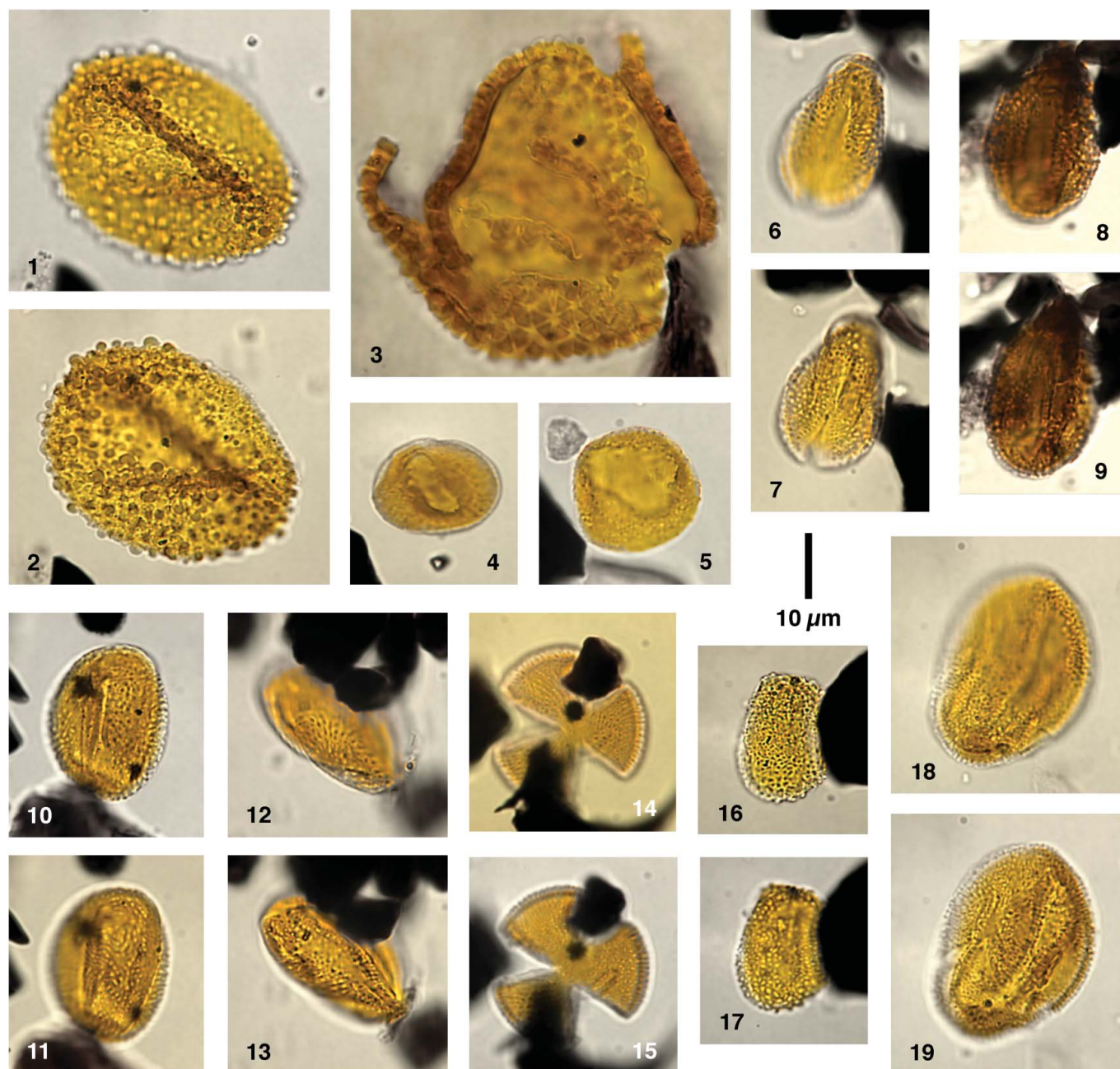


Plate 4. Monosulcate and tricolpate angiosperm pollen from the Glen Rose Formation. 1, 2. *Racemonocolpites* cf. *exoticus* (79-26 1.2, W44.2). 3. *Stellatopollis* sp. (79-28, Y43.2). 4, 5. *Tucanopollis* spp. (4: 79-26 1.2, P42.0; 5: 79-25, L51.2). 6, 7. *Rousea* cf. *georgensis* (79-26 1.1, J37.2). 8, 9. *Rousea* sp. (79-26 1.1, H36.1). 10–13. *Striatopollis* aff. *paraneus* (10, 11: 79-26 1.1, U43.3; 12, 13: 79-26 1.4, U47.3). 14, 15. *Striatopollis* sp. (79-26 1.3, P53.4). 16, 17. *Tricolpites* aff. *fragosus* (79-21, S39.4). 18, 19. *Tricolpites* aff. *crassimurus* (79-21, P42.2); what may appear to be a slight tendency for striation (upper right) is apparently an optical artifact caused by overlap of the exine on the two sides of the grain.

considered such forms incertae sedis, but their angiospermous affinities were subsequently confirmed by studies of exine structure (Doyle et al. 1975; Walker & Walker 1984) and association with angiosperm stamens and carpels (Pedersen et al. 1991; Friis et al. 1999, 2011). Based on the data available then from other areas, he dated Zone I as Barremian or Aptian and

Zone II as Albian. Because of the large number of species (22) that appear in Subzone II-A, he suggested that there was a hiatus between Zones I and II.

Doyle & Hickey (1976), Hickey & Doyle (1977) and Doyle & Robbins (1977) proposed a more detailed zonation, based primarily on samples from two wells near Delaware City, Delaware

Plate 3. Gymnosperm and monosulcate angiosperm pollen from the Glen Rose Formation. 1. *Sergipea* sp. (79-25, L52.1). 2. *Clavatipollenites hughesii* (79-26 1.2, T56.0). 3–6. *Clavatipollenites minutus* (3, 4: 79-21, T56.0; 5, 6: 79-21, T52.4). 7, 8. *Clavatipollenites* cf. *minutus* (79-26 1.3, U49.4). 9–12. *Clavatipollenites rotundus* (9, 10: 79-25, X36.3; 11, 12: 79-21, W42.3). 13, 14. *Clavatipollenites* aff. *rotundus* (79-21, E36.0). 15, 16. *Clavatipollenites tenellis* (79-21, H32.0). 17, 18. *Clavatipollenites* sp. 1 (79-26 1.1, G48.1). 19, 20. *Clavatipollenites* sp. 2 (79-26 1.2, H32.4). 21–23. *Dichastopollenites* sp. (79-29, L55.0). 24, 25. *Clavatipollenites* sp. 3 (79-29, M46.1). 26, 27. *Clavatipollenites* sp. 4 (79-26 1.3, T42.3). 28, 29. *Crassipollis* aff. *chaloneri* (79-26 1.2, L51.2). 30, 31. *Pennipollis peroreticulatus* (79-21, H32.0).

(studied in preliminary fashion by Brenner 1967). The most important result for the present study was recognition of about three species of reticulate tricolpates in upper Zone I, including Arundel Clay localities that Brenner (1963) assigned to upper Zone I (Allen Clay Mine, United Clay Mine) and the Fredericksburg and Baltimore megafossil localities of Fontaine (1889) and Berry (1911). Such samples also contain reticulate monosulcates with thickened sulcus margins that are similar to but more coarsely sculptured than pollen that Brenner (1963) identified as *Liliacidites dividuus*, described from the Cenomanian Dakota Formation of Minnesota by Pierce (1961) as *Retimonocolpites dividuus*, which Brenner observed only in Zone II. Doyle & Hickey (1976), Hickey & Doyle (1977) and Doyle & Robbins (1977) suggested that these horizons are early Albian, based primarily on Kemp (1968, 1970) and Laing (1975), who found similar tricolpates and monosulcates, described by Kemp (1968) as *Clavatipollenites rotundus*, in the first Albian ammonite zone in England, the *tardefurcata* Zone. However, Doyle (1992) argued that the Zone I–II boundary was some way down in the Aptian, based primarily on comparisons between pollen in the Arundel Clay and the Aptian of Egypt (Schrank 1983; Penny 1986, 1988a).

New evidence on this problem has come from work on Aptian–Albian coastal sections in Portugal (Heimhofer et al. 2005, 2007, 2012; Hochuli et al. 2006; Horikx et al. 2016), which consist of near-shore marine sediments that are well dated by dinoflagellates. The mesofossil floras of Friis et al. (1994, 2006, 2010, 2011), which together with floras from Potomac Zone II contain the most intensively studied flowers of early angiosperms, are from continental deposits farther inland. Hochuli et al. (2006) argued that their data indicate a significant hiatus between Potomac Zones I and II, as proposed by Brenner (1963), but with Zone I extending up into the earliest Albian and Zone II beginning in the middle Albian. One argument was based on the ratio of tricolpate to monosulcate angiosperm species. In Portugal tricolpates first appear in beds dated as earliest Albian (or possibly latest Aptian; Heimhofer et al. 2012) and are still less diverse than monosulcates in the early middle Albian, whereas at the

base of Zone II tricolpates are already as diverse as monosulcates. In the lower part of the Portuguese lower Albian there are only three species of tricolpates, all of which are reticulate, plus *Clavatipollenites rotundus*, as in upper Zone I. However, in the upper part of the lower Albian these are joined by striate tricolpates, which are not known in Zone I. Similar pollen is known in flowers (probably Buxales) from some Portuguese mesofossil localities (Pedersen et al. 2007). It should be noted that these are not the oldest striate tricolpates globally; such pollen is known from the Aptian of Brazil (Heimhofer & Hochuli 2010), Gabon (Doyle et al. 1977; Doyle 1992) and Egypt (Penny 1988b), in the Northern Gondwana province of Brenner (1976). However, they have not been reported before the Albian in Southern Laurasia.

4.2. Correlation of the Glen Rose samples with the Potomac Group and Portugal

Many spore and pollen groups in our samples of the Glen Rose Formation occur in both Zone I and Zone II of the Potomac Group, but others are more restricted. The more informative taxa are most consistent with the hypothesis that the study interval corresponds in age to a hiatus between Zones I and II in the Potomac, and to the late early Albian in Portugal (Figure 4). Some taxa are Zone II index species of Brenner (1963), which could have appeared either at the beginning of Zone II time or during a hiatus between the two zones, if there was one, while others appear related to Zone II species but not identical to them. Several taxa that appear and are common in lower Zone II are lacking.

Three spore types in our samples are among those that Brenner (1963) listed as Zone II index species: *Ceratosporites parvus* (Plate 1, figures 5, 6), *Staplinisporites caminus* (Plate 1, figure 7) and *Reticulatisporites arcuatus* (Plate 2, figure 10). Another form (Plate 3, figures 28, 29) is reminiscent of the Zone II index species described by Brenner (1963) as *Monosulcites chaloneri*, distinguished by large, low verrucae, which Brenner suggested might be a monolete spore but Górczán & Juhász (1985) interpreted as monosulcate angiosperm pollen and transferred to

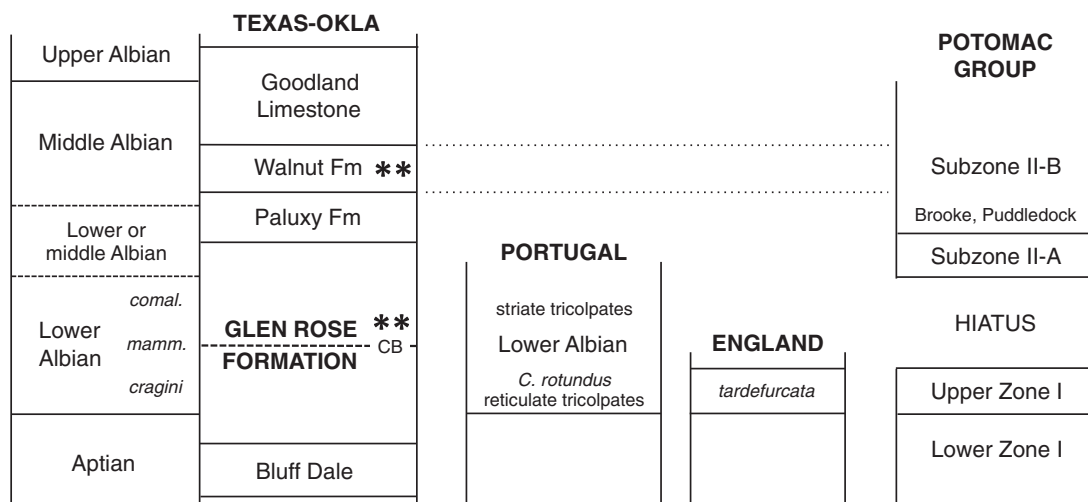


Figure 4. Proposed correlations of the Glen Rose Formation and related units in Texas and Oklahoma (OKLA) with sections in Portugal, England and the Potomac Group. CB, *Corbula* bed; **, position of palynofloras from the Glen Rose Formation (described here) and the Fredericksburg Group of Oklahoma (Hedlund & Norris 1968; Srivastava 1975). See text for full names of ammonite zones.

the genus *Crassipollis* (Góczán & Juhász 1984). However, the Glen Rose pollen has smaller verrucae and a thinner exine than the Potomac form, suggesting it is a distinct species, so its precise stratigraphic significance is uncertain.

The most common angiosperm grains are monosulcates of the sort usually assigned to *Clavatipollenites* or *Retimonocolpites*. The distinction between these two genera is unclear, and indeed Kemp (1968) considered them synonyms. Pierce (1961) defined *Retimonocolpites* as having reticulate sculpture, whereas *Clavatipollenites* was originally thought to have clavate or 'retipilate' sculpture (Couper 1958; Brenner 1963), but since the first scanning electron microscopic (SEM) studies (Doyle et al. 1975; Hughes et al. 1979; Walker & Walker 1984) it has been known that such grains have a reticulate (semitectate) tectum supported by columellae. *Retimonocolpites* is often used for forms in which the reticulum is more conspicuous than the columellae under light microscopy, and *Clavatipollenites* for those in which the columellae are more evident, but these two conditions form a continuum, and not surprisingly the line between the two genera has been drawn differently by different authors. Another problem is that Pierce (1961) described the type species of *Retimonocolpites*, *R. dividuus*, as having a sulcus that extends more than halfway around the grain, which is not the case for most pollen later assigned to the genus. We use the name *Clavatipollenites* for most species of this complex, whereas Heimhofer et al. (2007) assigned more of them to *Retimonocolpites*.

One common type (Plate 3, figures 15, 16) is similar to pollen first seen in upper Zone I that Doyle & Robbins (1977) compared with the Louisiana Paluxy species *Clavatipollenites tenellis* (Phillips & Felix 1971b). This is similar to but larger and more coarsely columellar than Zone I and II pollen compared to *Clavatipollenites hughesii* (Doyle et al. 1975; Walker & Walker 1984), which also occurs in our samples (Plate 3, figure 2). Heimhofer et al. (2007) reported similar pollen, as *Clavatipollenites* cf. *tenellis*, from the late Aptian and early Albian of Portugal. Probably the most common angiosperm, *Clavatipollenites* sp. 1 (Plate 3, figures 17, 18), approaches *C. tenellis* in size and shape but is much more finely sculptured. This is more similar to *Clavatipollenites* sp. 2 of Heimhofer et al. (2007) from the early Albian of Portugal. Grains with sculpture intermediate between that of *C. tenellis* and *C. sp. 1* also occur (Plate 3, figures 19, 20), suggesting that these types represent several morphologically overlapping species that may not be readily distinguishable without SEM.

Other grains with a more distinct, sometimes looser reticulum and thickened sulcus margins (Plate 3, figures 9–12) are similar to Potomac pollen that Brenner (1963) identified as *Liliacidites dividuus* (Pierce) Brenner, and especially more coarsely sculptured grains from upper Zone I that Doyle & Robbins (1977) designated aff. *Retimonocolpites dividuus*. These are probably identical to *Clavatipollenites rotundus* of Kemp (1968), which appears in the earliest Albian *tardefurcata* Zone in England, and *Retimonocolpites* sp. 7 of Heimhofer et al. (2007), which enters in the earliest Albian in Portugal. Some grains of this general type, designated *Clavatipollenites* aff. *rotundus* (Plate 3, figures 13, 14), have thicker muri and may represent one or two related species. Another (*Clavatipollenites* sp. 3; Plate 3, figures 24, 25) is like *C. rotundus* in having a distinct, loose reticulum with an abrupt border at the sulcus but shows no thickening of the sulcus margins.

Other monosulcate groups are less informative for placing the Glen Rose samples relative to the Zone I–II boundary. Many grains (Plate 3, figures 3–6) are smaller and more clearly reticulate than *C. hughesii* but similar to Potomac pollen assigned to or compared with (aff.) *Clavatipollenites minutus*, which ranges through Zones I and II. Probable trichotomosulcate variants of this complex (Plate 2, figures 7, 8) are similar to pollen that Groot & Groot (1962) described from the Albian of Portugal as *Apiculatisporis vulgaris*, which they assumed was a trilete spore. There is at least one species of *Pennipollis* (Plate 3, figures 30, 31), characterized by a coarse, loose reticulum with no columellae below, which ranges throughout the Potomac and the Aptian and Albian of Portugal and England and has been considered a post-Barremian guide fossil (Hughes et al. 1979; Upchurch & Doyle 1981; Penny 1988a; Doyle 1992; Heimhofer et al. 2007; Doyle & Endress 2014). One grain (Plate 4, figure 3) resembles *Stellatopollis barghoornii* from Subzone II-B in the Potomac but is too poorly preserved for precise identification; the genus ranges from Barremian through Albian sediments in Europe and Africa (Doyle et al. 1977; Penny 1991; Hughes 1994; Ibrahim 2002; Heimhofer et al. 2007).

Some Glen Rose monosulcates have not been reported from the Potomac Group, but it is uncertain whether they were absent due to ecological or geographic effects or do occur but have not been recognized. These include large grains with irregular gemmate to clavate sculpture elements similar to *Racemonocolpites exoticus* (Plate 4, figures 1, 2) from the late Albian of Kansas (Ward 1986), also reported from the late Aptian to middle Albian of Portugal (Heimhofer et al. 2007). One coarsely reticulate pollen type appears to represent *Dichastopollenites* (Plate 3, figures 21–23), characterized by a sulcus extending more than halfway around the grain, which was first described by May (1975) from the Cenomanian of Utah and Arizona and is diverse in the early and middle Albian of Portugal (Heimhofer et al. 2007). Half-grains of this group may have been observed in the Potomac but mistaken for reticulate monosulcate pollen. There are also isolated grains of one or two species of *Tucanopollis* (Plate 4, figures 4, 5), first described from the Barremian and Aptian of Northern Gondwana (Regali et al. 1974; Regali 1989). The lack of Potomac reports is probably due to non-recognition, since Friis et al. (1995) found *Tucanopollis* pollen adhering to fruits named *Appomattoxia* from the Albian of Virginia.

Glen Rose tricolpates are less common and diverse than angiospermous monosulcates, but they are more diverse than tricolpates in upper Zone I. Some have reticulate sculpture, as in upper Zone I and the lowest Albian of England (Kemp 1968) and Portugal (Heimhofer et al. 2007). One (Plate 4, figures 18, 19) resembles the most common tricolpate type in upper Zone I, designated aff. *Tricolpites crassimurus* by Doyle & Robbins (1977), which has uniform finely reticulate-foveolate sculpture and thicker exine at the poles. In another, *Rousea* cf. *georgensis* (Plate 4, figures 6, 7), the reticulum grades from fine at the poles to coarser at the equator (the defining character for the genus *Rousea*). Tricolpate pollen with graded sculpture was not reported from upper Zone I by Doyle & Robbins (1977) or the lower Albian of England by Kemp (1968), but it was observed in upper Zone I by Doyle (1992) and the lowest Albian of Portugal by Heimhofer et al. (2007). Another graded-reticulate type,

Rousea sp. (Plate 4, figures 8, 9), has a thicker exine and more robust muri.

In contrast to upper Zone I, other tricolpates have striate-reticulate sculpture (with a tendency for parallel alignment of the muri making up the reticulum), as in the late early Albian in Portugal (Heimhofer et al. 2007) and Potomac Zone II. These are not as conspicuously striate as the Zone II species *Striatopollis paraneus* and *S. vermimurus* (Brenner) Srivastava, and they sometimes appear reticulate unless studied under oil immersion. One type, with fine reticulate-striate sculpture (Plate 4, figures 10–13), is most similar to *S. paraneus*. Doyle & Robbins (1977) did not report *S. paraneus* below Subzone II-B, but they figured a grain close to *S. vermimurus*, which has more coarsely striate-rugulate sculpture, from Subzone II-A; both types have been associated with buxalean flowers (Drinnan et al. 1991). Another striate type (*Striatopollis* sp.) has a more fused, probably finely foveolate tectum (Plate 4, figures 14, 15).

Another tricolpate type (*Tricolpites* aff. *fragosus*) has a coarser reticulum at the poles than in other parts of the grain (Plate 4, figures 16, 17). A similar pattern of grading, the opposite of that seen in *Rousea*, is characteristic of *Tricolpites fragosus* from the middle Albian of Oklahoma (Hedlund & Norris 1968), which does not appear until lower Subzone II-B in the Potomac. However, the lumina in the Glen Rose pollen are less markedly larger at the poles and the muri form a more distinct reticulum than in typical *T. fragosus*, where the graded pattern is formed by foveolae of differing sizes in a smooth tectum. This suggests that the Glen Rose type is a distinct species and may therefore have a different range than typical *T. fragosus*. Horikx et al. (2016) identified *T. aff. fragosus* from the late early Albian of Portugal, but their pollen differs more from the Glen Rose, Potomac and type material in being larger and thinner walled.

Although the exact number of species is difficult to determine, monosulcate angiosperms are more than twice as diverse as tricolpates. By contrast, in Potomac Subzone II-A the diversity of the two pollen classes is roughly equal, as noted by Hochuli et al. (2006). In this respect, the Glen Rose angiosperm assemblage is more similar to that of the early Albian of Portugal. Overall, Subzone II-A tricolpates cover a broader morphological range than Glen Rose tricolpates (Doyle & Robbins 1977, pl. 2, figs 3–20). They include forms that differ from those in the Glen Rose samples in being smaller and reticulate (aff. *Tricolpites micromunus* (Groot & Penny) Singh), smaller and psilate (aff. *Cupuliferoidaepollenites parvulus* (Groot & Penny) Dettmann), more oblate (aff. *Tricolpites sagax*) and coarsely striate-rugulate (aff. *Striatopollis vermimurus*), all presumably derived features relative to the first tricolpates. The absence of such types supports the hypothesis that the Glen Rose horizons studied are older than the base of Zone II. Horikx et al. (2016) reported pollen close to two of these, *T. sagax* and *S. vermimurus*, from the late early Albian of Portugal, suggesting that they may not all appear at the same time.

If it could be assumed that only evolutionary processes were involved, the great increase in diversity of tricolpate pollen between Potomac Zones I and II might be taken as evidence for a long missing interval. However, less time might be required if much of this increase was due to rapid poleward migration of eudicots from Northern Gondwana into Laurasia driven by global warming, as proposed by Heimhofer et al. (2005), Coiffard & Gomez (2012) and Coiffard et al. (2012).

4.3. Relation to younger units in the Gulf Coast

Our only sample from the upper member of the Glen Rose Formation, at Paluxy Townsite, was unfossiliferous, but Beach (1981a) had several productive samples from this interval. Most of the angiosperms, although difficult to identify from Beach's plates, are broadly comparable to types in our study, including reticulate monosulcates of the *C. rotundus* group (identified as *Liliacidites dividuus* and *Retimonocolpites peroreticulatus*) and both reticulate and finely striate tricolpates. However, there are two taxa not found in our samples that may reflect a younger age. One is *Asteropollis*, with a four- or five-branched sulcus, first described from the Fredericksburg of Oklahoma (Hedlund & Norris 1968), which appears in lower Subzone II-B in the Potomac. Heimhofer et al. (2007) recorded *Asteropollis* in both the Aptian and Albian in Portugal, but this was a result of including pollen with a three-branched sulcus (trichotomosulcate) as well as the more distinctive four- and five-branched sulcus of the Oklahoma type material. The oldest grain with a four-branched sulcus that Heimhofer et al. (2007) illustrated was from the late early Albian, and re-examination of older specimens showed that all of these were trichotomosulcate (U. Heimhofer, pers. comm.). As discussed by Doyle & Endress (2014), this appears to be true of other pre-Albian reports of *Asteropollis*. The second taxon consists of small, smooth tricolpates identified as *Cupuliferoidaepollenites parvulus*; as noted above, similar pollen (aff. *C. parvulus*) occurs in Subzone II-A but not in our Glen Rose samples. Hochuli et al. (2006) argued that the presence of typical *C. parvulus* in Subzone II-B of the Potomac Group indicated a late Albian age, but Beach's report (if correct) would support the contention of Massoni et al. (2015, p. 9) that smooth tricolpates of this type extend down further in the Albian.

The best-known Albian palynoflora in the region is from the 'Walnut' clay facies in southernmost Oklahoma, at the base of the Fredericksburg Group, described by Hedlund & Norris (1968) and Srivastava (1975, 1981). Hedlund & Norris (1968) studied three samples from the underlying Antlers (Paluxy) Sand, but all their illustrated angiosperm pollen was from the 'Walnut' and thus clearly above the regional Trinity–Fredericksburg disconformity. The middle–late Albian boundary based on ammonites falls within the overlying unit, the Goodland Limestone (Young 1966, 1967a, 1967b, 1986; Scott et al. 2003). The angiosperms are markedly more diverse than in our Glen Rose samples, especially the tricolpates (12 out of 18 angiosperm species identified by Hedlund & Norris 1968). These include several taxa that appear in Potomac Subzone II-A, such as *Tricolpites sagax*, *Tricolpites micromunus* and *Striatopollis vermimurus*, and others first seen in lower or middle Subzone II-B, including *Asteropollis* and possibly related forms with several colpoid apertures (*Stephanocolpites fredericksburgensis* = *Hammenia* Ward), *Tricolpites fragosus*, '*Retitricolpites*' *geranioides* (Couper) Brenner (renamed *Rousea brenneri* by Singh 1983), *Penetetrapites mollis* and *Striatopollis paraneus*. Doyle et al. (1975) also noted *Stellatopollis*, not reported by Hedlund & Norris (1968), in slides deposited at the US National Museum. Based on these observations, Doyle (1977) argued that the 'Walnut' assemblage correlates with the middle of Subzone II-B in the Potomac. Among several new 'Walnut' species, Srivastava (1975) added triporoidate tetrads that he named

Senectotetradites amiantopollis (transferred to *Virgo* by Ward 1986), which are similar to tetrads that appear in lower Subzone II-B (aff. *Ajatipollis* sp. A of Doyle & Robbins 1977). Similar pollen, identified as *Virgo amiantopollis* by Heimhofer et al. (2007) and *Ajatipollis* sp. 1 by Horikx et al. (2016), extends further back in Portugal, into the late early Albian.

These comparisons raise questions on the age of the base of Potomac Zone II. Assuming that the 'Walnut' flora correlates with the middle of Subzone II-B, the fact that its angiosperm element is so much more diverse than our Glen Rose assemblage suggests that equivalents of lower Zone II could extend down well into the Paluxy Formation or the upper Glen Rose. This would be consistent with the limited palynofloral data from higher in the Glen Rose Formation (Beach 1981a). The Paluxy leaf flora of Ball (1937) may also be relevant, since it includes palmately lobed leaves (*Araliaephyllum paluxyense*) that are similar to fossils identified as *Araliaephyllum* by Fontaine (1889) from his '72d mile-post near Brooke' locality in Virginia, which is not dated palynologically but is probably close in age to his nearby 'Bank near Brooke' locality (lower Subzone II-B). However, the position of Ball's flora within the Paluxy Formation is not established.

Unfortunately, the relation of the uppermost Glen Rose and Paluxy interval to standard substages of the Albian is poorly controlled by faunal data. Ammonites above the *comalensis* Zone in the Glen Rose Formation are endemic engonocerids, and the area was not fully connected to the open ocean until deposition of the Goodland Limestone (Scott et al. 2003). Based on rather indirect ammonite correlations of the Walnut Formation with the middle part of the middle Albian, Young (1966) suggested that the post-*comalensis* part of the Glen Rose (called the *Metengonoceras* sp. Zone in Young 1986) correlates with the first two ammonite zones (*Hoplites benettianus* and *Hoplites dentatus*) of the middle Albian in England. If this is correct, Zone II most likely begins in the middle Albian, as assumed by Hochuli et al. (2006), Doyle & Upchurch (2014) and Massoni et al. (2015). The hiatus between Zones I and II might either straddle the early–middle Albian boundary or lie in the middle Albian, as proposed by Hochuli et al. (2006). By contrast, Scott et al. (2003), using graphic correlation methods to extrapolate stage boundaries from other areas to the Trinity River valley (northeast of the Glen Rose type area), estimated that the early–middle Albian boundary falls only a little below the top of the Paluxy Formation, above the Trinity–Fredericksburg disconformity in the middle of the formation. If this is correct, the base of Zone II and the preceding hiatus could be well down in the early Albian. If so, lower Subzone II-B leaf and mesofossil localities such as Bank near Brooke (Fontaine 1889; Hickey & Doyle 1977; Upchurch 1984; Crane et al. 1993) and Puddledock, Virginia (Crane et al. 1994; Friis et al. 2011), considered middle Albian by Doyle & Upchurch (2014) and Massoni et al. (2015), could be either early middle or late early Albian.

4.4. Summary of stratigraphic results

To summarize, these results fit the hypothesis that our Glen Rose samples correlate with an interval between Zones I and II that is missing in the Potomac Group, but present in the late early Albian of Portugal. The fact that ammonites in this part of

the Glen Rose Formation correlate with the *mammillatum* Zone in Europe (Young 1974) further confirms that the missing Potomac interval is at least in part late early Albian. This is consistent with palynological evidence that upper Zone I correlates with the lowest Albian in Portugal and the *tardefurcata* Zone in England, which correlates with the *cragini* Zone in the lower Glen Rose Formation (Young 1974).

This scheme might be tested and extended by future palynological studies of underlying and overlying horizons in Texas. Thus we would predict that the lower Glen Rose Formation (*cragini* Zone) should have an angiosperm flora with reticulate tricolpates and members of the *Clavatipollenites rotundus* group but not striate tricolpates, as in the lowest Albian of Portugal and the *tardefurcata* Zone in England. Palynological and leaf paleobotanical studies of the upper Glen Rose and the overlying Paluxy Formation could clarify where equivalents of Zone II begin in this section. In the absence of diagnostic ammonites, studies of dinoflagellates might provide new independent evidence on the age of this interval and thereby refine the age of the base of Zone II. Studies of dinoflagellates in the present samples might contribute to placement of the early–middle Albian boundary in the Texas section if they could clarify whether the samples fall near the end of the early Albian or significantly earlier within it.

As discussed in Doyle & Endress (2014), most of the Portuguese mesofossil localities of Friis et al. (1994, 2006, 2011) may be close to the Glen Rose samples in age, i.e. late early Albian, rather than either late Aptian or early Albian (as assumed by Friis et al. 2006, 2011): ca. 15% of the angiosperm taxa are tricolpate, some of them striate (Pedersen et al. 2007). The rich Torres Vedras locality (Friis et al. 2010) is perceptibly older, but rather than being Barremian–early Aptian (Friis et al. 2006, 2010, 2011), it may be near upper Zone I in age, since it contains *Pennipollis*, indicative of a post-Barremian age (reviewed in Doyle & Endress 2014), plus *C. rotundus*-like monosulcates (Friis et al. 2010, pl. IV) and reticulate tricolpates similar to those in upper Zone I, the lowest Albian of England and the lowest Albian in the Portuguese coastal sections (Heimhofer et al. 2007).

4.5. Paleoecology and paleogeography

The dominance of *Classopollis* and *Exesipollenites* in the Glen Rose Formation, compared to their more modest role in the Potomac Group, is clearly of paleoecological significance. Abundance of *Classopollis*, associated with evidence for a hot and dry climate, is one of the main features that distinguished the Northern Gondwana province of Brenner (1976) from his Southern Laurasian province (except in apparently wetter areas near the paleoequator where Araucariaceae and ferns were more common: Doyle et al. 1982; Schrank 1990; Brenner 1996; Doyle 1999). The common occurrence of striate ephedroid pollen (*Ephedripites*) is another similarity to Northern Gondwana and putative indicator of aridity, as is the lower species diversity of spores than in the Potomac. However, the Glen Rose flora also includes a consistent low frequency of bisaccate pollen (Pinaceae, Podocarpaceae), which only penetrated into the northern fringe of Northern Gondwana, and other spore and pollen types shared with the Potomac Group. This could mean that Texas lay

in a transition zone between the two provinces. The presence of more distinctive Gondwanan taxa, namely *Sergipea* and *Tucanopolis*, both first described from Brazil (Regali et al. 1974; Regali 1989), indicates a floristic connection as well as similar climate. Another possible indication of floristic differentiation within North America is the prominent Glen Rose spore genus *Acradosporites*, originally described by Srivastava (1975) from the Goodland Limestone of Texas, which is not known in the Potomac.

The relative role of climatic zonation, geographic barriers and local factors in determining these trends is uncertain. *Classopollis* was locally dominant in other parts of Southern Laurasia in the Early Cretaceous, notably in marine-influenced facies, such as beds dominated by *Pseudofrenelopsis* and *Dioonites* (Bennettiales) in the lower Potomac Group (Upchurch & Doyle 1981). This suggests that the dominance of *Classopollis* and low diversity of spores in the Glen Rose Formation could be as much a function of the local lagoonal environment as of climate. Temporal changes in climate could be superimposed on geographic and local environmental differences. Brenner (1963) recognized a decline in *Classopollis* and *Exesipollenites* and a rise in bisaccate pollen between Zones I and II, which could be due either to cooling or to increased rainfall. The latter would be more consistent with evidence for CO₂-driven global warming beginning in the early Albian, which Heimhofer et al. (2005), Coiffard & Gomez (2012) and Coiffard et al. (2012) have argued stimulated the poleward spread of tricolpate eudicots from Northern Gondwana into Laurasia.

The situation in the Glen Rose Formation may have analogies in the Iberian Peninsula, which appears to have straddled the boundary between a warm and humid belt to the north (with a typical Southern Laurasian flora) and a hot and semiarid or arid belt to the south (Heimhofer et al. 2008, 2012). In the Algarve Basin in southwestern Portugal, *Classopollis* was dominant and spores occurred at low frequency throughout the early Aptian to early Albian, despite evidence from clay mineralogy for greater humidity in the early Aptian and more aridity in the late Aptian to early Albian (Heimhofer et al. 2008). Because of the presence of bisaccate and araucariaceous pollen and schizaeaceous and gleicheniaceaceous fern spores, and the rarity or absence of distinctive Northern Gondwanan elements, Heimhofer et al. (2008) attributed the abundance of *Classopollis* to dominance of Cheirolepidiaceae in coastal habitats rather than a transition to Northern Gondwana. However, Horiks et al. (2016) reported polyporate *Cretacaeiporites* pollen, a typical Northern Gondwana group that is not known in North America, from the late early Albian onward in the Lusitanian Basin, north of Lisbon. In this basin, Heimhofer et al. (2012) showed that *Classopollis* was dominant in the earliest Albian (though less so than in Algarve), but spores became abundant in the late early Albian, the interval that we correlate with the Glen Rose samples. They interpreted this as evidence for a transient southward shift of the northern wet belt due to a climatic fluctuation. The fact that our samples have fewer spores could mean that north central Texas was farther south of the boundary between humid and arid zones, like Algarve; that the fluctuation was a European phenomenon that did not affect Texas; or that a similar fluctuation did occur in Texas but was obscured by a vast area of circum-lagoonal vegetation.

5. Conclusions

The late early Albian palynoflora described here from the Glen Rose Formation provides a firm tie point for correlation of other less well-dated continental sections. Thus, it confirms the hypothesis based on Aptian–Albian sequences in Portugal that there is a hiatus between Zones I and II in the Potomac Group, and that this hiatus is at least in part of late early Albian age. However, studies of older and younger units are desirable for both stratigraphic and paleoecological purposes. Palynofloras from higher in the Glen Rose and the Paluxy Formation are needed to elucidate the development of the angiosperm flora between our mid-Glen Rose horizon and the next well-described interval in the Gulf Coast, the middle Albian ‘Walnut’ facies of Oklahoma, and to refine the age of the base of Potomac Zone II. Studies of dinoflagellates could provide further evidence on ages in the section, particularly in the upper Glen Rose Formation, where the only ammonites are endemic taxa with little utility for intercontinental correlation.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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