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Turonian flora of New Jersey, USA

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Abstract. An extraordinarily diverse flora was discovered in sediments of the Old Crossman Clay Pit, Raritan Formation (New Jersey, USA). The age of these rocks has been estimated as Turonian (~ 90 MYBP, Late Cretaceous) by palynological and stratigraphic correlations. The environment in which the sediments were deposited is described as fluvial (non-marine) with levee, back levee and swamp conditions. The fossils, preserved as charcoal, maintain their three-dimensional structure, and an excellent morphological and anatomical preservation, offering a unique opportunity for studying characters rarely available for plant fossils. This flora encompasses mosses, ferns, gymnosperms and angiosperms, and a preliminary study is presented here with special emphasis on selected taxa. The Raritan sediments have yielded the oldest records for flowers of hamamelidaceous, capparealean, ericalean, and fagalean affinities and the oldest Clusiaceae as well as the oldest unequivocal monocot. Although the relationships of some taxa are still uncertain, for others the relationships are clear. Thus far, this flora has enlightened our knowledge of several plant groups, in particular the angiosperms. Based on the paleoposition of New Jersey in southern Laurasia in a low-middle latitude on the north side of the Tethyan Sea, a tropical to subtropical climate was previously proposed for the Raritan Formation. The elements of the Old Crossman Clay Pit locality are consistent with this conclusion.

Key words. Raritan Formation. Paleoflora. Cretaceous. Mosses. Ferns. Seed plants.

Introduction

During the last decade, our knowledge on the evolution of the seed plants, especially of the angiosperms, has increased enormously. Due to the discovery of exceptionally well-preserved fossils and extraordinary diverse paleofloras, it has been possible to gain new insights on the appearance of taxa and their phylogenetic relationships. One of these floras was recovered from the Raritan fluvial sediments that encompass the Atlantic Coastal Plain.

The fossils reported here were collected from the Old Crossman Clay Pit locality, Raritan Formation that is exposed in New Jersey. Jengo (1995) in the latest study on the Raritan and Magothy formations pointed out that the Old Crossman Clay Pit is an interfacies between the Old Bridge and the Sayreville Sands. The Raritan sediments constitute a series of interlensing gravels, sands and clay deposited in fluvial channels and avulsion or overbank paleoenvironment (Brenner, 1963; Jengo, 1995). Groot *et al.* (1961) proposed a Turonian age (Late Cretaceous; ~90 MYBP) for the Old Crossman Clay Pit; subsequently, this age has been corroborated by many others (Brenner, 1963; Grimaldi *et al.*, 1989; Harland *et al.*, 1989).

The aim of this report is to address briefly some of the taxa of the Old Crossman Clay Pit flora. The assemblage includes mosses (gametophytes), ferns (rhizomes, petioles and sterile and fertile pinnules), gymnosperms (foliage, cones, and wood) and angiosperms (flowers, complete floral organs, fruits, seeds, and wood).

Materials and methods

The fossils of the Old Crossman Clay Pit locality are charcoalified and three-dimensional with extraordinary preservation of characters including cellular features. To extract the fossils from the matrix, the unconsolidated sediments were dissolved in warm water and sieved through successively finer screens. The resultant organic material was cleaned with strong detergent to remove excess clay. Sand was removed by gently swirling to suspend the fossils and then decanting the suspension of organic materials. Other adherent minerals were removed by treating the fossils with hydrofluoric acid followed by several rinses with distilled water. Fossils were air-dried and sorted with a Zeiss SV-8 stereosmicrospe. In preparation for examination with a Hitachi 4500

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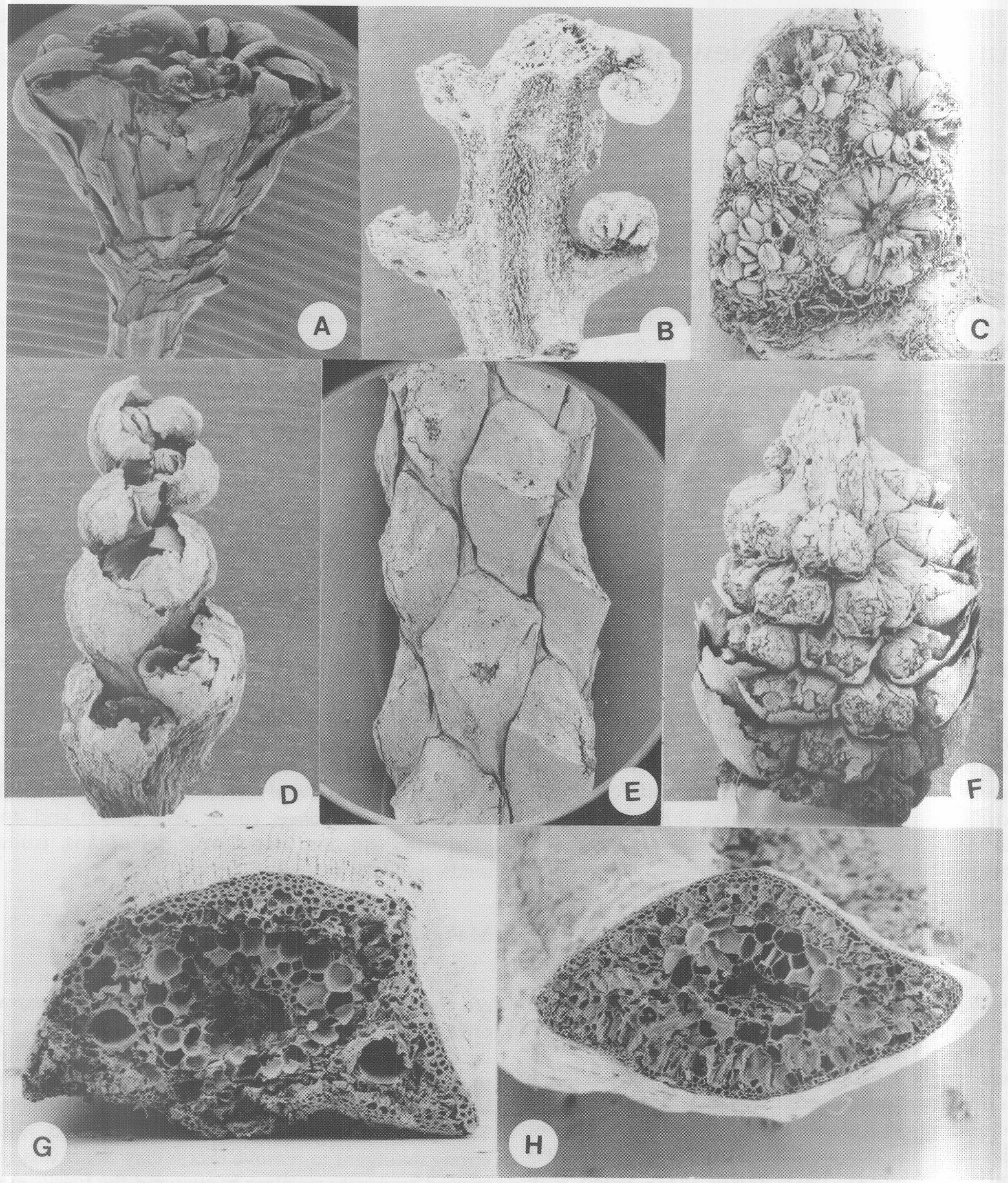

Figure 1. A, ***Eopolytrichum antiquum*** Konopka *et al.*, cf? (Polytrichaceae). Male gametophyte showing the overlapping perigonial bracts, CUPC-Stub# 293 (21X). **B-C,** ***Boodlepteris turoniana*** Gandolfo (Gleicheniaceae); **B,** overall view of an inmature frond. Observe the circinate bipinnate pinnae. Note the trichomes, CUCP 1023 (42X); **C,** overall view of one pinnule with 5 sori, CUCP 1040 (32X). **D,** ***Lygodium bierhorstiana*** Gandolfo *et al.* Front view of a sorophore showing single sporangia, CUCP 1059 (42X). **E,** ***Brachyphyllum*** sp. (Cheirolepidiaceae?), CUCP-Stub#1063 (21X). **F-H,** Pinaceae; **F,** ***Amboystrobus cretacicum*** Gandolfo *et al.* Side view of a male cone. Note the hellicaly arranged microsporophylls. Each microsporophyll bears two microsporangia, CUCP 1082 (28X); **G,** ***Prepinus parlinensis*** Robinson. Cross-section of a leaf, CUCP 1084 (91X); **H,** ***Prepinus*** sp. Cross-section of a leaf, CUPC 1088 (91X).

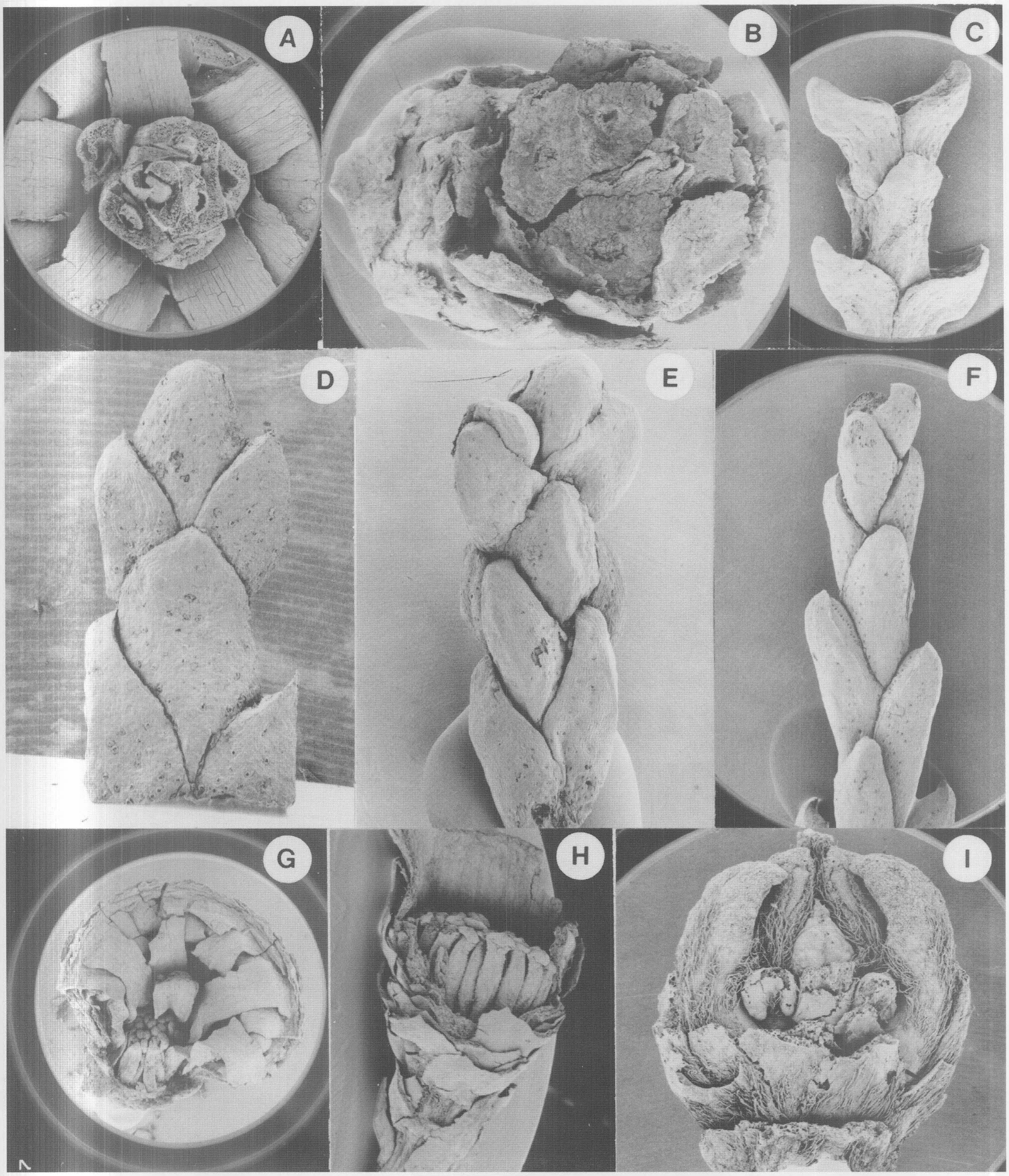

Figure 2. A-B, Pinaceae; **A,** top view of a dwarf shoot of ***Prepinus*** sp. showing the bract and the hellicaly arranged leaves, CUPC 1093 (14X); **B,** top view of a dwarf shoot of ***Pinus quinquefolia***, CUCP 1097 (21X). **C-D,** Cupressaceae; **C,** Cupressaceae sp. 1, CUPC-Stub#1001 (14X); **D,** Cupressaceae sp. 2, CUPC-Stub#708 (32X). **E-F,** Taxodiaceae; **E,** Taxodiaceae sp. 1, CUPC-Stub#1017 (32X); **F,** Taxodiaceae sp. 2, CUPC-Stub#1011 (21X). **G-I,** Magnoliidae; **G,** ***Detrusandra mystagoga*** Crepet and Nixon, CUPC 1188 (14X). **H,** ***Cronquistiflora sayrevillensis*** Crepet and Nixon, CUPC 1175 (11X). **I,** ***Perseanthus crossmanensis*** Heredeen *et al.*, CUPC 1153 (21X).

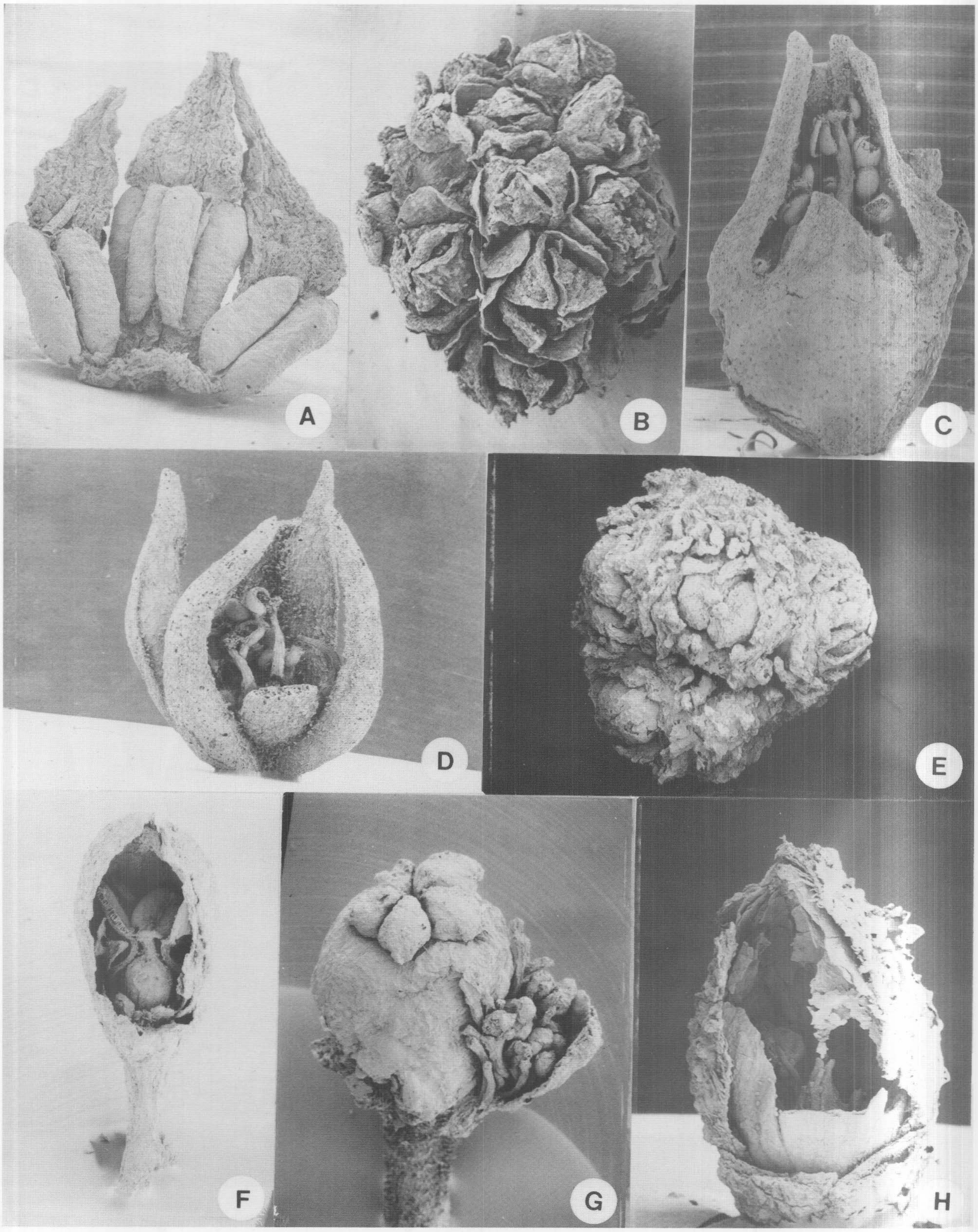

Figure 3. A, Magnoliidae: ***Chloranthistemon crossmanensis*** Heredeen *et al.*, CUPC 1004 (70X). **B-E,** Hamamelidae; **B,** Hamamelidaceae male inflorescence, CUPC 1156 (32X); **C,** female Fagaceae flower, CUPC-Stub#269 (42X); **D,** male Fagaceae flower, CUPC-Stub#740 (35X); **E,** Altingioideae female inflorescence, CUPC 1064 (26X). **F-H,** Dilleniidea; **F,** ***Dressiantha bicarpellata*** Gandolfo *et al.*, CUPC 1074 (42X); **G,** ***Paleoclusia chevalieri*** Crepet and Nixon, CUPC 1192 (53X); **H,** ***Paleoenkianthus sayrevillensis*** Nixon and Crepet, CUPC 1100 (51X).

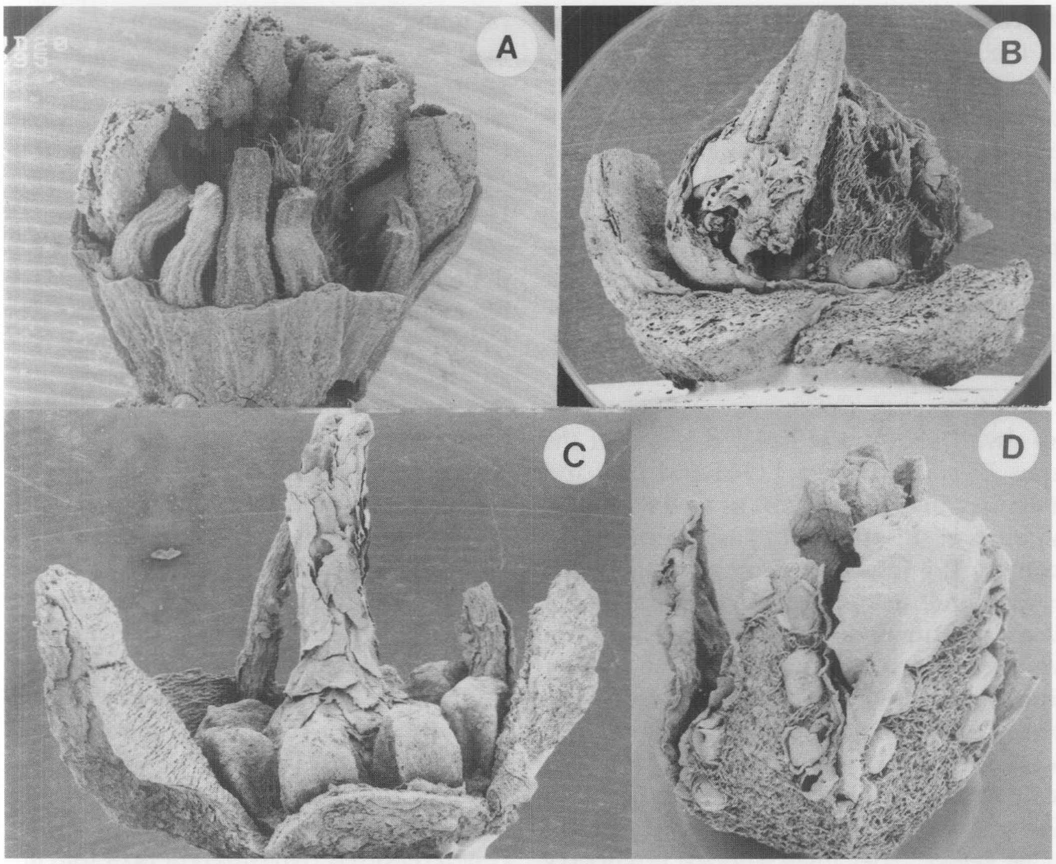

Figure 4. **A-D**, Dilleniidae; **A-B**, Ericaceae; **A**, Ericaceae sp. 1, CUPC-Stub#295 (25X); **B**, Ericaceae sp. 2, CUPC-Stub#499 (21X); **C**, Ericoid flower, CUPC 1107 (28X); **D**, Pyrolaceae sp. 1, CUPC-Stub#253 (33X).

scanning electron microscope (SEM), the selected specimens were mounted on stubs and sputter-coated with gold/palladium. Specimens are housed in the Paleobotany Collection of the L.H. Bailey Hortorium, Cornell University.

Components of the flora

The Old Crossman Clay flora includes a moss, two species of ferns, at least four families of gymnosperms and several genera of angiosperms. The following paragraphs summarize our current knowledge of floral diversity as it is known from vegetative and reproductive remains.

Bryophytes

Bryophytes are represented in the flora by sterile and fertile male gametophytes.

Polytrichaceae. The Raritan fossils are comparable to those described by Konopka *et al.* (1997) as *Eopolytrichum antiquum* (Polytrichaceae). The gametophytes consist of rosettes formed by overlapping bracts forming the perigonia, and among the bracts, there are numerous antheridia associate with paraphyses (figure 1.A).

Pteridophytes

Two families within the leptosporangiate ferns have been described from the Raritan flora.

Gleicheniaceae. Gandolfo *et al.* (1997) described the fossil fern *Boodlepteris turoniana* belonging to the family Gleicheniaceae. *Boodlepteris turoniana* is based on rhizomes, petioles, and sterile and fertile pinnules (figures 1.B-C). The fossils were included in a cladistic analysis, which suggested that they represented a single taxon and established that *Boodlepteris* is more closely related to the extant genus *Stromatopteris* than to the remaining extant members of the family.

Schizaeaceae. Ratcliffe *et al.* (1995) and Gandolfo *et al.* (2000b) also described fossil sorophores of *Lygodium* (figure 1.D). Although this new fossil species comprises only fertile pinnules, the characters preserved allowed the authors to determine its affinities with the family Schizaeaceae as well as with the genus *Lygodium*.

Gymnosperms

Gymnosperms are abundant in this assemblage. They are represented by shoots, leaves, reproductive structures (male and female cones and isolated sterile and fertile bracts). Penny (1947) studied the conifers of the Magothy/Raritan Formation and he identified the families Cupressaceae, Pinaceae, Taxodiaceae, Araucariaceae and Cheirolepidiaceae. So far, we have identified four of those families, although more detailed studies are being carried out to confirm their taxonomic placement at the generic level (Gandolfo *et al.*, 2000a).

Cheirolepidiaceae?. Fossils assignable to this extinct family are characterized by short, triangular hellicaly arranged scales. These specimens (figure 1.E) exhibit similarities with the genus *Brachyphyllum*.

Pinaceae. Gandolfo *et al.* (1996, in press) report the presence of dwarf shoots and isolated leaves of the extinct genus *Prepinus* (figures 1.G-H and 2.A) and the extant genus *Pinus* (figure 2.B) as well as a male cone with pollen *in situ* (figure 1.F) assignable to the family Pinaceae. The fossils have preserved external morphological and anatomical characters. Fossil wood, dwarf and spur shoots, leaves, pollen and reproductive structures assignable to the family Pinaceae have been described previously (for more references see Gandolfo *et al.*, in press).

Cupressaceae. This family is represented by portions of branches that bear thick, scale leaves (figures 2.C-D). The leaves have parallel margins, triangular apices and are keeled. They have whorled phyllotaxy (closely appressed to the stem), and they are placed in alternating whorls of two (decussate phyllotaxis) showing the characteristic pattern of the extant Cupressaceae (De Laubenfels, 1953).

Taxodiaceae. Other remains consist of leafy shoots, with spirally arranged leaves that are linear, have a decurrent base, and acute apex. The leaves are bifacially flattened (figures 2.E-F). These remains were placed taxonomically within this family because in profile view they show the typical S-shaped (falcate) form, spiral phyllotaxis, stomata unevenly distributed and for being amphistomatic, a combination of features diagnostic of the Taxodiaceae (De Laubenfels, 1953).

Angiosperms

The Raritan Formation is attractive because the dominant group in the vegetation is the angiosperms (Brenner, 1963). Five of the six subclasses of dicots and one subclass of monocots (*sensu* Cronquist, 1981) are represented at the locality. The Raritan sediments have yielded the oldest records for flowers of hamamelidaceous, capparealean, ericalean, and fagalean affinities and the oldest Clusiaceae as well as the oldest unequivocal monocot.

Magnoliidae. Crepet and Nixon (1994, 1998a) described *Detrusandra mystagoga* (figure 2.G) and *Cronquistiflora sayrevillensis* (figure 2.H) based on floral remains. These two species have magnoliid affinities. Flowers of *Perseanthus crossmanensis* within the Lauraceae (figure 2.I) and *Chloranthistemon crossmanensis* which represents stamens of Chloranthaceae (figure 3.A) have also been recovered from this locality (Herendeen *et al.*, 1993, 1994).

Hamamelididae. Three families belonging to this subclass are represented in this flora. Male and female inflorescences with affinities to transitional Hamamelidaceae (figure 3.B) were described by Crepet *et al.* (1992). The Hamamelidaceae subfamily Altingioideae is also represented by inflorescences, flowers and fruits (figure 3.E) (Zhou *et al.*, in press). Nixon and Crepet (1994) reported the presence of bisexual and staminate flowers that share characters within the modern flowers of Fagaceae (figures 3.C-D).

Dilleniidae. Gandolfo *et al.* (1998a) reported oldest record for flowers and pollen assignable to the order Capparales. *Dressiantha bicarpellata* show a combination of characters of the five families within the Capparales (figure 3.F). *Paleoclusia chevalieri* (figure 3.G), an extinct member of the family Clusiaceae, was described by Crepet and Nixon (1998b). Flowers with ericoid affinities are abundant in this flora. Nixon and Crepet (1993a, 1994) and Crepet (1996) reported two different taxa that share characters with the extant members of Ericaceae, *Paleoenkianthus sayrevillensis* (figure 3.H) and the taxa represented in plates 2 (figs. 4-10) and 3 (figs. 1-6) in Crepet (1996) (figures 4.A-B). Crepet (1996) presented also a taxon (plates 4, 5 and 6) that is, in general aspect, similar to those modern Pyrolaceae (figure 4.D). Another taxon related to the Ericales was described by Nixon *et al.* (in press) and Weeks *et al.* (1996) (figure 4.C).

Rosidae. Gandolfo *et al.* (1998b) described a series of flowers and fruits as representing the taxon *Tylerianthus crossmanensis* (figure 5.A), related to the family Hydrangeaceae. Although the authors placed *T. crossmanensis* within the family Hydrangeaceae based on the position of the fossil in a cladistic analysis, the fossil shares features with the family Saxifragaceae as well.

Caryophyllidae. Only one flower featuring characters of this subclass was found in the Old Crossman Clay Pit locality. Nixon and Crepet (1993b) described a flower bud (figure 5.B) with a suite of characters that suggest the possibility of a relationship with modern Caryophyllidae.

Alismatidae. Gandolfo *et al.* (1998e) reported the finding of fossil flowers of the saprophytic family Triuridaceae. Based on several cladistic analyses (Gandolfo *et al.*, 1998c, 1998d) this family is represented by at least 3 fossil species in the Crossman flora (figures 5.C-F).

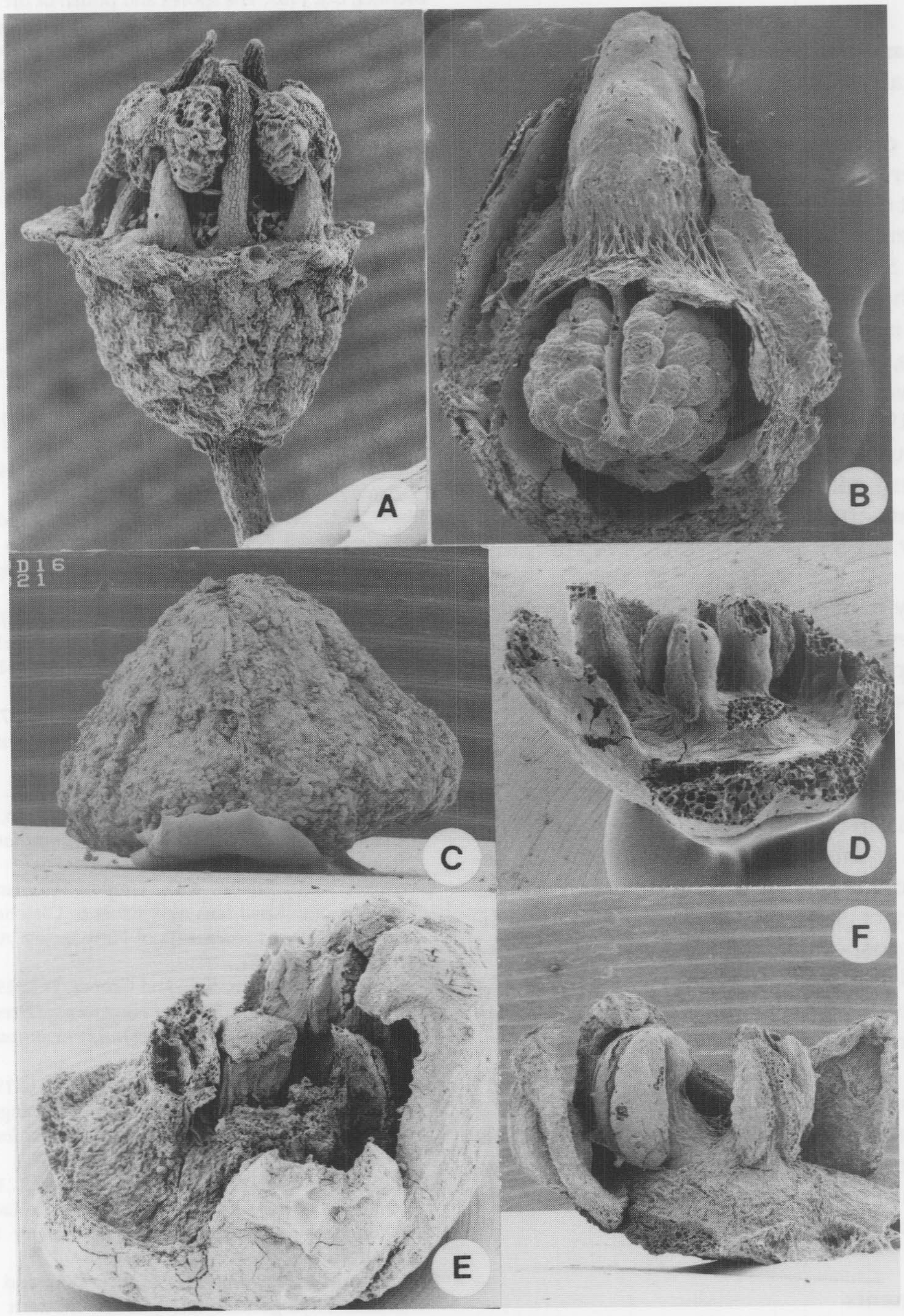

Figure 5. A, Rosidae ***Tylerianthus crossmanensis*** Gandolfo *et al.*, CUPC 1047 (70X). **B,** Caryophyllidae. Dissection of a caryophylloid bud, CUPC-Caryophyll#1 (84X). **C-F,** Alismatidae, Triuridaceae; **C,** side view of a bud, CUPC-Stub#321 (49X); **D,** Truiridaceae sp. 1, dissection of a flower showing the free stamens, CUPC-Stub#1115 (49X); **E,** Triuridaceae sp. 2, dissection of a flower showing the central pistillode, CUPC-Stub#599 (49X); **F,** Triuridaceae sp. 3, dissection of a flower showing the basally fused stamens, CUPC-Stub#903 (35X).

Paleoclimate

Berry (1916) postulated warm temperate rain forest environmental conditions for this formation based on megafossils; and although the angiosperm pollen assemblages confirmed this type of environment (Groot *et al.*, 1961), the presence of spores and megafossils of Schizaeaceae and Gleicheniaceae and the abundant pollen of Cycadaceae, Podocarpaceae, Araucariaceae and Pinaceae (Gray and Groot, 1966; Brenner, 1963) suggests that the paleoclimate was subtropical to tropical rather than temperate. Fossil flowers described from the Raritan sediments strengthen the likelihood presence of a subtropical to tropical climate for the Raritan Formation at the time of deposition.

Conclusions

The Turonian fossil angiosperms from New Jersey have dramatically changed our view of angiosperm history. These fossils reveal that the angiosperms were far more diverse early in their history than has previously been supposed (*e.g.*, Friis *et al.*, 1987). We now know that each extant subclass of angiosperms is already represented in the fossil record by ninety million years ago. Suites of advanced characters now associated with hymenopteran and lepidopteran pollinators including: bilateral symmetry, pollen in polyads, resins, fused corollas and others are represented in flowers of this age (Nixon and Crepet, 1993a, 1993b, 1994; Crepet, 1996; Crepet and Nixon, 1996, 1998b). Further, angiosperm families now associated with these pollinators are present in Turonian fossil sediments, providing evidence that certain modern, highly specific, plant pollinator relationships can be traced all the was back to the Turonian. Complimentary data on insect fossil history from the same locality reveal a strong correspondence between the history of pollinators and the angiosperms they pollinate (Crepet, 1996; Grimaldi, 1999). Preliminary comparison of Turonian angiosperm diversity with angiosperm diversity in early Tertiary sediments suggests that approximately half of modern angiosperm taxa evolved within that interval, and further, that the preponderance of these are now associated with derived insect pollinators. This observation suggests that we are only beginning to understand the full diversity of angiosperms that existed during the Cretaceous and that studies of floras of similar age from other parts of the world may reveal early histories of still other extant angiosperms families and genera. Finally the discovery of fossil Triuridaceae from Turonian deposits and the coordinated reappraisal of the previously reported record of monocot history is raising interesting questions about the timing of monocotyledon evolution and their interrelationships (Gandolfo *et al.*, 1998e, 1998c, 1998d).

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