

PALAEOENVIRONMENT OF LATE NEOGENE LACUSTRINE SEDIMENTS AT THE GRAY FOSSIL SITE, TENNESSEE, USA

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Abstract: A new palaeopalynological investigation was conducted on 15 samples from four test-pits at the Gray Fossil Site (Bear Pit, Elephant Pit, Test Pit 2-2010, and Rhino Pit). In total, 50 morpho-species of miospores (including five species of spores, eight species of gymnosperm pollen, and 37 species of angiosperm pollen) and 18 morpho-species of freshwater algal micro-remains were identified. One new morphological species, related to zygospores of the Zygnemataceae, *Stigmozygodites grayensis* sp. nov., is proposed. The assemblage of fossil algae recovered provides insights into the palaeoenvironmental conditions of the uppermost (125 cm) part of the Gray Fossil Site sedimentary cover, deposited after the formation of a number of sinkholes, and the fill of the palaeo-sinkholes. Most of the algae identified prefer meso- to eutrophic conditions and are characteristic of stagnant to slowly flowing shallow fresh water. Therefore, the lacustrine fossiliferous sediments at the Gray Fossil Site represent pond deposits. The palaeopalynological analysis revealed differences in the composition of the miospore and algal assemblages of the pits studied, suggesting that the Test Pit 2-2010, Bear, and Elephant pits are similar and may have been formed in the same pond, while the presence of a higher percentage of algae in the Rhino Pit may indicate sedimentation in a separate water body.

Key words: palaeopalynology, sinkhole, non-pollen palynomorphs (NPPs), freshwater algae, palaeoenvironment, Neogene, North America

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INTRODUCTION AND GEOLOGICAL SETTING

Located in Washington County in the northeastern corner of Tennessee in the USA, the Gray Fossil Site (GFS) represents a rare Neogene deposit in the eastern half of North America and still the only fossil site of this age in the southern Appalachians. It has yielded a diverse array of fossils of both animals and plants (e.g., Zobia *et al.*, 2011; Mead *et al.*, 2012; Ochoa *et al.*, 2012 and references cited herein), which have provided an unusual window for an insight into the conditions of palaeoecology, palaeoclimate, and palaeobiogeography in the southeast USA during the late Neogene, a critical transition period that witnessed dramatic changes in climate and vegetation (Cerling *et al.*, 1997; Zachos *et al.*, 2008). The site was initially interpreted as the fills of a palaeosinkhole within the Cambro-Ordovician Knox Group (Shunk *et al.*, 2006). Recently, the study of two palynological cores suggested that the site is composed of multiple sinkholes/sub-basins that could represent asynchronous events, preserving multiple basin-fill histo-

ries in sediments as old as early Palaeogene (Zobia *et al.*, 2011). On the basis of a high-resolution gravity study of the 4000 m² GFS area of the Cambro-Ordovician Knox Group carbonates, Whitelaw *et al.* (2008) detected the presence of 11 depo-centers (or sub-basins) that are aligned along northwest (joint) and northeast (strike) structural trends.

The GFS deposits extend laterally approximately 26,000 m² and consist of about 40 m of dark-coloured sediment of lacustrine origin (Shunk *et al.*, 2006). The sediment can be subdivided into three distinct facies, named graded, transition, and laminated, in ascending order (Shunk *et al.*, 2006). The overlying fossiliferous laminated facies is about 4 m thick, covered by subaerial alluvium and colluvium layers, more than 5 m thick (Shunk *et al.*, 2006). The animal and plant megafossils uncovered are all from the organic-rich, laminated sediments, which are biostratigraphically dated as between 7.0 and 4.5 Ma, i.e. the Hemphillian Land Mammal Age (latest Miocene to earliest Pliocene), on the

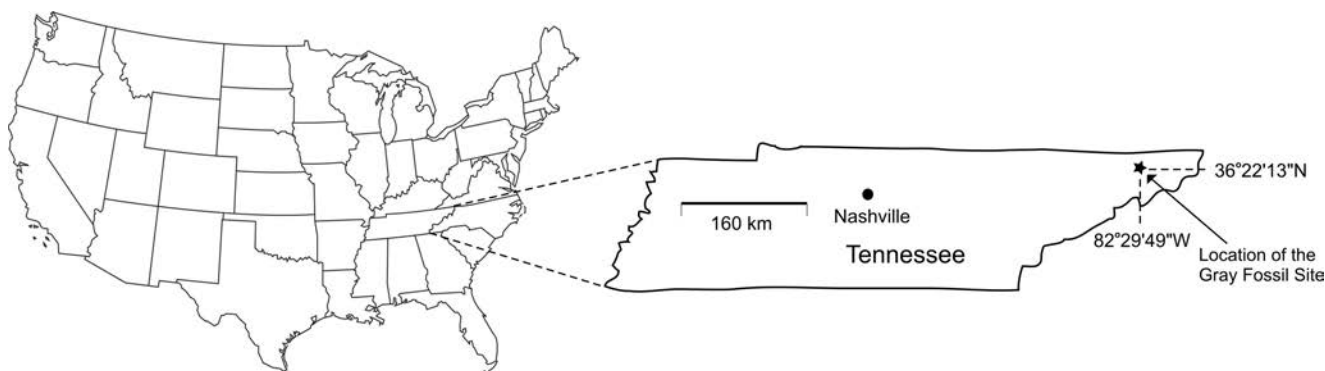


Fig. 1. Location of Gray Fossil Site (modified after Liu and Jacques, 2010)

basis of the presence of the rhino *Teleoceras* and short-faced bear *Plionarctos* (Wallace and Wang, 2004; Shunk *et al.*, 2006). The presence of laterally continuous laminated sediments that include well-recognized periodicities in rhythmites was further interpreted as representing annually generated varves that correspond to seasonal variations in sedimentation (Shunk *et al.*, 2009). The reconstructed Neogene vegetation at the GFS is a closed to open woodland setting with oak and hickory trees, mixed with diverse exotic climbing vines and shrubs in a warm temperate to subtropical climate (Gong *et al.*, 2010; Liu and Jacques, 2010; Ochoa *et al.*, 2012). The associated faunal taxa around and in the sinkholes are diverse and abundant and include tapirs, red pandas, Eurasian badgers, as well as helodermatid lizard, anurans, salamanders, turtles, alligators, snakes, birds, and others (Parmalee *et al.*, 2002; Wallace and Wang, 2004; Schubert and Wallace, 2006; Hulbert *et al.*, 2009; Board-

man and Schubert, 2011; Mead *et al.*, 2012). In addition, stable isotope analyses of bulk and serial samples of fossil tooth enamel from all ungulates at the GFS suggest minor differences in seasonal temperature and/or precipitation (DeSantis and Wallace, 2008). To date, no palaeolimnological research has been conducted on the characteristics of the pond waters in the palaeosinkholes.

This paper presents the results of a palaeopalynological investigation on samples collected from four fossiliferous test-pits within the GFS. The main attention is paid to the occurrence of miospores and the associated organic-walled algal microfossils in the samples studied. The investigation provides new data concerning the algal communities within the GFS Neogene water bodies and their surrounding vegetation, supplementing the knowledge on palaeoenvironment and palaeoecology of the site, as well as conditions within water bodies developed within Neogene sinkholes.

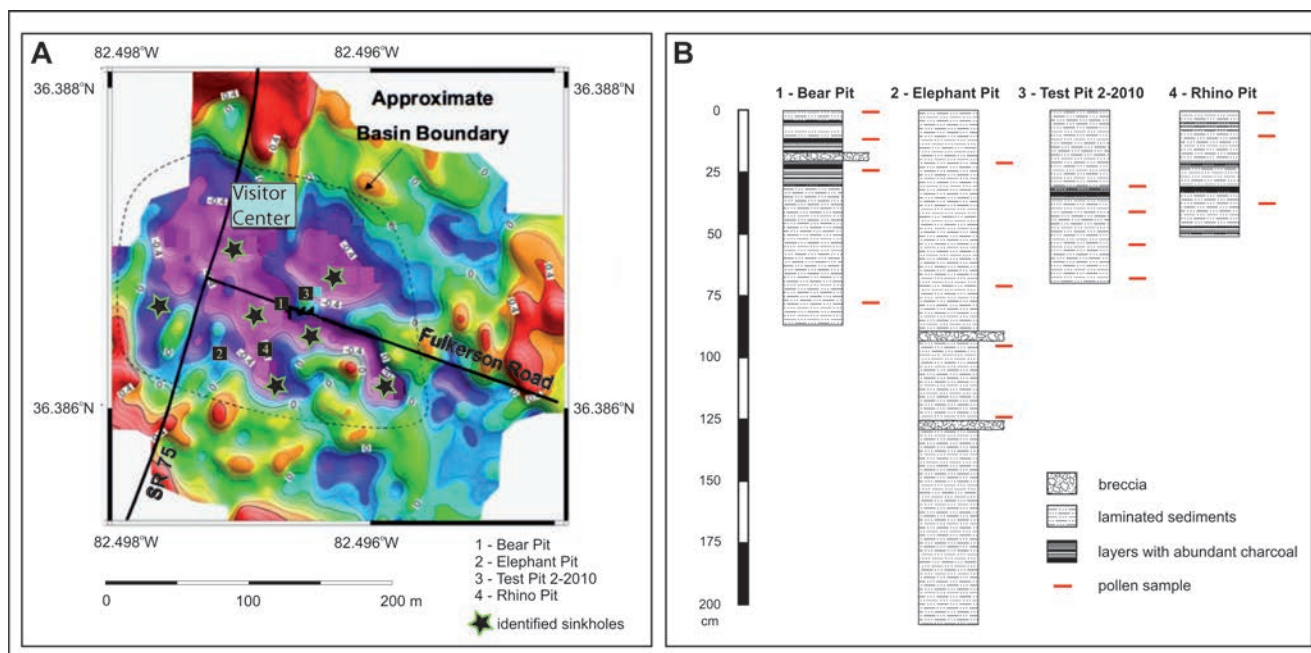


Fig. 2. A. Distribution of identified sinkholes on the gravimetric map of the Gray Fossil Site of Whitelaw *et al.* (2008), modified after Ochoa *et al.* (2012). B. Four profiles of test-pits sampled in the present study (modified after Ochoa *et al.*, 2012)

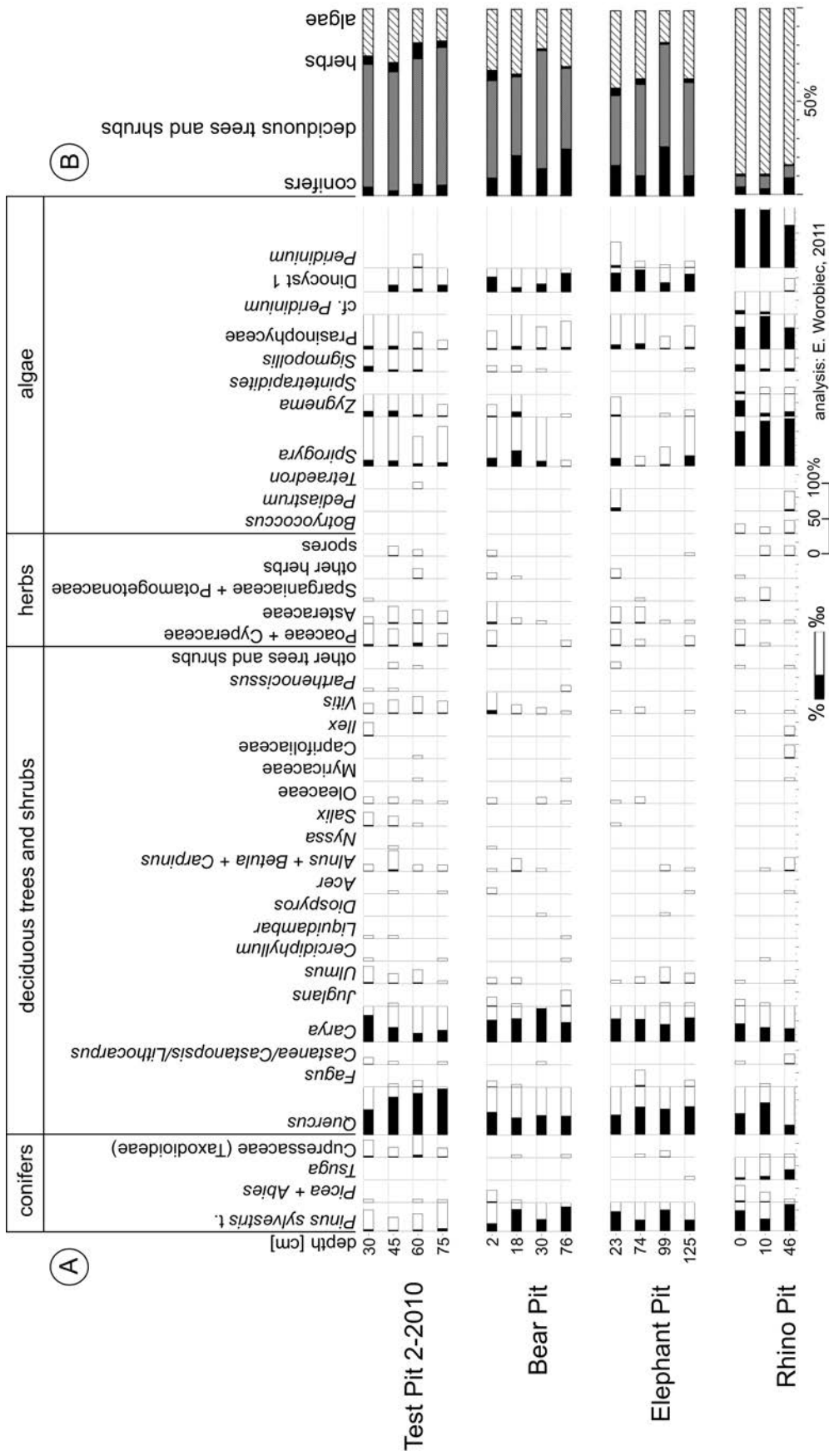


Fig. 3. Four percentage diagrams of selected miopore and algal taxa in the pits studied (Test Pit 2-2010, Bear Pit, Elephant Pit, and Rhino Pit), presented one under another. The pits are ordered according to their similarities (see text). **A.** Frequencies of certain miopore and algal taxa. Black bars show frequencies of miopores and algae (see right scale); white bars show frequencies $\times 10$. **B.** Percentages of major palynomorph groups

Table 1

Semi-quantitative distribution of recovered palynomorphs in the present study

TAXON	BOTANICAL AFFINITY	Test Pit 2-2010	Bear Pit	Elephant Pit	Rhino Pit
SPORES					
<i>Foveotriletes</i> sp.	unknown				*
<i>Laevigatosporites</i> sp.	Polypodiaceae, Davalliaceae	*			*
<i>Neogenisporis</i> sp.	Gleicheniaceae, Cyatheaceae				*
<i>Rudolphisporis major</i> (Stuchlik) Stuchlik	Anthocerotaceae	*	*		
<i>Stereisporites</i> sp.	<i>Sphagnum</i>	*			
other spores	Pteridaceae?, other ferns?	*	*	*	*
GYMNOSPERMS					
<i>Abiespollenites</i> sp.	Pinaceae: <i>Abies</i>		*		*
<i>Inaperturopollenites concedipites</i> (Wodehouse) Krutzsch	Cupressaceae: <i>Taxodium</i> , <i>Glyptostrobus</i>	**	*	*	*
<i>Inaperturopollenites dubius</i> (Potonié et Venitz) Thomson et Pflug	Cupressaceae: <i>Taxodium</i> , <i>Glyptostrobus</i>	*			
<i>Piceapollis</i> sp.	Pinaceae: <i>Picea</i>	*	*		*
<i>Pinuspollenites</i> spp. - <i>Pinus sylvestris</i> L. type	Pinaceae: <i>Pinus</i>	**	****	****	****
<i>Zonalapollenites</i> spp.	Pinaceae: <i>Tsuga</i>			*	**
ANGIOSPERMS					
<i>Aceripollenites</i> sp.	Sapindaceae: <i>Acer</i>	*	*	*	*
<i>Alnipollenites verus</i> Potonié	Betulaceae: <i>Alnus</i>	*	*	*	*
<i>Calystegiapollis</i> sp.	Convolvulaceae: <i>Calystegia</i>	*			
<i>Caprifoliipites</i> sp.	Caprifoliaceae	*			*
<i>Carpinipites carpinoides</i> (Pflug) Nagy	Betulaceae: <i>Carpinus</i>	*			*
<i>Caryapollenites simplex</i> (Potonié) Raatz	Juglandaceae: <i>Carya</i>	****	****	****	****
<i>Celtipollenites</i> sp.	Ulmaceae: <i>Celtis</i>			*	
<i>Cercidiphyllites minimireticulatus</i> (Trevisan) Ziemińska-Tworzydło	Cercidiphyllaceae: <i>Cercidiphyllum</i>	*	*		*
<i>Chenopodipollis stellatus</i> (Mamezar) Krutzsch	Amaranthaceae (incl. Chenopodiaceae)				*
<i>Corsinipollenites</i> sp.	Onagraceae	*		*	
<i>Cupuliferoipollenites oviformis</i> (Potonié) Potonié	Fagaceae: <i>Castanea</i> , <i>Castanopsis</i> , <i>Lithocarpus</i>	*	*		*
<i>Cyperaceapollis neogenicus</i> Krutzsch	Cyperaceae	**	*	*	*
<i>Diospyropollenites ovalis</i> Skawińska	Ebenaceae: <i>Diospyros</i>		*	*	
<i>Faguspollenites</i> sp.	Fagaceae: <i>Fagus</i>	*	*	*	*
<i>Graminidites</i> sp.	Poaceae: Pooideae	*	*	*	*
<i>Ilexpollenites margaritatus</i> (Potonié) Raatz	Aquifoliaceae: <i>Ilex</i>	*			*
<i>Intratrirporopollenites cordataeformis</i> (Wolff) Mai	Malvaceae: Tilioideae				*
<i>Juglanspollenites verus</i> Raatz	Juglandaceae: <i>Juglans cinerea</i> L. type	*	*	*	*
<i>Malvacearumpollis</i> sp.	Malvaceae: Malvoideae	*			
<i>Myricipites</i> sp.	Myricaceae	*	*		*
<i>Nyssapollenites</i> sp.	Cornaceae: <i>Nyssa</i>	*	*		
<i>Oleoidearumpollis</i> sp./ <i>Fraxinipollenites</i> sp.	Oleaceae: <i>Fraxinus</i> ?	*	*	*	
<i>Parthenopollenites marcodurensis</i> (Pflug et Thomson) Traverse	Vitaceae: e.g. <i>Parthenocissus</i>	*	*		
<i>Periporopollenites stigmaticus</i> (Potonié) Thomson et Pflug	Altingiaceae: <i>Liquidambar</i>	*	*		
<i>Potamogetonacidites</i> sp.	Potamogetonaceae: <i>Potamogeton</i>				*
<i>Quercopollenites</i> sp.	Fagaceae: <i>Quercus</i>	****	****	****	****
<i>Salixipollenites</i> sp.	Salicaceae: <i>Salix</i>	*		*	
<i>Sparganiaceapollenites microreticulatus</i> Grabowska et Ważyńska	Sparganiaceae	*		*	*
<i>Spinulaepollis arceuthobioides</i> Krutzsch	Santalaceae: <i>Arceuthobium</i>				*
<i>Thalictropipollis thalictroides</i> Stuchlik	Ranunculaceae: <i>Thalictrum</i>			*	
<i>Tricolporopollenites</i> sp.	Rosaceae?	*			*
<i>Trivestibulopollenites betuloides</i> Pflug	Betulaceae: <i>Betula</i>	*	*	*	*
<i>Tubulifloridites ambrosinae</i> Nagy	Asteraceae: <i>Ambrosia</i>	*	*	*	
<i>Tubulifloridites granulatus</i> Nagy	Asteraceae: Asteroideae	**	*	**	*

(* = 1–10, ** = 11–50, *** = 51–100, **** = more than 100). The pits are listed in order, according to their similarities. Miospores taxa and botanical affinity according to Stuchlik *et al.* (2001, 2002, 2009)

Table 1 continued

TAXON	BOTANICAL AFFINITY	Test Pit 2-2010	Bear Pit	Elephant Pit	Rhino Pit
ANGIOSPERMS					
<i>Ulmipollenites</i> sp.	Ulmaceae: <i>Ulmus</i>	**	*	**	*
<i>Umbelliferoipollenites</i> sp.	Apiaceae		*		
<i>Vitisipollenites</i> sp.	Vitaceae: <i>Vitis</i>	**	**	*	*
ALGAL MICROFOSSILS					
<i>Botryococcus braunii</i> Kützing	Chlorophyta: <i>Botryococcus</i>				*
Dinocyst 1	Dinophyceae	***	****	****	*
<i>Leiosphaeridia</i> sp.	Prasinophyceae	**	**	**	****
<i>Ovoidites elongatus</i> (Hunger) Krutzsch	Chlorophyta: Zygnemataceae: <i>Spirogyra</i>	**	***	***	****
<i>Ovoidites grandis</i> (Pocock) Zippi	Chlorophyta: Zygnemataceae: <i>Spirogyra</i>	*	*	*	**
<i>Ovoidites spriggii</i> (Cookson et Dettmann) Zippi	Chlorophyta: Zygnemataceae: <i>Spirogyra</i>	*	**	*	****
<i>Ovoidites</i> sp.	Chlorophyta: Zygnemataceae: <i>Spirogyra</i>	*			
<i>Pediastrum boryanum</i> (Turp.) Menegh.	Chlorophyta: <i>Pediastrum</i>				*
<i>Pediastrum integrum</i> Nägeli	Chlorophyta: <i>Pediastrum</i>			**	
<i>Peridinium</i> sp.	Dinophyceae: <i>Peridinium willei</i> or <i>P. volzii</i> ?	*		**	****
<i>Sigmopollis pseudosetarius</i> (Weyland et Pflug) Krutzsch et Pacltová	Chlorophyta?, other algae?	*	*		*
<i>Sigmopollis punctatus</i> Krutzsch et Pacltová	Chlorophyta?, other algae?	**	*	*	**
<i>Spintetrapidites quadriformis</i> Krutzsch et Pacltová	Chlorophyta				**
<i>Spintetrapidites</i> sp. 1	Chlorophyta?				*
<i>Stigmozygodites mediostigmus</i> Krutzsch et Pacltová	Chlorophyta: Zygnemataceae: <i>Zygnema</i>	**	**	*	***
<i>Stigmozygodites microfoveoloides</i> Krutzsch et Pacltová?	Chlorophyta: Zygnemataceae: <i>Zygnema</i> ?		*	*	**
<i>Stigmozygodites grayensis</i> E. Worobiec sp. nov.	Chlorophyta: Zygnemataceae: <i>Zygnema</i>	**	*		
<i>Tetraedron minimum</i> (A. Braun) Hansgirg	Chlorophyta: Chlorococcaceae: <i>Tetraedron</i>	*			
EPIPHYLLOUS FUNGI					
Microthyriales indiff.	Ascomycota: Microthyriales	*	***	**	*
Summary					
Number of pollen grains and spores counted		847	854	831	616
Number of algal microfossils counted		236	370	427	4351

(* = 1–10, ** = 11–50, *** = 51–100, **** = more than 100). The pits are listed in order, according to their similarities. Miospores taxa and botanical affinity according to Stuchlik *et al.* (2001, 2002, 2009)

MATERIAL AND METHODS

A total of 15 samples were collected from four test-pits (Bear Pit, Elephant Pit, Test Pit 2-2010, and Rhino Pit) at the GFS (Figs 1, 2). All the samples were taken from the fossiliferous laminated facies, as illustrated in Fig. 2B. Samples for palynomorph analysis were prepared by means of a modification of Erdtman's acetolysis method, using HF to remove the mineral matter (Faegri and Iversen, 1975; Moore *et al.*, 1991), and were rinsed in a 5- μ m filter cloth. The microscope slides were made, using glycerine jelly as a mounting medium and cover-slips 24 \times 24 mm. The rock samples, palynological residues, and slides are stored in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.

Five to seven slides were made from each sample. Depending on the abundance of palynomorphs, one to seven slides from each sample were examined in detail, counting more than 200 miospores plus all the organic-walled algal microfossils encountered. Data from all spore-pollen spectra were used to construct pollen diagrams (Fig. 3A). The percentages of particular taxa were calculated from the total

sum of pollen grains and spores. The percentages of algal micro-remains were computed separately in relation to the total sum of miospores plus algae, using the POLPAL computer program (Nalepka and Walanus, 2003). The relative proportions of palynomorph groups in all examined samples were calculated (Fig. 3B). Selected microphotographs of miospores and algal micro-remains are shown in Figures 4–6.

RESULTS OF SPORE-POLLEN AND ALGAL ANALYSES

All of the studied samples yielded well-preserved palynomorphs suitable for detailed analysis. The recorded spectra are rather poorly differentiated and a total of 50 morpho-species from 45 genera of miospores (including five species of spores, eight species of gymnosperm pollen, and 37 species of angiosperm pollen), as well as 18 morpho-species from 9 genera of algal micro-remains were identified (Figs 4–6, Tab. 1). Besides miospores and algae, moss and fungal spores, fragments of plant tissues (including mosses) and sporocarps of epiphyllous fungi were recorded.

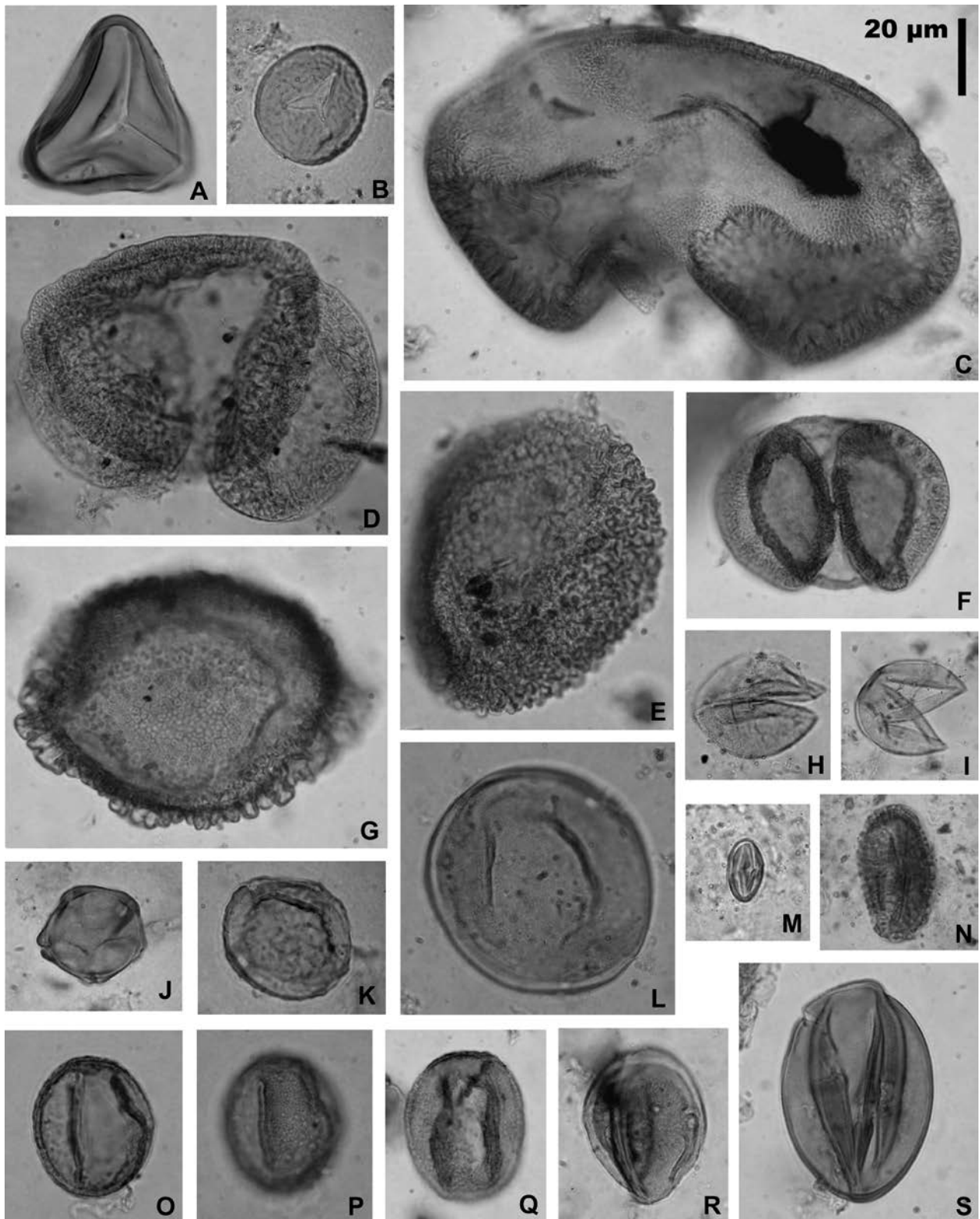


Fig. 4. Spores and pollen grains from Gray Fossil Site; one scale for all photographs. **A.** *Neogenisporis* sp., Rhino Pit, depth 46 cm, **B.** Pteridaceae?/*Salvinia*?, Test Pit 2-2010, depth 45 cm, **C.** *Piceapollis* sp., Rhino Pit, depth 10 cm, **D.** *Abiespollenites* sp., Rhino Pit, depth 0 cm, **E.** *Zonalapollenites verrucatus*, Rhino Pit, depth 46 cm, **F.** *Pinuspollenites labdacus*, Bear Pit, depth 30 cm, **G.** *Zonalapollenites maximus*, Rhino Pit, depth 10 cm, **H.** *Inaperturopollenites concedipites*, Test Pit 2-2010, depth 30 cm, **I.** *Inaperturopollenites dubius*, Test Pit 2-2010, depth 45 cm, **J.** *Alnipollenites verus*, Test Pit 2-2010, depth 45 cm, **K.** *Ulmipollenites* sp., Test Pit 2-2010, depth 45 cm, **L.** *Caryapollenites simplex*, Test Pit 2-2010, depth 45 cm, **M.** *Cupuliferoipollenites oviformis*, Test Pit 2-2010, depth 30 cm, **N.** *Ilexpollenites margaritatus*, Test Pit 2-2010, depth 30 cm, **O.** **P.** *Quercopollenites* sp. (same specimen, various foci), Bear Pit, depth 18 cm, **Q.** *Quercopollenites* sp., Elephant Pit, depth 74 cm, **R.** *Nyssapollenites* sp., Test Pit 2-2010, depth 45 cm, **S.** *Diospyrospollenites ovalis*, Bear Pit, depth 30 cm

In the material studied, the spores of ferns are very rare, as only few specimens were found. Gymnosperms are represented by Pinaceae, mainly *Pinus sylvestris* L. type (1.9–37.7% of pollen spectrum) and *Tsuga* (0–14.5%), as well as Cupressaceae (subfamily Taxodioideae – *Taxodium/Glyptostrobus* type, 0–3.9%). More frequent are pollen grains of angiosperms, with a strong domination of *Quercus* (14.0–64.7%) and *Carya* (12.6–48.0%). Frequencies of other angiosperm taxa, however, do not exceed 2.5–3.0%, except *Vitis* (up to 6.0%). Pollen grains of *Ulmus*, *Juglans*, *Fagus*, Oleaceae (*Fraxinus*?), *Alnus*, *Betula*, *Castanea/Castanopsis/Lithocarpus*, *Acer*, as well as herbs of Cyperaceae, Poaceae and Asteraceae (including *Ambrosia*) were also encountered regularly (Figs 4, 5).

Microfossils of freshwater algae are present in all samples studied (Figs 5, 6). Their frequencies vary from 17.1% up to 88.2%. Their composition varies among the pits, with peridinioid dinoflagellate cysts and microfossils of green algae being the most frequent. Chlorophyta are represented mainly by the morphological genera *Ovoidites* and *Stigmozygodites*, related to green algae of the family Zygnemataceae – most probably *Spirogyra* and *Zygnema*. Additionally, some microfossils related to Prasinophyceae (*Leiosphaeridia* sp.) as well as *Sigmopollis* occur. Most of the identified morpho-species of algal microfossils (except *Pediastrum* and *Tetraedron*) represent their resting cells.

Palynological analysis revealed differences in composition of miospore and algal assemblages in the different pits (Fig. 3, Tab. 1). The pollen assemblages from the Bear and Elephant pits are the most similar to each other (Fig. 3A). Frequencies of conifers, deciduous trees and shrubs, herbs, and algae in both pits are also similar (Fig. 3B). However, a subtle difference is seen between them in the composition of the algal assemblages, in which *Pediastrum integrum* and *Peridinium* are not present in the Bear Pit.

In the Test Pit 2-2010 miospores are the most diversified among the pits studied, represented by more than 37 morpho-species. When compared to other pits, Test Pit 2-2010 has the lowest frequency in *Pinus* (1.9–4.6%), but the highest in the Taxodioideae pollen (1.4–3.9%). Moreover, it contains the highest frequency in herbs, though less than 10%. Despite the absence of *Pediastrum integrum* and the presence of only four specimens of *Peridinium*, the overall algal assemblages in the Test Pit 2-2010 are similar to those recovered from the Bear and Elephant pits, suggesting that all three pits may represent the same pond (Fig. 2).

In the three pits mentioned above, the frequencies of algal micro-remains do not exceed 50% (16.3–28.4% in the Test Pit 2-2010, 21.4–34.4% in the Bear Pit, and 17.5–40.8% in the Elephant Pit). In contrast, samples from the Rhino Pit are strongly dominated by algal microfossils (81.6–88.2%, represented by 15 morpho-species), among which dinoflagellates (2500 specimens of *Peridinium* and only 4 specimens of *Dinocyst* 1), and Zygnemataceae (*Ovoidites* and *Stigmozygodites*) are the most dominant. Additionally, *Spintetrapidites*, *Botryococcus*, and *Pediastrum boryanum* occur only in the Rhino Pit. The presence of *Tsuga* pollen (3.4–14.5%) in the Rhino Pit is a peculiar feature of its miospore content. Pollen of *Tsuga* was not recorded from the Test Pit 2-2010 and the Bear Pit, and only

one specimen was recovered from the Elephant Pit. Therefore, it likely implies that the Rhino Pit may represent a completely different pond (Fig. 2).

NEW MORPHOLOGICAL SPECIES RELATED TO ZYGNEMATACEAE ZYGOSPORES

Phylum CHLOROPHYTA Pascher, 1914

Order ZYGNEMATALES Bessey, 1907

Family ZYGNEMATACEAE Kützing, 1843

Genus *Stigmozygodites* Krutzsch et Pacltová, 1990

Type species: *Stigmozygodites multistigmus* (Potonié 1931) Krutzsch et Pacltová 1990

Stigmozygodites grayensis E. Worobiec new species

Fig. 6A–C

Holotype: The Test Pit 2-2010, depth 45 cm, slide no. 5, position stage coordinates 41.5/83.5 (Fig. 6A, B). Paratype: The Bear Pit, depth 2 cm, slide no. 2, position stage coordinates 47.2/91.5 (Fig. 6C).

Etymology: The specific epithet *grayensis* refers to the Gray Fossil Site from where the microfossils were recorded.

Material: 18 specimens: 16 specimens from the Test Pit 2-2010 (eight specimens from the 30 cm depth sample, five specimens from the 45 cm depth sample, and three specimens from the 60 cm depth sample) as well as two specimens from the Bear Pit (one specimen from the 2 cm depth sample, and one specimen from the 18 cm depth sample).

Dimensions: 52–61 µm in diameter.

Diagnosis: Zygosporae spherical, circular in outline. Wall composed of several layers. The most external and internal layers smooth and thin. Middle layer smooth, densely covered with distinct foveae.

Description: Zygosporae spherical, circular in outline, about 52–61 µm in diameter. Wall composed of several layers. The most external and internal layers smooth and thin. Middle layer smooth, densely covered with distinct foveae (about 4.0–5.5 µm in diameter and 2.5–4.0 µm apart).

Remarks: Comparison: *Stigmozygodites grayensis* differs from the morphologically nearest species *S. zonestigmus* Krutzsch et Pacltová mainly by more layers in its wall, dense cover of regularly distributed distinct foveae, and bigger size. *S. grayensis* differs from *S. mediostigmus* Krutzsch et Pacltová mainly by its wall, which is composed of several layers.

Stigmozygodites grayensis distinctly differs from *Cinctiporipollis*? sp. recorded from the Paleocene–Eocene deposits at the GFS (Zobaa *et al.*, 2011), mainly in the spherical shape and its several-layer-wall structure. In contrast, *Cinctiporipollis*? sp. illustrated by Zobaa *et al.* (2011) is a flat form, closely resembling the zygosporae of another zygnemataceous genus *Debarya* (see “Type 214: *Debarya* sp.”, pl. 7, fig. 214a–d in van Geel *et al.*, 1989).

Botanical affinity: Morphologically these microfossils are closely related to the zygosporae of the recent genus *Zygnema*, especially to e.g., *Z. lamellatum* (Rao) Krieger (see p. 154, figs 604–606 in Kadłubowska, 1972; p. 180, fig. 255 in Kadłubowska, 1984), that occurs today in Asia (India) and Africa, and *Z. pawneanum* Taft (see p. 166, figs 678, 679 in Kadłubowska, 1972; p. 197, fig. 289 in Kadłubowska, 1984), that occurs today in USA (Oklahoma, Louisiana, Ohio, and Florida) and Africa. It should be noted that the morphology of these microfossils bears similarities to a variety of nematode eggs and cysts. It is difficult to establish unequivocally their association with algal microfossils (see McConnell and Zavada, 2013).

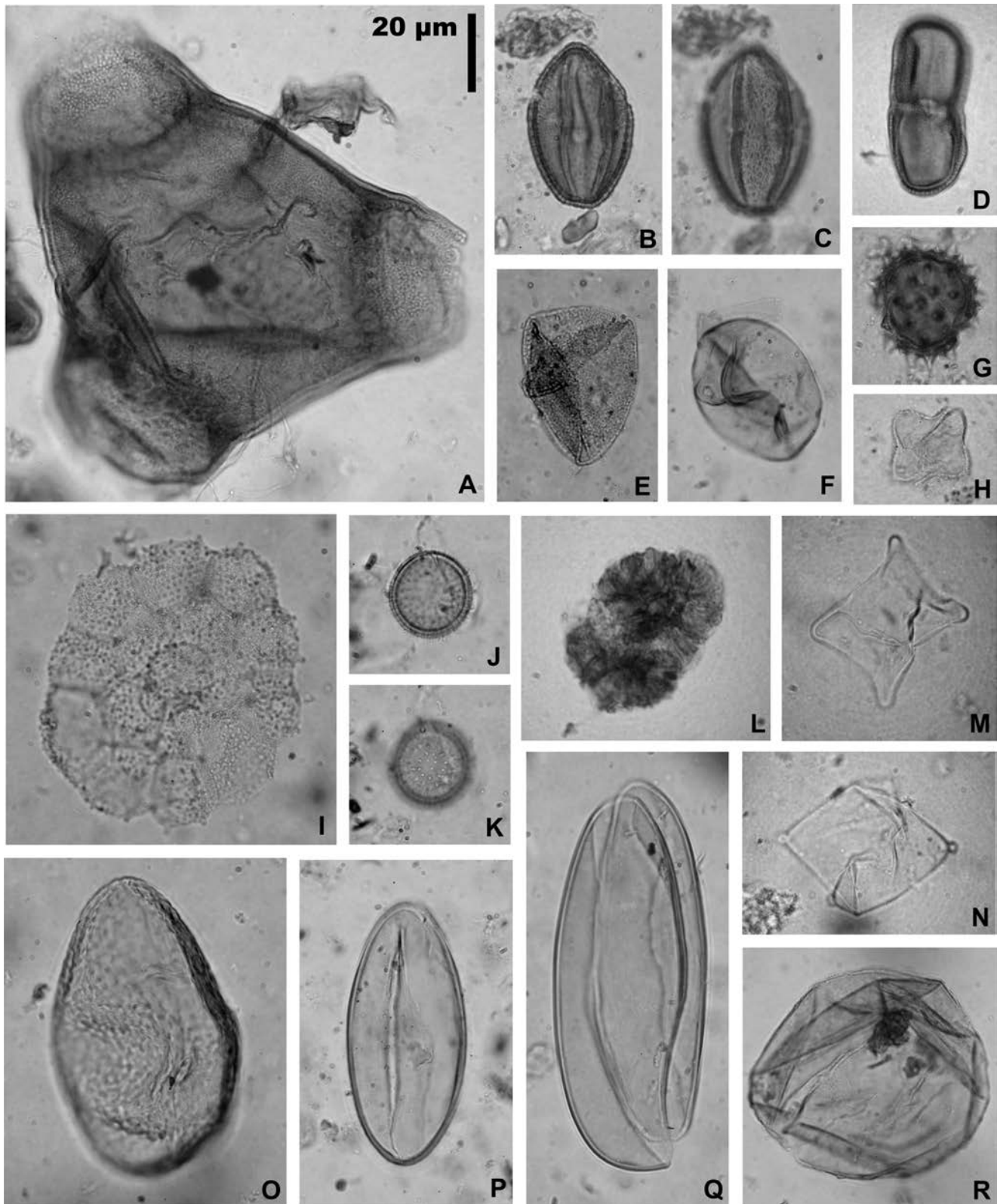


Fig. 5. Pollen grains and algal microfossils from Gray Fossil Site; one scale for all photographs. **A.** *Corsinipollenites* sp., Elephant Pit, depth 23 cm, **B, C.** *Parthenopollenites marcodurensis* (same specimen, various foci), Test Pit 2-2010, depth 45 cm, **D.** *Umbelliferopollenites* sp., Bear Pit, depth 18 cm, **E.** *Cyperaceapollis neogenicus*, Test Pit 2-2010, depth 60 cm, **F.** *Graminidites* sp., Test Pit 2-2010, depth 60 cm, **G.** *Tubulifloridites granulosus*, Test Pit 2-2010, depth 75 cm, **H.** *Tetradron minimum*, Test Pit 2-2010, depth 60 cm, **I.** *Pedastrum integrum*, Elephant Pit, depth 23 cm, **J, K.** *Sigmopollis pseudosetarius* (same specimen, various foci), Test Pit 2-2010, depth 45 cm, **L.** *Botryococcus braunii*, Rhino Pit, depth 46 cm, **M.** *Spintetrapidites quadriformis*, Rhino Pit, depth 0 cm, **N.** *Spintetrapidites* sp. 1, Rhino Pit, depth 0 cm, **O.** *Ovoidites* sp., Test Pit 2-2010, depth 45 cm, **P.** *Ovoidites elongatus*, Test Pit 2-2010, depth 30 cm, **Q.** *Ovoidites grandis*, Elephant Pit, depth 23 cm, **R.** *Leiosphaeridia* sp., Elephant Pit, depth 23 cm

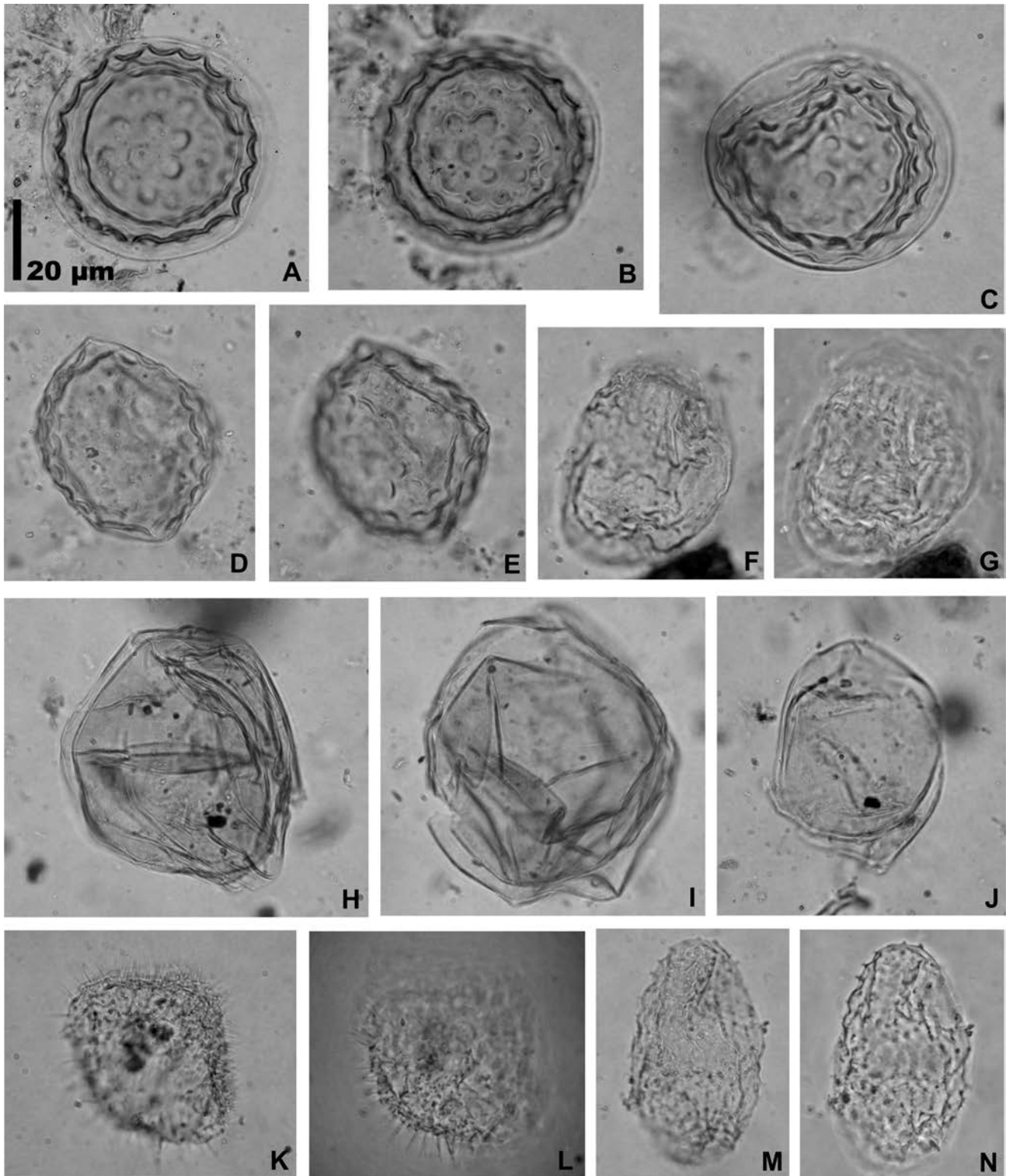


Fig. 6. Algal microfossils and other non-pollen palynomorphs from Gray Fossil Site; one scale for all photographs. **A, B.** *Stigmozygodites grayensis* sp. nov., holotype (same specimen, various foci), Test Pit 2-2010, depth 45 cm, **C.** *Stigmozygodites grayensis* sp. nov., paratype, Bear Pit, depth 2 cm, **D, E.** *Stigmozygodites mediostigmus* (same specimen, various foci), Test Pit 2-2010, depth 45 cm, **F, G.** *Stigmozygodites microfoveolatooides*? (same specimen, various foci), Rhino Pit, depth 0 cm, **H, I.** *Peridinium* sp., Rhino Pit, depth 0 cm, **J.** *Peridinium* sp., Rhino Pit, depth 10 cm, **K, L.** Dinocyst 1 (same specimen, various foci), Bear Pit, depth 18 cm, **M, N.** Parasite egg? (same specimen, various foci), Rhino Pit, depth 0 cm

Type locality: The Gray Fossil Site, Washington County, north-eastern Tennessee, USA (36°22'13"N, 82°29'49"W).

Type level: Near the top layer of the laminated facies.

Stratigraphic distribution: Late Hemphillian (7–4.5 Ma, latest Miocene to earliest Pliocene).

Deposition of types: Department of Palaeobotany, Władysław Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland. Slide collection Gray Fossil 3(5).

PALAEOCOMMUNITIES OF PLANTS AND ALGAE AND THEIR PALAEOENVIRONMENTAL SIGNIFICANCE

Pollen analysis has revealed a significant role of two genera – *Quercus* and *Carya*, as previously recognized (Ochoa *et al.*, 2012). These trees were the main components of an oak-hickory forest, with a small admixture of other plants, such as *Ulmus*, *Juglans*, *Pinus*, *Vitis*, among others. This provides partial support for DeSantis and Wallace (2008), who indicated the presence of a C₃ carbon fixation dominated ancient local flora, using stable isotope analyses of bulk and serial samples of fossil tooth enamel from all ungulates at the GFS. The palaeocommunity appears to be comparable to the modern oak-hickory forests in the eastern deciduous forest of North America (Braun, 1950). However, fossil seeds and endocarps from the same pits suggest that the palaeoflora surrounding the water bodies could not be floristically comparable to the modern oak-hickory forest, owing to the occurrence of numerous exotic plant genera with strong East Asian affinities, such as *Sinomenium*, *Vitis*, *Sargentodoxa*, *Illicium*, and *Carya* (Gong *et al.*, 2010; Liu and Jacques, 2010). The palaeovegetation as a whole in the region might not have been able to reach its climax as a dense forest, mainly because it was frequently under disturbance by abiotic factors, such as forest fires, drought, and large herbivores (Jiang and Liu, 2008; Shunk *et al.*, 2009; Zobaa *et al.*, 2011; Ochoa *et al.*, 2012). It is fairly clear that there is no modern vegetation analogous to the palaeoflora.

On the basis of sedimentological criteria, Shunk *et al.* (2006) interpreted the GFS sediments as recording storm flow influxes into a palaeolake. Multiple layers of silt and clay, with less common layers of larger clasts, attest to a predominantly low-energy aquatic environment, one with at least some through-flow of water (Mead *et al.*, 2012). The occurrence of freshwater algal micro-remains in the studied pits also supports the presence of water bodies developed in the pre-existing GFS karst sinkholes. However, there were no pollen grains of typical aquatic plants recorded. Moreover, pollen grains of herbs that could have surrounded the water bodies (e.g., Cyperaceae, Poaceae, and Asteraceae) are infrequent. Except for the discovery of some swampy plant macrofossils (*Taxodium* and *Nyssa*), aquatic plant remains at the GFS have not yet been recorded. The absence of aquatic plants at the GFS might be related to the low water quality, owing to the high primary productivity of algae (see discussion below and Dodson, 2005); while the rarity of swampy herbs could be attributed to a 'dense' clump plant cover surrounding the palaeopond/lake that made the development nearby of extensive herbaceous vegetation impossible.

Spirogyra and *Zygnema* (filamentous green algae from the family Zygnemataceae, Chlorophyta) and dinoflagellates (Peridinioids), as well as Prasinophyceae and *Sigmopollis*, were major components of the algal palaeocommunities recovered. Most of the identified algae prefer meso- to eutrophic conditions, and are characteristic of stagnant or slowly flowing shallow fresh water (van Geel, 1976; Worobiec, 2010, 2011, and literature cited therein). This appears to be consistent with the depositional environment in the palaeolake inferred by Shunk *et al.* (2009), who considered that the water body might represent a small lake with a poorly oxygenated bottom. Furthermore, most representatives of algae from the family Zygnemataceae occur in small stagnant bodies of water, in paddy fields, near the margins of lakes, sometimes also in moist soils or bogs (Kadłubowska 1972, 1984; van der Hoek *et al.*, 1995; Johnson, 2005; Naselli-Flores and Barone, 2009). These algae reproduce by means of various "spores", but in fossil material only zygospores (forming during conjugation) and probably aplano-spores can be preserved (Kadłubowska, 1972, 1984; van Geel and Grenfell, 1996). In temperate climatic conditions Zygnemataceae conjugate in shallow (often less than 0.5 m), relatively warm water. Dormant hypnozygotes may be exposed to desiccation (e.g., in summer) without damage to the living contents (van Geel, 2001). The presence of these resting cells in the pits studied suggests that the sinkhole pond water was shallow, permitting easy warming and possible periodical drying up. This scenario conforms to the warmer and drier climatic conditions deduced, quantitatively reconstructed by Liu and Zavada (2009) using plant fossils identified from the GFS. Another line of evidence for the warmer and drier palaeoclimate, prevailing in the region of eastern Tennessee during the late Neogene, is the common occurrence of charcoals all over the fossiliferous laminated layers, contributed by forest fires (Jiang and Liu, 2008; Liu and Zavada, 2009). On the other hand, the presence of epiphyllous fungi sporocarps in samples from all the pits studied (Tab. 1) and the palaeoclimatic reconstruction of the GFS fossil flora (Liu and Zavada, 2009) likely indicate a rather high mean annual precipitation (over 1000 mm) in the late Neogene. It would be most probable that the higher precipitation during the wettest months made possible the development of the Microthyriales epiphyllous fungi, whereas during the driest months the water bodies in the palaeosinkhole might have dried up and forest fires could have occurred.

Pediastrum algae are common phytoplankton of lakes and ponds and therefore are of significance in palaeoenvironmental reconstruction. For example, the extant *Pediastrum boryanum* generally occurs in eutrophic waters (Komárek and Jankovská, 2001), while *Pediastrum integrum* can be found mainly in oligotrophic and dystrophic water biotopes (Komárek and Jankovská, 2001). Interestingly, *P. boryanum* algae were recovered from the Rhino Pit, whereas *P. integrum* algae were encountered in the sample from the top of the Elephant Pit. This provides further evidence that the two pits were formed under a quite different environment, as pointed out above.

Generally, although the extant dinoflagellates are quite common in marine environments, freshwater dinoflagella-

tes are represented by about 220 recent species and can be valuable in determining water conditions (Bourrelly, 1970; Herrmann, 2010; McCarthy *et al.*, 2011). The absence of *Botryococcus* algae in the three pits and the sparse presence in the Rhino Pit, as well as the simultaneous abundance of freshwater dinoflagellates in all of the four pits (Fig. 3, Tab. 1), presumably indicate a depositional environment of alkaline and probably eutrophic water conditions (Herrmann, 2010). Additionally, the species of *Sigmopollis* (with unknown botanical affinity) are associated with stagnant or slowly moving shallow, mesotrophic to eutrophic, freshwater conditions (Pals *et al.*, 1980; van Geel *et al.*, 1983). Owing to the presence of diverse and abundant aquatic and water-loving animals at the GFS, for example over 80 extinct tapirs found at a single pit (Mead *et al.*, 2012), the relatively small pond easily could have become eutrophic. The alkaline conditions facilitated bone preservation, whereas under acidic conditions in ponds developed within other Neogene sinkholes, e.g. from Poland (Worobiec and Szulc, 2010; Szulc and Worobiec, 2012), animal macrofossils are not normally present.

CONCLUSIONS

The algal assemblages recovered from the four pits strongly suggest differences in deposition in separate water bodies (ponds), particularly between the Rhino Pit and the other three pits. This interpretation is well in accordance with the results of previous investigations of this site, supporting the occurrence of multiple sub-basins separated by elevated bedrock blocks (Clark *et al.*, 2005; Whitelaw *et al.*, 2008; Zobaa *et al.*, 2011). In addition, the distinct sporomorph assemblages from these pits, further reflects differences in the surrounding vegetation during the deposition of particular infills. Possibly these differences might have corresponded to various times of sedimentation. The pollen assemblages of the Bear and Elephant Pits show clear similarities in composition, suggesting most similar ages of these sinkhole infills.

The present study distinctly enriches the list of the Neogene sporomorph taxa recorded at this locality. The pollen flora from the Neogene sediments of the site includes trees and shrubs, such as *Pinus*, *Tsuga*, *Quercus*, *Carya*, *Ulmus*, *Betula*, *Fraxinus*, *Celtis*, *Alnus*, *Salix*, as well as herbs of *Ambrosia*-type, Cyperaceae, Gramineae, Apiaceae (named Umbelliferae), and Caryophyllaceae (Ochoa *et al.*, 2012). The present study confirms the occurrence of these taxa and reveals the presence of more than 30 other species.

The results also provide insight into the palaeoenvironmental conditions of the ponds, developed in the palaeosinkhole. They were shallow fresh ponds with meso- to eutrophic conditions, due to shallow water that easily might have been warmed, and the water bodies might have dried up periodically. In addition, alkaline conditions in these ponds would have helped to facilitate bone preservation.

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