

# New macro- and micropaleobotanical data on the Paleogene flora from the Hvoyna Basin (Central Rhodopes, Bulgaria)

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**Abstract.** The current study presents new macro- and micropaleobotanical data about the fossil flora from the Hvoyna Basin (Central Rhodopes). The studied material originates from the fine terrigenous sediments of a sandstone-argillite and conglomerate-argillite formation found in the area of the Orehovo (macroflora) and Hvoyna (microflora) villages. So far, four locations of the Paleogene flora have been known in the region, namely, Hvoyna, Malevo, Orehovo, and Pavelsko, but only four species were known from the sediments near village of Orehovo. Based on new research, 14 more species have been found in the area. Five of them – *Cassiophyllum ambiguum*, *Cyperacites chavannesii*, *Dalbergia rectinervis*, *Sapindus ungeri*, and *Typha latissima* - are new to the fossil flora of the Hvoyna Basin. The microflora from Hvoyna village comprises 23 fossil taxa and 14 of them are new to that site. Based on the floristic composition, geofloristic, biostratigraphic and paleoecological analyses have been carried out. The new data confirm the high endemism of the paleoflora of the Rhodopes and the significance of that region in plant speciation. Climate data reconstructed using the Coexistence Approach method show a subtropical or warm temperate condition with MAT 16.8 - 18.0°C and annual rainfall of ca. 1200-2300 mm. Stratigraphic interpretation of the paleoflora supports the assumed Late Eocene to Early Oligocene age.

**Key words:** Eocene, Hvoyna, Oligocene, Orehovo, paleoclimate, paleoecology, paleoflora, palynology

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## Introduction

The Eocene–Oligocene transition was a climate shift from a largely ice-free greenhouse world to icehouse climate, involving the first major glaciation of Antarctica and the global cooling occurring about 34 million

years ago (Ma) and lasting about 790 kyr (Hutchinson & al. 2021). A global shift in the deep-sea  $\delta^{18}\text{O}$  representing a combination of deep-ocean cooling and growth of the land ice volume had marked that change. Along with that, multiple independent terrestrial proxies indicated cooling, major changes in the global flora

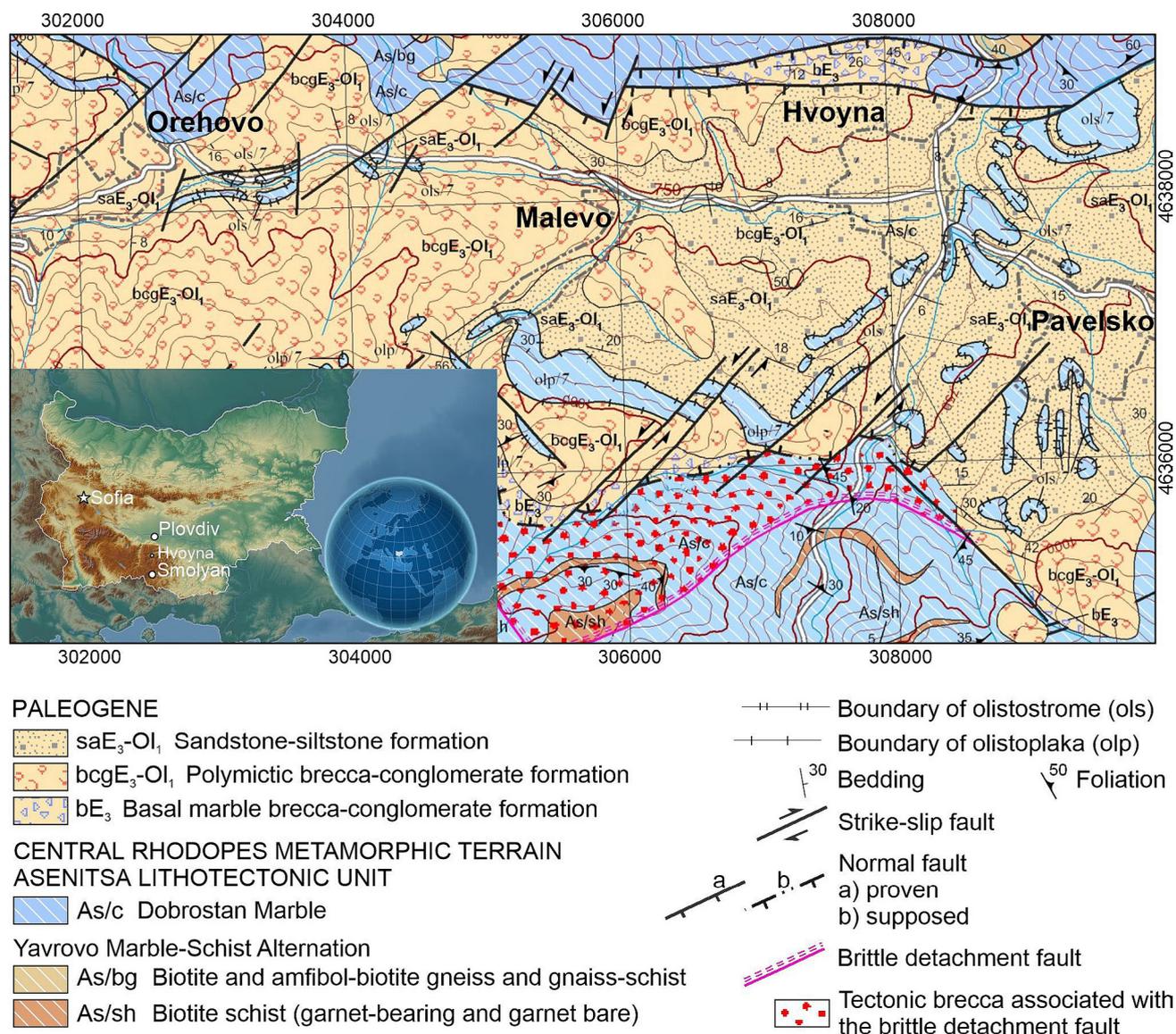


Fig. 1. Geological map of the Hvoyna Basin [redrawn from Sarov & al. (2008) with corrections].

record, and a shift towards colder-climate-adapted species marked by an increase of the arcto-tertiary and a decrease of the paleotropical plants. In this article, the authors have provided new evidence of the floristic and vegetation changes in the area of Hvoyna Depression (Central Rhodopes, Bulgaria) based on the analysis of macro- and microfloristic remains.

Paleogene flora of the Hvoyna Basin has been an object of thorough paleobotanical, paleoecological and biostratigraphic studies (Černjavská & al. 1988). Based on palynomorphs, 30 paleotaxa from 17 families were described, as well as 76 fossil species from 34

families, based on macroremains. The fossil material was collected from four locations in that Basin. They were situated close to Pavelsko, Hvoyna, Malevo, and Orehovo villages (Smolyan District). Subsequently, data on the flora in the Basin was published by Palamarev & Petkova (1990, 1994). Mention deserves the fact that the so far identified fossil species from the Orehovo location were only four: *Gleichenia rhodopaea* Palam. & Petkova, *Dryophyllum dewalquei* Sap. & Mar., *Eugenia splendens* Petr., G. Margit & M. Margit, and *Rhodomyrtophyllum sinuatum* (Bandulska) H. Walther. Particularly important was the first spe-

cies, so far identified only in the Hvoyna Basin. The new studies in the Orehovo region helped record 14 new species for the location, five of which were new for the paleoflora of the Hvoyna Basin. Along with the four already known taxa, the Orehovo paleoflora has expanded its composition up to 18 species.

Palynological studies have enhanced the data on the fossil flora from the region of Hvoyna village with 14 species, identified during the present studies.

## Geological setting

Paleogene section of the Hvoyna Depression (Fig. 1) is presented by sedimentary and volcanic rocks. During the last 1:50 000 mapping (Sarov & al. 2008), three formations and numerous large-scale olistostromes and olistoplasakas have been identified, taking into account also the lateral relationships (intertonging and gradations). Stratigraphic subdivision of the sedimentary section includes the following units (from bottom to top): a basal marble breccia-conglomerate formation, a polymictic breccia-conglomerate formation and a sandstone-siltstone formation. The sandstone-siltstone formation was built up by rhythmic alternations of sandstones, siltstones, argillites, minor marlstones, and clayey limestones.

Based on abundant micro- and macropaleobotanic material, Černjavska & al. (1988) indicated the Formation's age within the interval of Late Eocene to Early Oligocene. According to Kitanov in Kozhuharov & al. (1960), the sandstones and siltstones were no younger than the Late Eocene. Conventional dating in the available literature varied within the range of Middle Eocene (Vatsev 1988), Priabonian (Kozhuharova & Kozhuharov 1962) and Oligocene (Kozhuharov & al. 1994). Sarov & al. (2008) accepted the same Late Eocene–Early Oligocene age, which coincided with the dating of similar sections in the Central Rhodopes depressions of Arda, Smolyan and Izvor-Peshtera.

The formation crops out in the eastern part of the Depression, in the vicinity of Pavelsko and Hvoyna villages. Westwards of Hvoyna village, two wide strips have been formed, which narrow gradually also westwards. The southern strip is up to 1 km wide southwestwards of Malevo village, and the northern strip stretches along the Oreshtitsa River Valley. Small outcrops have been found eastwards and southwards of Orehovo village (Fig. 2). The formation grades vertically or laterally from the polymictic breccia-conglomerate formation or intertongues with it. The upper boundary of the formation represents a lateral and vertical gradation towards the uppermost tonguing of the polymictic breccia-conglomerates. It could be traced out westwards of Hvoyna village, on



Fig. 2. Orehovo flora-bearing sedimentary strata.

the left bank of river Oreshitsa, as well as north- and northwestwards of peak Lukanets. Eastwards of river Chepelarska, the sandstones and siltstones are cut by a present-day erosional surface. The microflora and macroflora in the present study originate from the fine terrigenous sediments of a sandstone-argillite and conglomerate-argillite formation found in the area of Hvoyna and Orehovo villages.

## Material and methods

Leaf imprints on a sedimentary sandstone rock have been studied near Orehovo village. They were 25 in number and were stored in the Paleobotanical Collection of IBER – BAS. The Angiosperm Leaf Morphology Scheme of Dilcher (1974) was used to determine the leaf imprints. Arrangement of the corresponding taxa in the article followed the scheme of the Angiosperm Phylogeny Group (APG 1998). The photographs were taken with a Panasonic DC-FZ82 digital camera.

Two samples of sandstone-argillite sediments near the Hvoyna village were subjected to pollen analysis following the standard technique for disintegration of Cenozoic sediments. One of the samples was barren, while the second provided enough palynomorphs for analysis. Pollen analysis was carried out with Olympus B52 microscope and photomicrographs were taken with an Olympus digital camera.

To quantify climate conditions, we use the Coexistence Approach (CA) method, which is frequently applied on all types of Cenozoic palaeofloras using the climatic requirements of the Nearest Living Relatives known for a fossil assemblage. More details on the method are given in Utescher & al. (2014). The Palaeoflora Database (Utescher & al. 2024) is used as source for climate requirements of fossil taxa.

## Results and discussion

The systematic section presented below contains data on each fossil species identified as a macrofossil; this

data features its geographic and stratigraphic distribution in the Rhodopean Paleogene, and its specificities and importance for the paleoflora of the Hvoyna Basin. The nearest living relative (NLR) is given respectively for each fossil species, as well as its ecological requirements. The composition of the macroflora is presented in Table 1. The microflora is analyzed in terms of the taxonomic composition, stratigraphic distribution, ecological requirements, and geofloristic elements. The results are summarized in Table 2.

Divisio *Pinophyta*

Family *Taxodiaceae* Warm.

*Doliosirobus* Marion

***Doliosirobus taxiformis*** (Sternb.) Kvaček

1833. *Cystoseirites taxiformis* Sternberg, p. 35, Pl. 18, Figs 1-3.

1966. *Cryptomeria* cf. *sternbergii* auct. non Gardner; Palamarev & Petkova, p. 51, Pl. 1, Fig. 2; Pl. 2, Figs 3-4, Pl. 4, Fig. 1; Figs-text 1a-b.

1971. *Doliosirobus taxiformis* (Sternb.) Kvaček, p. 118, Pl. 31, Figs 8-12, 15-16; Pl. 32, Figs 1-5.

1975. Palamarev & Petkova, p. 208, Pl. 4, Figs 1-3.

1988. Černjavská & al., p. 30, Pl. 1, Figs 5-6.

1991. Palamarev & Petkova, p. 26, Pl. 2, Figs 4-6; Pl. 3, Figs 1-4, Pl. 4, Figs 1,4-6.

1995. Palamarev & Staneva, p. 116.

1999a. Palamarev & al., p. 8, Pl. 8, Fig. 3.

**Material.** An imprint of a twig with leaves, No 12b (Pl. I, Fig. 1)

**Location and stratigraphic range.** A widely distributed species in the Rhodopean Paleogene found in more than 20 locations (Palamarev & al. 2005). It was also widely distributed in Europe during the Eocene, while the upper boundary of its stratigraphic range was the Upper Oligocene in East Europe (Kvaček 2002). In the Hvoyna Basin, it was so far known from the locations in Hvoyna and Pavelsko villages (Palamarev & Petkova 1991).

**Table 1.** Taxonomic composition of the Orehovo macroflora: location, stratigraphic distribution in the Paleogene of the Rhodopes, and their NLR belonging to the floristic kingdoms.

| No                    | Taxon                                  | Hvoyna Basin |        |          |        | Others Rhodopes localities | Stratigraphic range in the Rhodopes | Floristic Kingdom of NLR |
|-----------------------|----------------------------------------|--------------|--------|----------|--------|----------------------------|-------------------------------------|--------------------------|
|                       |                                        | Orehovo      | Hvoyna | Pavelsko | Malevo |                            |                                     |                          |
| <b>Gleicheniaceae</b> |                                        |              |        |          |        |                            |                                     |                          |
| 1                     | <i>Gleichenia rhodopaea</i>            | +            | +      | -        | -      | -                          | UEo-LOli                            | PT                       |
| <b>Taxodiaceae</b>    |                                        |              |        |          |        |                            |                                     |                          |
| 2                     | <i>Doliosrobos taxiformis</i> *        | 1            | +      | -        | +      | +                          | UEo-LOli                            | PT                       |
| <b>Pinaceae</b>       |                                        |              |        |          |        |                            |                                     |                          |
| 3                     | <i>Pinus palaeorhodopaensis</i> *      | 1            | -      | +        | -      | +                          | UEo-LOli                            | NT                       |
| <b>Lauraceae</b>      |                                        |              |        |          |        |                            |                                     |                          |
| 4                     | <i>Daphnogene cinnamomea</i> *         | 1            | -      | +        | -      | +                          | UEo-LOli                            | PT                       |
| 5                     | <i>Daphnogene lanceolata</i> *         | 1            | +      | +        | -      | +                          | UEo-LOli                            | PT                       |
| 6                     | <i>Neolitsea palaeosericea</i> *       | 3            | +      | -        | -      | +                          | UEo-LOli                            | PT                       |
| <b>Cyperaceae</b>     |                                        |              |        |          |        |                            |                                     |                          |
| 7                     | <i>Cyperacites chavannesii</i> *       | 1            | -      | -        | -      | +                          | UEo-LOli                            | CS                       |
| <b>Typhaceae</b>      |                                        |              |        |          |        |                            |                                     |                          |
| 8                     | <i>Typha latissima</i> *               | 2            | -      | -        | -      | +                          | UEo-LOli**                          | CS                       |
| <b>Fabaceae</b>       |                                        |              |        |          |        |                            |                                     |                          |
| 9                     | <i>Cassiophyllum ambiguum</i> *        | 1            | -      | -        | -      | +                          | UEo-Loli                            | PT-NT                    |
| 10                    | <i>Dalbergia rectinervis</i> *         | 1            | -      | -        | -      | +                          | UEo-LOli**                          | PT                       |
| <b>Fagaceae</b>       |                                        |              |        |          |        |                            |                                     |                          |
| 11                    | <i>Eotrigonobalanus furcinervis</i> *  | 7            | +      | +        | -      | +                          | UEo-LOli                            | PT                       |
| 12                    | <i>Lithocarpus palaeorhodopensis</i> * | 2            | -      | +        | -      | +                          | UEo-LOli                            | PT                       |
| 13                    | <i>Dryophyllum dewalquei</i>           | +            | +      | +        | -      | +                          | UEo-LOli                            | PT-NT                    |
| <b>Myrtaceae</b>      |                                        |              |        |          |        |                            |                                     |                          |
| 14                    | <i>Eugenia splendens</i>               | +            | -      | +        | -      | +                          | UEo-LOli                            | AU                       |
| 15                    | <i>Macclintockia basinervis</i> *      | 1            | +      | -        | -      | -                          | UEo-LOli                            | AU                       |
| 16                    | <i>Rhodomyrtophyllum sinuatum</i>      | +            | +      | +        | -      | +                          | UEo-LOli                            | NT-AU                    |
| <b>Sapindaceae</b>    |                                        |              |        |          |        |                            |                                     |                          |
| 17                    | <i>Sapindus ungeri</i> *               | 1            | -      | -        | -      | +                          | UEo-LOli                            | PT                       |
| <b>Sapotaceae</b>     |                                        |              |        |          |        |                            |                                     |                          |
| 18                    | <i>Bumelia minor</i> *                 | 2            | +      | +        | -      | +                          | UEo-LOli                            | NT                       |

**Legend.** \* - new taxa found in the Orehovo paleoflora; \*\* - stratigraphic range changes; **UEo** – Upper Eocene; **LOli** – Lower Oligocene; **UOli** – Upper Oligocene; **PT** – Paleotropical; **NT** – Neotropical; **AU** – Australian; **CS** – cosmopolitan.

**Comparison.** According to Palamarev & Petkova (1991), the genus *Doliosrobos* was ancient and combined the characteristics of two monotypic contemporary genera – *Cryptomeria* and *Taiwania* - which represented the family *Cupressaceae*. *Cryptomeria japonica* (L. f.) D. Don grows in forests on

deep, well-drained soils, subject to warm, moist conditions. It is intolerant of poor soils and cold, and of a drier climate ([http://www.efloras.org/flora-taxon.aspx?flora\\_id=2&taxon\\_id=200005392](http://www.efloras.org/flora-taxon.aspx?flora_id=2&taxon_id=200005392)). *Taiwania cryptomerioides* Hayata is native to Southeast Asia, growing in the mountains of Cen-

**Table 2.** Taxonomic composition of the microflora from the Hvoyna Basin, Hvoyna section: botanical affinity, plant community elements, geofloristic elements, stratigraphic range of the taxa. The new species to the microflora of Hvoyna are marked with an asterisk (\*).

| No                                      | Taxon                                                                                            | Botanical affinity                                                                   | Plant community's element                 | Geofloristic element | Stratigraphic range |
|-----------------------------------------|--------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|-------------------------------------------|----------------------|---------------------|
| <b>Osmundaceae</b>                      |                                                                                                  |                                                                                      |                                           |                      |                     |
| 1                                       | <i>Echinatisporis</i> cf. <i>cycloides</i> Krutzsch*                                             | <i>Selaginella</i>                                                                   | swamp forest                              | P/A                  | Oli-Mio             |
| <b>Gleicheniaceae</b>                   |                                                                                                  |                                                                                      |                                           |                      |                     |
| 2                                       | <i>Gleicheniidites</i> fsp. *                                                                    | <i>Gleicheniaceae</i>                                                                | mesophytic forest                         | P1                   | Eo-Mio              |
| <b>Lygodiaceae</b>                      |                                                                                                  |                                                                                      |                                           |                      |                     |
| 3                                       | <i>Trilites multivalatus</i> (Pfl.) Krutzsch*                                                    | cf. <i>Lygodium</i>                                                                  | mesophytic forest                         | P1                   | LOli-Mio            |
| <b>Schizaeaceae</b>                     |                                                                                                  |                                                                                      |                                           |                      |                     |
| 4                                       | <i>Cicatricosisporites chatensis</i> Krutzsch subsp. <i>chatensis</i>                            | <i>Schizaeaceae</i> ; cf. <i>Anemia</i>                                              | mesophytic forest                         | P2                   | UEo-Mio             |
| 5                                       | <i>Ischyosporites asolidus</i> (Krutzsch) Krutzsch                                               | <i>Schizaeaceae</i>                                                                  | mesophytic forest                         | P2                   | Eo-Oli              |
| <b>Pteridaceae</b>                      |                                                                                                  |                                                                                      |                                           |                      |                     |
| 6                                       | <i>Polypodiaceoisporites gracillimus</i> subsp. <i>granoverrucatus</i> Krutzsch                  | <i>Pteridaceae</i>                                                                   | mesophytic forest                         | P                    | Oli-Mio             |
| <b>Thelypteridaceae</b>                 |                                                                                                  |                                                                                      |                                           |                      |                     |
| 7                                       | <i>Laevigatosporites</i> cf. <i>discordatus</i> Pfl.*                                            | <i>Thelypteridaceae</i>                                                              | swamp forest                              | A                    | Oli-Pli             |
| <b>Davaliaceae</b>                      |                                                                                                  |                                                                                      |                                           |                      |                     |
| 8                                       | <i>Verrucatosporites pseudoalienus</i> Krutzsch*                                                 | <i>Davaliaceae</i>                                                                   | mesophytic forest                         | P2                   | Oli-Pli             |
| <b>Polypodiaceae / Dennstaedtiaceae</b> |                                                                                                  |                                                                                      |                                           |                      |                     |
| 9                                       | <i>Verrucatosporites</i> cf. <i>favus</i> (Pot.) Th. & Pfl.                                      | <i>Polypodiaceae</i> / <i>Dennstaedtiaceae</i>                                       | mesophytic forest                         | P2                   | Oli-Pli             |
| <b>Taxodiaceae</b>                      |                                                                                                  |                                                                                      |                                           |                      |                     |
| 10                                      | <i>Inaperturopollenites hiatus</i> Th. & Pfl.*                                                   | <i>Taxodiaceae</i>                                                                   | swamp forest                              | A1                   | Eo-Pli              |
| 11                                      | <i>Inaperturopollenites</i> fsp.                                                                 | cf. <i>Glyptostrobus</i>                                                             | swamp forest                              | A1                   | Eo-Pli              |
| <b>Pinaceae</b>                         |                                                                                                  |                                                                                      |                                           |                      |                     |
| 12                                      | <i>Pityosporites microalatus</i> (Pot.) Th. & Pfl.                                               | cf. <i>Cathaya</i>                                                                   | coniferous forest                         | P                    | Eo-Pli              |
| <b>Podocarpaceae</b>                    |                                                                                                  |                                                                                      |                                           |                      |                     |
| 13                                      | <i>Podocarpidites libelus</i> (Pot.) Krutzsch*                                                   | <i>Podocarpaceae</i> ,<br><i>Podocarpus</i>                                          | coniferous forest                         | P                    | Eo-Mio              |
| <b>Poaceae</b>                          |                                                                                                  |                                                                                      |                                           |                      |                     |
| 14                                      | cf. <i>Graminidites</i> fsp.*                                                                    | cf. <i>Bambusoideae</i> / <i>Arundinarieae</i>                                       | mesophytic to wet forest, open grasslands | P/A                  | Eo-Pli              |
| <b>Sparganiaceae</b>                    |                                                                                                  |                                                                                      |                                           |                      |                     |
| 15                                      | <i>Sparganiaceapollenites</i> fsp.*                                                              | <i>Sparganiaceae</i>                                                                 | aquatic communities                       | A                    | UEo-Pli             |
| <b>Arecaceae</b>                        |                                                                                                  |                                                                                      |                                           |                      |                     |
| 16                                      | <i>Monocolpopollenites</i> fsp.*                                                                 | <i>Arecaceae</i>                                                                     | mesophytic forest                         | P                    | Eo-Mio              |
| <b>Fagaceae</b>                         |                                                                                                  |                                                                                      |                                           |                      |                     |
| 17                                      | <i>Tricolporopollenites (Castaneoideaeipollis) cingulum</i> ssp. <i>fuscus</i> (Pot.) Th. & Pfl. | <i>Castanea</i> ,<br><i>Castanopsis</i> ,<br><i>Passania</i> ,<br><i>Lithocarpus</i> | mesophytic forest                         | P2                   | Eo-Mio              |
| <b>Juglandaceae</b>                     |                                                                                                  |                                                                                      |                                           |                      |                     |
| 18                                      | <i>Caryapollenites</i> cf. <i>circulus</i> (Pfl.) Krutzsch                                       | <i>Carya</i> sp.                                                                     | riparian forest                           | P2/A1                | UEo-LOli            |
| 19                                      | <i>Momipites (Engelhardtioipollenites) quietus</i> (Pot.) Nichols*                               | <i>Engelhardtia</i> sp.                                                              | mesophytic forest                         | P1                   | UEo-Mio             |

| No                   | Taxon                                                   | Botanical affinity    | Plant community's element | Geofloristic element | Stratigraphic range |
|----------------------|---------------------------------------------------------|-----------------------|---------------------------|----------------------|---------------------|
| 20                   | <i>Pterocaryapollenites</i> fsp.*                       | cf. <i>Pterocarya</i> | riparian forest           | A1                   | Oli-Pli             |
| 21                   | <i>Plicapollis pseudoexcelsus</i> (Krutzsch) Krutzsch * | <i>Juglandaceae</i>   | mesophytic forest         | P1                   | UEo-MMio            |
| <b>Bombacaceae</b>   |                                                         |                       |                           |                      |                     |
| 22                   | <i>Bombacidites</i> cf. <i>palaeogenicus</i> Krutzsch*  | <i>Bombacaceae</i>    | mesophytic forest         | P1                   | UEo                 |
| <b>Indeterminate</b> |                                                         |                       |                           |                      |                     |
| 23                   | <i>Tricolporopollenites</i> fsp.                        | unknoun               | -                         | -                    | -                   |

**Legend.** Geofloristic elements: **P** - generally paleotropical element; **P1** - tropical element; **P2** - subtropical element; **A** - generally arctotertiary element; **A1** - warm temperate element; **A2** - cool temperate element.

Stratigraphic range: **Eo** - Eocene; **UEo** - Upper Eocene; **LOli** - Lower Oligocene; **UOli** - Upper Oligocene; **Oli** - Oligocene; **Mio** - Miocene; **MMio** - Middle Miocene; **Pli** - Pliocene.

tral Taiwan, and locally, in coniferous, broad-leaved or mixed evergreen valley forests, in warm or warm temperate regions with high summer and autumn rainfalls, but drier winters in SW China (Guizhou, Hubei, Sichuan, Yunnan, Tibet) and the adjoining Myanmar, and in North Vietnam; 500-2800 m a.s.l. ([http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=200005401](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=200005401)).

Family *Pinaceae* Lindl.

Genus *Pinus* L.

***Pinus palaeorhodopaensis*** Palam.

1991. *Pinus palaeorhodopaensis* Palam. in Palamarev & Petkova, p. 24, Pl. 1, Figs 2, 5; Pl. 2, Figs 2-3.

1995. Palamarev & Staneva, p. 116.

2001. Palamarev & al., p. 280, Pl. 2, Fig. 5.

**Material.** An imprint of a brachyblast, with four needle-shaped leaves, No 8 (Pl. I, Fig. 2)

**Location and stratigraphic range.** That species is endemic to the Rhodope Mts. It has been so far known from the locations of Dolno Fatovo, Borino and Polkovnik Serafimovo (Palamarev & al. 2005). Its stratigraphic area is Upper Eocene - Lower Oligocene.

**Comparison.** Palamarev & Petkova (1991) mentioned as probable NLR to it the recent species of *P. wallichiana* A.B. Jacks, *P. torreyana* Carr., *P. lawso-*

*nii* Roegl., and *P. dalatensis* De Ferré. Of those four species, only the leaves of *P. lawsonii* were in bundles of 3-4(-5) (Farjon & Styles 1997). Considering that in the presently studied material there were four leaves in the brachyblast, the authors have assumed that particular species, distributed only in S Mexico, was best suited as NLR. *P. lawsonii* occurs in forests and woodlands, at 1300-2600 m a.s.l., in warm-temperate to temperate climate, with 600-1500 mm of annual precipitation and a November-to-May dry season. It grows in sites with sandy shallow soil (Farjon & Styles 1997). Its cold hardiness limit varied between -1°C and +4.4°C (Bannister & Neuner 2001).

Divisio *Magnoliophyta*

Family *Lauraceae* Juss.

Genus *Daphnogene* Unger

***Daphnogene cinnamomea*** (Rossm.) Knobloch

1840. *Phyllites cinnamomeus* Rossmässler, p. 23, Pl. 1, Figs 1-8.

1964. *Cinnamomophyllum cinnamomeum* (Rossm.) Kol.; Kolakovski, p. 100, Pl. 38, Fig. 5.

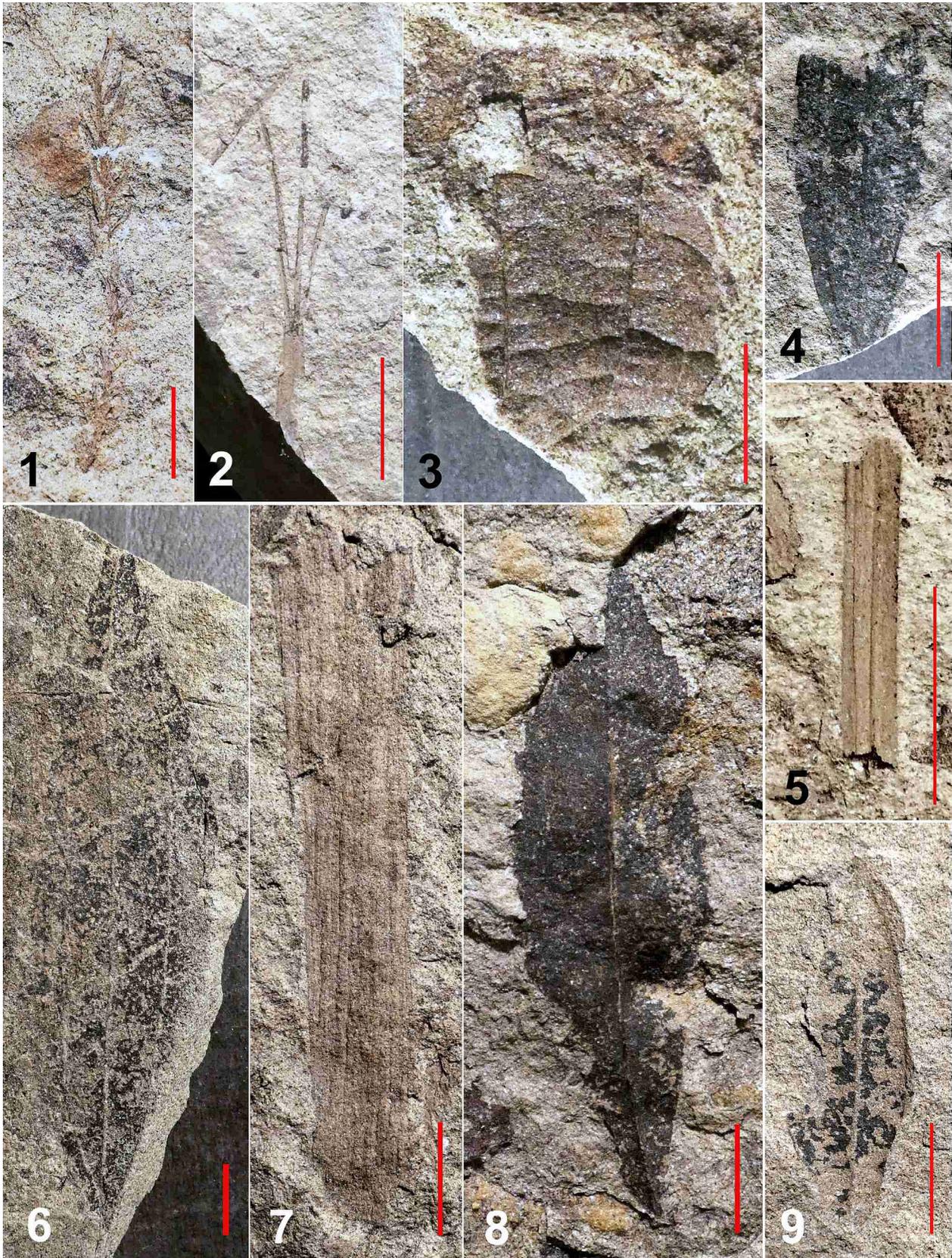
1968. *Daphnogene cinnamomea* (Rossm.) Knobloch, p. 139, Pl. 2, Fig. 6, Pl. 4, Fig. 2.

1995. Palamarev & Staneva, p. 117.

1999a. Palamarev & al., p. 9, Pl. 1, Fig. 6; Pl. 2, Figs 1-2.

1999b. Palamarev & al., p. 30.

2001. Palamarev & al., p. 281, Pl. 2, Fig. 7.



**Plate I.** Photographs of macrofossil material

1. *Doliosrobis taxiformis*; 2. *Pinus palaeorhodopaensis*; 3. *Daphnogene cinnamomea*; 4. *D. lanceolata*; 5. *Cyperacites chavannesii*; 6. *Neolitsea palaeosericea*; 7. *Typha latissima*; 8. *Eotrigonobalanus furcinervis*; 9. *Cassiophyllum ambiguum* (measuring bar – 1 cm).

**Material.** Part of a leaf imprint, No 19 (Pl. I, Fig. 3)

**Location and stratigraphic range.** On the territory of Bulgaria, this species occurred only in the Rhodopes (in Pavelsko, Polkovnik Serafimovo, Borino, Boukovo, and Eleshnitsa paleofloras) (Palamarev & al. 2005). *Daphnogene cinnamomea* is a characteristic species for Eocene floras in Europe, however, on the territory of Eastern Rhodopes it was identified only on the sedimental rocks of the Valche Pole Molasse formation, dated as Late Oligocene – Early Miocene (Bozukov & al. 2008). Kolakovski (1964) registered the species in the Upper Miocene of Georgia, where the upper stratigraphic boundary of the species probably lay.

**Comparison.** That fossil species has morphological features similar to the recent *Cinnamomum verum* J. Presl, distributed in Sri Lanka. The species can be found at elevations up to 2000 m. It requires a warm and wet climate, with average temperatures of about 27°C, and no heat or cold extremes. Rainfalls shall amount to 2000-2500 mm and must be well-distributed across the year. Although there can be months with less precipitation, no prolonged dry season is tolerated and rain is expected to fall about 150 days per year. The species prefers a fertile, sandy, moisture-retentive but easily drained soil, in full sun or partial shade (<https://pfaf.org/user/Plant.aspx?LatinName=Cinnamomum+verum>).

#### *Daphnogene lanceolata* Unger

1850a. *Daphnogene lanceolata* Unger, p. 167, Pl. 37, Figs 1-7.

1932. *Cinnamomum lanceolatum* (Unger) Heer; Konjaroff, p. 54, Pl. 22, Fig. 2; p. 98, Pl. 27, Figs 10-11; Pl. 28, Fig. 1; p. 129, Pl. 43, Fig. 3; p. 222, Pl. 64, Figs 2-4; p. 239, Pl. 72, Figs 2-3.

1988. *Daphnogene lanceolata* Unger; Černjavská & al., p. 3, Pl. 3, Fig. 1.

1995. Palamarev & Staneva, p. 117, Pl. 1, Fig. 2.

1998. Palamarev & al., pp. 14-15.

1998. Bozukov, p. 5, Pl. 4, Fig. 3.

1999a. Palamarev & al., p. 9, Pl. 2, Figs 7-8.

1999b. Palamarev & al., p. 31, Pl. 1, Fig. 5.

2001. Palamarev & al., p. 281, Pl. 1, Fig. 1.

2008. Bozukov & al., p. 174, Pl. 1, Fig. 6.

**Material.** A leaf imprint No10 (Pl. 1, Fig. 4)

**Location and stratigraphic range.** A widely distributed species in Bulgaria's Cenozoic flora, occurring in more than 15 locations and with a very wide stratigraphic range from Upper Eocene to Lower Pliocene (Palamarev & al. 2005). In the Rhodopean Paleogene, it has been known from eight locations, with a stratigraphic range of Upper Eocene – Upper Oligocene.

**Comparison.** That fossil species has morphological features similar to the recent *Cinnamomum tenuifolium* (Makino) Sugim. (= *C. pedunculatum* Nees, *C. japonicum* Sieb.) distributed in SE China, S Japan, S Korea, and Taiwan. Its typical habitat is in lowland evergreen forests, between 300 and 1000 m a.s.l., often near the coastline (<https://www.treesandshrubsonline.org/articles/cinnamomum/cinnamomum-japonicum/>).

Genus *Neolitsea* (Benth.) Merrill

*Neolitsea palaeosericea* Takht.

1963. *Neolitsea palaeosericea* Takhtajan, p. 202, Pl. 6, Figs 5-7.

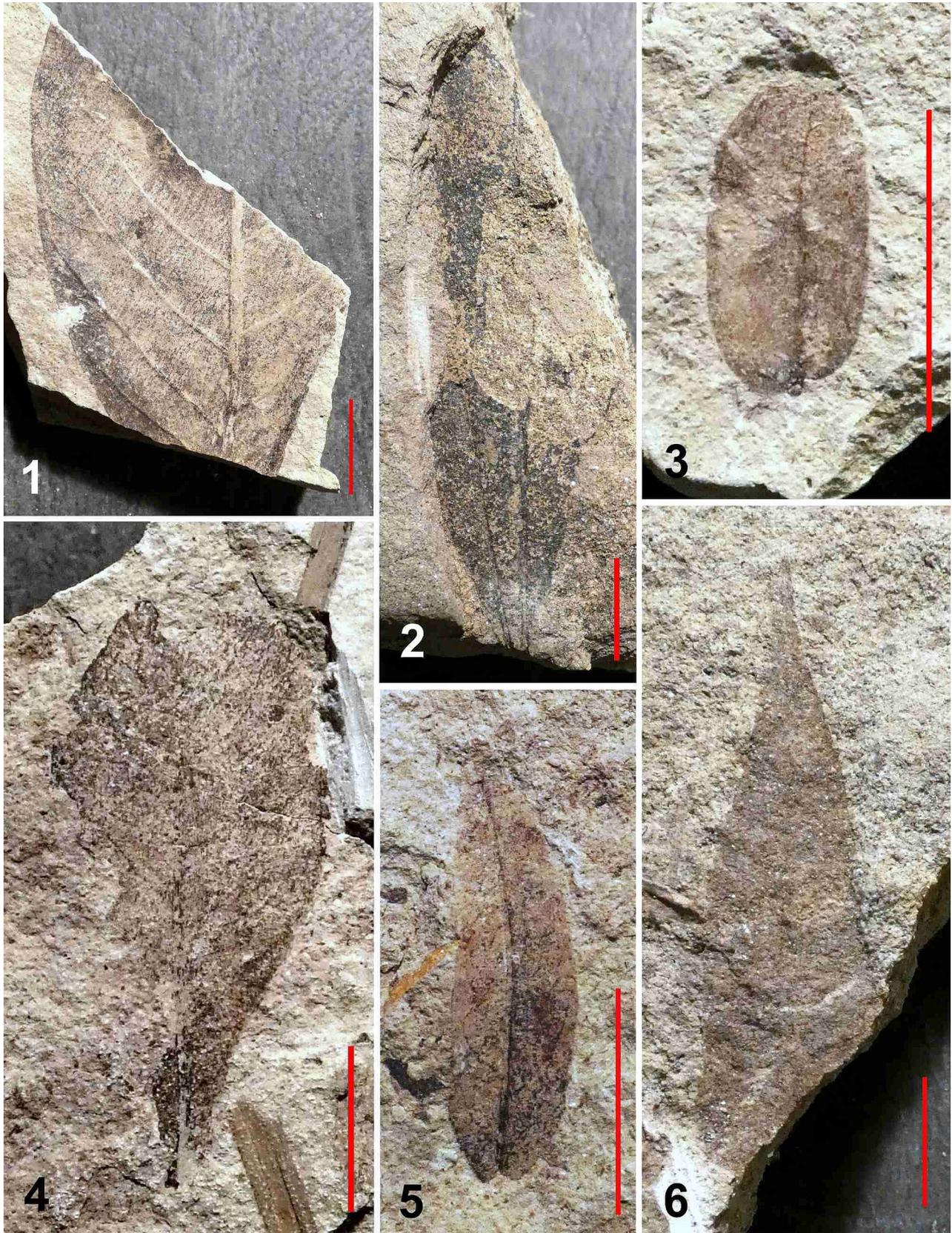
1988. Černjavská & al., p. 30, Pl. 3, Fig. 3.

1998. Bozukov, p. 6, Pl. 2, Fig. 1.

2008. Bozukov & al., p. 174, Pl. 3, Fig. 7.

**Material.** Three leaf imprints, Nos 2, 3, 6 (Pl. I, Fig. 6)

**Location and stratigraphic range.** That fossil species has been identified so far in three locations on the territory of Bulgaria. All three are in the Rhodopes. The first one is at Hvoyna, from the sedimentary basin with the same name, dated at Late Eocene – Early Oligocene (Černjavská & al. 1988); second comes the location at Valche Pole, dated at Late Oligocene – Early Miocene (Bozukov & al. 2008); and the third is at



**Plate II.** Photographs of macrofossil material:

1. *Lithocarpus palaeorhodopensis*; 2. *Macclintockia basinervis*; 3. *Dalbergia rectinervis*; 4. *Bumelia minor*; 5. *Sapindus ungeri*; 6. *Eotriginobalanus furcinervis* (measuring bar – 1 cm).

Satovcha, dated at Middle Miocene (Bozukov 1998). Considering the fact that the species was described in the Late Miocene sediments of Georgia (Takhtajan 1963), it could be assumed that it had migrated from the Rhodopes along the southern coastline of the Eastern Parathetys towards the territory of Georgia, where it was identified with the latest dating.

**Comparison.** According to Takhtajan (1974), based on the morphological characteristics of the leaves, that fossil species is close to the recent species *Neolitsea sericea* (Bl.) Koidz. It is an evergreen small tree, abundantly growing in subtropical and warm-temperate evergreen forests found in SE China, S Japan, S Korea, and Taiwan. Its natural habitat lies on the forest margins and slopes ([https://www.ffpri.affrc.go.jp/labs/prdb/eng/neolitsea\\_ser.html](https://www.ffpri.affrc.go.jp/labs/prdb/eng/neolitsea_ser.html)).

Family *Cyperaceae* Juss.

Genus *Cyperacites* Schimp.

*Cyperacites chavannesii* (Heer) Schimp.

1855. *Cyperus chavannesii* Heer, p. 72, Pl. 22, Fig. 7.

1870. *Cyperacites chavannesii* (Heer) Schimper, p. 415.

1962a. Palamarev, p. 16, Fig. 1b.

1998. Palamarev & al., p. 14.

1999a. Palamarev & al., p. 21, Pl. 4, Fig. 7.

**Material.** An imprint of a leaf fragment, No 23 (Pl. I, Fig. 5)

**Location and stratigraphic range.** That fossil species has a limited geographical distribution. Its stratigraphic range, however, is comparatively wide: Upper Eocene to Middle Miocene (Palamarev & al. 2005).

**Comparison.** That fossil species has morphological features similar to the recent *Cladium mariscus* L. The latter is a cosmopolitan taxon, with a main distribution area in Europe and the Mediterranean, but it is also found in N Africa and W Asia. It grows in wetland environments, in shallow ponds, on the shores of lakes, lagoons and water canals, and in the humid grasslands

surrounding them (Teochropoulos & al. 2006).

Family *Typhaceae* Juss.

Genus *Typha* L.

*Typha latissima* A. Braun

1851. *Typha latissima* A. Braun in Stizenberger, p. 75, (nomen).

1961. Palamarev, p. 178, Fig.-text 3.

1998. Palamarev & al., p. 15.

2000. Bozukov, p. 29, Pl. 5, Figs 2, 6.

2001. Palamarev & al., p. 292.

**Material:** Two imprints of leaf fragments, Nos 5, 12a (Pl. I, Fig. 7)

**Geographic and stratigraphic range:** That fossil species has been identified in many localities on the territory of Bulgaria. Its stratigraphic range is Lower Oligocene – Upper Pliocene (Palamarev & al. 2005). The new find expands the range to include also the Upper Eocene.

**Comparison.** That fossil species has morphological features similar to the recent *T. latifolia* L. It is a cosmopolitan species, always found in or near water, from 0 to 2300 m a.s.l. It grows mostly in fresh water but also occurs in slightly brackish marshes ([http://www.efloras.org/florataxon.aspx?flora\\_id=1&taxon\\_id=220013917](http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=220013917)).

Family *Fabaceae* Lindl.

Genus *Cassiophyllum* Geyl.

*Cassiophyllum ambiguum* (Unger) Palam., Kitan. fil., Bozukov & Staneva

1850a. *Cassia ambigua* Unger, p. 492.

1964. Palamarev, p. 24, Fig.-text 23.

1967. Palamarev, p. 95.

1999a. *Cassiophyllum ambiguum* (Unger) Palamarev & al., p. 17, Pl. 7, Fig. 4.

1999b. Palamarev & al., p. 37, Pl. 2, Fig. 6.

**Material.** An imprint of a leaflet No 22 (Pl. I, Fig. 9)

**Location and stratigraphic range.** A comparatively rare species in the Bulgarian paleoflora, though with a broad stratigraphic range: from Upper Eocene to Middle Miocene (Palamarev & al. 2005).

**Comparison.** According Palamarev & al. (1999a), fossils of that type had many common traits with representatives of the tribe *Sophoreae*, distributed in the tropical and subtropical areas of America and Asia ([http://efloras.org/browse.aspx?flora\\_id=2&name\\_str=sophoreae&btnSearch=Search&chkAllFloras=on](http://efloras.org/browse.aspx?flora_id=2&name_str=sophoreae&btnSearch=Search&chkAllFloras=on) sophorae).

Genus *Dalbergia* L. f.

*Dalbergia rectinervis* Ettingsh.

1869. *Dalbergia rectinervis* Ettingshausen, p. 223, Pl. 55, Fig. 14.

1999b. Palamarev & al., p. 35, Pl. 1, Fig. 13.

2009. Bozukov & al., p. 274, Pl. 2, Fig. 4.

2021. Bozukov & al., p.102, Pl. 1, Fig. B.

**Material.** An imprint of a leaflet, No 24 (Pl. II, Fig. 3)

**Location and stratigraphic range.** That fossil species has been identified in three locations of the Paleogene flora in Bulgaria, with a stratigraphic range from Upper Eocene (Bozukov & al. 2021) to Upper Oligocene (Bozukov & al. 2009). It was registered for the first time in the Mediterranean flora by Bilin (Ettingshausen 1869), and its upper stratigraphic range in Europe was Upper Miocene in Georgia (Kolakovski 1964).

**Comparison.** According to Kolakovski (1964), that fossil species had morphological traits close to those of *Dalbergia assamica* Bentham (= *D. balansae* Prain). It is a tree in mixed and open forests, among bushes, on mountain slopes, and at riversides, at altitudes of 300-1700 m in SE China, E India, Laos, Myanmar, Thailand, and Vietnam ([http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=242316769](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=242316769)).

Family *Fagaceae* Dumort.

Genus *Eotrigonobalanus* Walther & Kvaček

*Eotrigonobalanus furcinervis* (Rossm.) Walther & Kvaček

1840. *Phyllites furcinervis* Rossmässler, p. 33, Pl. 6, Fig. 25; Pl. 7, Fig. 26-31.

1932. *Quercus furcinervis* (Rossm.) Unger; Konjaroff, p. 129, Pl. 42, Figs 1-4; Pl. 46, Figs 1-3.

1962b. *Castanopsis furcinervis* (Rossm.) Kräusel & Weyland; Palamarev, p. 161, Pl. 1, Figs 1, 3; Pl. 2, Figs 1, 3-4; Pl. 3, Figs 1-5; Figs-text 1-2.

1966. Palamarev & Petkova, p. 57.

1975. Palamarev & Petkova, p. 219, Pl. 7, Fig. 1.

1988. *Dryophyllum furcinerve* (Rossm.) Schmalh.; Černjavská & al., p. 30.

1989. *Eotrigonobalanus furcinervis* (Rossm.) Walther & Kvaček in Kvaček & Walther, p. 581, pars, Pl. 33, Figs 1-6; Pl. 34, Figs 1-6; Pl. 35, Figs 1-7; Pl. 36, Figs 1-4; Pl. 39, Figs 1-4; Pl. 40, Figs 1-6; Pl. 41, Figs 1-4; Pl. 42, Figs 1-4; Pl. 43, Figs 1-6; Pl. 44, Figs 1-4; Pl. 45, Figs 1-4; Pl. 46, Figs 1-4 (non Pl. 47, Figs 1-3 = *Quercus lyellii* Heer).

1995. *Dryophyllum furcinerve* (Rossm.) Schmalh.; Palamarev & Staneva, p. 118.

1998. *Eotrigonobalanus furcinervis* (Rossm.) Walther & Kvaček; Palamarev & Mai, p. 243, Pl. 9, Figs 5-7.

1998. Palamarev & al., pp. 15, 19.

1999a. Palamarev & al., p. 13, Pl. 3, Fig. 6; Pl. 5, Figs 1-2.

1999b. Palamarev & al., p. 32, Pl. 2, Figs 1-2, 9.

2001. Palamarev & al., p. 286, Pl. 1, Figs 2-3, 5; Pl. 2, Fig. 2; Pl. 3, Fig. 3; Pl. 5, Fig. 2.

**Material.** Seven leaf imprints, Nos 1, 7, 9, 12c, 14, 16, 17 (Pl. I, Fig. 8; Pl. II, Fig. 6)

**Location and stratigraphic range.** An exceptionally widely distributed species in Bulgaria's Paleogene and in Europe in general. According to Palamarev & Mai (1998), its stratigraphic range was from Lower

Paleocene to Upper Oligocene (Lower Miocene). Bozukov & Ivanova (2015) reported a registered leaf imprint of that fossil species in the Middle Miocene flora of Satovcha (SW Bulgaria), where along with other Paleogene relicts, such as *Macclintockia basinervis* (Rossm.) Knobl. and *Cryptomeria rhenana* Kilpp., it had probably found its last refuge before becoming extinct on the territory of Europe.

**Comparison.** *Eotrigonobalanus* is an extinct genus, part of the „mixed-mesophytic forests”, constituted mainly from the families *Lauraceae*, *Fagaceae* and *Taxodiaceae* (Mai 1995). According to Kvaček (2004), the NLR of that species is *Trigonobalanus verticillata* Forman occurring on the slopes of mountain rivers in tropical SE Asia. It reaches altitudes of up to 1100 m.

Genus *Lithocarpus* Blume

***Lithocarpus palaeorhodopensis*** Palam. & Mai

1998. *Lithocarpus palaeorhodopensis* Palamarev & Mai, p. 237, Pl. 6, Figs 5-6; Pl. 10, Fig. 14; Pl. 11, Figs 5-7; Pl. 12, Fig. 1.

1999a. Palamarev & al., p. 13, Pl. 5, Fig. 3.

**Material.** Two leaf imprints, Nos 18, 26 (Pl. II, Fig. 1)

**Location and stratigraphic range.** So far, the species has been known from two locations in the Rhodopes: Pavelsko (Hvoyna Basin) and Eleshnitsa (NW Rhodopes). Belitsa (SW Bulgaria) is a third location in close proximity to the Rhodopes. According to Palamarev & Mai (1998), that species was a local endemic, with a stratigraphic range of Upper Eocene – Lower Oligocene.

**Comparison.** Palamarev & Mai (1998) have assumed as possible NLR to it the species *L. trachicarpa* Camus, *L. hypoglauka* (Hu) Rehd. and *L. sphaerocarpus* (Hickel & A. Camus) A. Camus based on the anatomical structure of the leaves, and the species *L. petelotii* Camus, *L. maingayi* (Beth.) Rehd. and *L. pulchra* (King) Markgr. based on its morphological characteristics. *L. trachicarpa* and *L. sphaerocar-*

*pus* are part of the broad-leaved evergreen forests, at 600-1300 m a.s.l. in SE China (Yunnan Province) to Vietnam. *L. hypoglauca* and *L. petelotii* participate in the composition of mixed mesophytic forests, at 1000-3000 m a.s.l. in SE China (Yunnan Province) to Vietnam. *L. maingayi* and *L. pulchra* grow primarily in the wet tropical biome, in Thailand in the south and up to the Malaysian Peninsula for the first, and in Borneo for the second, respectively (<https://powo.science.kew.org>).

Family *Myrtaceae* Juss.

Genus *Macclintockia* Heer

***Macclintockia basinervis*** (Rossm.) Knobloch

1840. *Phyllites basinervis* Rossmässler, p. 37, Pl. 9, Figs 41-42.

1962. *Macclintockia basinervis* (Rossm.) Knobloch, p. 121, Pl. 6, Fig. 5.

1988. *Cocculus* (*Macclintockia*) *kani* (Heer) Sap. & Mar.; Černjavská & al., p. 30, Pl. 1, Fig. 3.

1996. *Macclintockia basinervis* (Rossm.) Knobl.; Bozukov, p. 71, Pl. 1, Figs 1-5.

2000. Bozukov, p. 28, Pl. 3, Fig. 1.

2005. Bozukov, p. 12, Pl. 1, Figs 1-6.

2022. Bozukov & Ivanov, p. 149, Pl. 1, Fig. 1.

**Material.** A leaf imprint, No 4 (Pl. II, Fig. 2)

**Location and stratigraphic range.** That species is distributed in locations across the territory of the Rhodopes and has a broad stratigraphic range from the Upper Eocene to the Middle Miocene (Bozukov & Ivanov 2022). According to the same authors, the latter location of the species in Europe has been identified on the territory of SW Bulgaria (Late Serravalian = Volhynian).

**Comparison.** Bozukov & Ivanov (2022) give as NLR of that fossil species the recent *Melaleuca quinquenervia* (Cav.) S.T. Blake, native to New Caledonia, Papua New Guinea and coastal East Australia. That

species is distributed in estuarine swamps and on lake margins, where the annual rainfall is 1200-1400 mm. It is dominant in the swamp forests or dominates with species of the genus *Eucalyptus*. *M. quinquenervia* tolerates drought and salinity, but is intolerant of frost (<https://www.wettropics.gov.au/site/user-assets/docs/factsheets/wtmaVMWTB50a-59g.pdf>).

Family *Sapindaceae* Juss.

Genus *Sapindus* Tourn.

*Sapindus ungeri* Ettingsh.

1870. *Sapindus ungeri* Ettingshausen, p. 889, Pl. 2, Fig. 9.

1961. Palamarev, p. 186, Fig.-text 21.

1964. Palamarev, p. 27, Fig.-text 35.

1995. Palamarev & Staneva, p. 119, Pl. 3, Fig. 2.

1999b. Palamarev & al., p. 37, Pl. 4, Fig. 11.

**Material.** A leaf imprint, No 25 (Pl. II, Fig. 5)

**Location and stratigraphic range.** That fossil species is new to the Hvoyna Basin but known in the Rhodopean Paleogene (Palamarev & Staneva 1995; Palamarev & al. 1999b). Its stratigraphic distribution on the territory of Bulgaria is Upper Eocene – Middle Miocene.

**Comparison.** That fossil species has similar morphological characteristics with the recent *Sapindus rarak* DC. The latter species occurs in sparse forests at altitudes from 500 to 2100 m, in a vast region of SE Asia, including Bhutan, Cambodia, China (Yunnan Province), India, Indonesia, Laos, W Malaysia, Myanmar, Sri Lanka, Taiwan, Thailand, and Vietnam ([http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=200013221](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=200013221)).

Family *Sapotaceae* L.

Genus *Bumelia* Sw.

*Bumelia minor* (Unger) Unger

1850a. *Pyrus minor* Unger, p. 481.

1850b. *Pyrus minor* Unger, p. 53, Pl. 38, Figs 16-24.

1850b. *Bumelia oreadum* Unger, p. 42, Pl. 22, Figs 7-14.

1866. *B. minor* (Unger) Unger, p. 25, Pl. 6, Figs 11-19.

1995. *B. oreadum* Unger; Palamarev & Staneva, p. 118, Pl. 3, Fig. 4.

1999a. *B. minor* (Unger) Unger, Palamarev & al., p. 16, Pl. 8, Fig. 6.

1999b. Palamarev & al., p. 34, Pl. 1, Fig. 12.

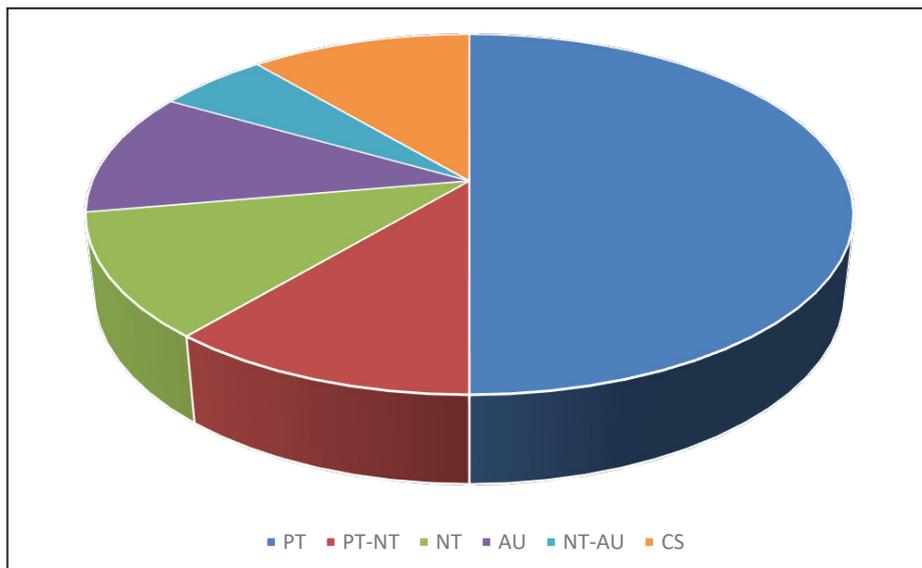
**Material.** Two leaf imprints, Nos 20, 21 (Pl. II, Fig. 4)

**Location and stratigraphic range.** That species is widely distributed in the Rhodopean Paleogene, but is new for the paleoflora of the Hvoyna Basin. Its stratigraphic range on the territory of Bulgaria is Upper Eocene - Middle Miocene (Palamarev & al. 2005).

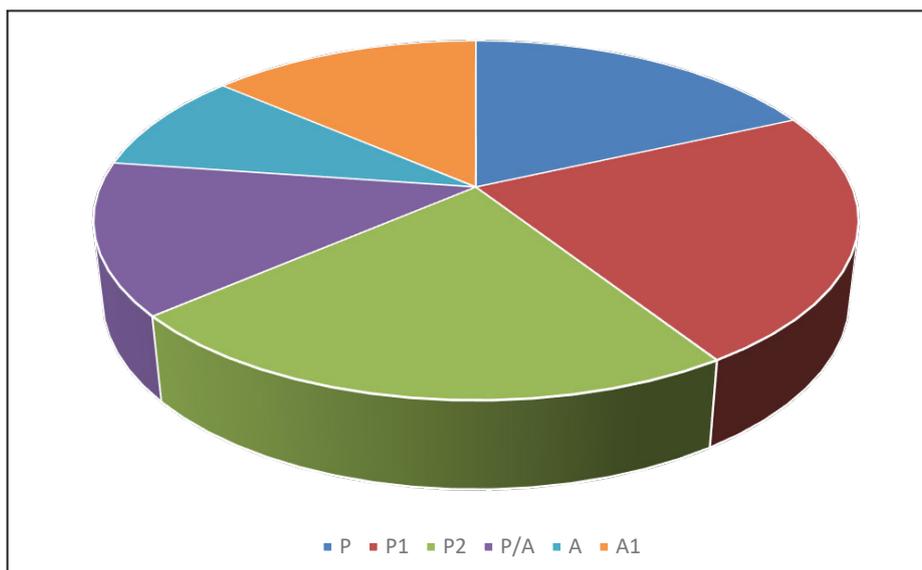
**Comparison.** According to Palamarev & Petkova (1987), two recent species could be accepted as NLR. The first is *Bumelia tenax* (L.) Wild. (= *Sideroxylon tenax* L.), distributed along the coastline of Florida Peninsula (USA). It grows on dry, sandy soil in pine forests, pine-oak woodlands and hummocks, at elevations of less than 100 m. ([http://www.efloras.org/florataxon.aspx?flora\\_id=1&taxon\\_id=250092176](http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250092176)).

The second is *B. retusa* Sw. [= *Sideroxylon americanum* (Mill.) T.D. Penn], which grows in dry broadleaf evergreen formations – forests/woodlands/shrublands (coppice and scrublands) across the island groupings of the Lucayan Archipelago, as well as in Cuba and Jamaica (<https://worldfloraonline.org/taxon/wfo-0000310562>).

As illustrated in Table 1, 11 families, 17 genera and 18 species have been identified in the Orehovo paleoflora. Mention deserves the fact that the families *Lauraceae*, *Fagaceae* and *Myrtaceae* have been represented by the maximum for that paleoflora number of genera, species belonging to one family, as well as by the maximum number of leaf imprints. *Eotrigonobalanus furcinervis* dominated all species with seven leaf imprints. That accounted approximately for 30 percent of the collected imprints by the authors and



**Fig. 3.** Ratio between floristic kingdoms of NLRs in the macroflora from Orehovo (Abbreviations acc. Table 1).



**Fig. 4.** Ratio between geofloristic element in the microflora from Hvoyna (Abbreviations acc. Table 2).

of the already published materials on *Gleichenia rhodopaea*, *Dryophyllum dewalquei*, *Eugenia splendens*, and *Rhodomyrtophyllum sinuatum* (Černjavská & al. 1988; Palamarev & Petkova 1990, 1994). The formerly collected data on the distribution of *Eotriginobalanus furcinervis* in Bulgaria (Palamarev & al. 2005) revealed its exceptional importance for the Bulgarian Paleogene floras. The great number of its locations across S Bulgaria relating to the Upper Eocene – Lower Oligocene interval outlined its coenose-forming role in that part of the country. Palamarev

& Petkova (1975) assumed that the *E. furcinervis* coenoses had formed a well-outlined belt in that region at the end of the Eocene, in place of the coenoses of genus *Dryophyllum*. In fact, the genus *Dryophyllum* was represented in the paleofloras of the Hvoyna Basin (Orehovo, Pavesko), but in rather limited numbers (Černjavská & al. 1988; Palamarev & Mai 1998). The widest distribution of *E. furcinervis* was registered in the Oligocene and was testified by the number of its locations and its quantitative participation in the local paleofloras (Palamarev & al. 2005). That fact also

coincided with the mass development of the species in Central Europe (Knobloch 1962; Petrescu 1968; Kvaček & Walther 1998; Palamarev & Mai 1998). Velitselos & al. (2014) and Sari & Gülen (2021) have reported finds of that species in the Upper Oligocene of Thrace, on the territory of Greece and Turkey. At the end of the Oligocene and the beginning of the Miocene, the species had strongly reduced its area and, after the Tortonian, did not settle anywhere in Europe (Palamarev & Petkova 1975). Single imprints were registered in the Middle Miocene flora of Satovcha (SW Rhodopes) (Bozukov & Ivanova 2015), where along with other Paleogene relicts like *Macclintockia basinervis* and *Cryptomeria rhenana* Kilpper (Bozukov 2001), *Eotrigonobalanus furcinervis* had found its last refuge on the territory of Bulgaria, and presumably in Europe.

Domination of the families *Lauraceae*, *Fagaceae* and *Myrtaceae* over the others participating in the paleoflora of Orehovo proved that mainly arboreal paleocoenoses of subtropical humid oak (*Dryophyllum*, *Eotrigonobalanus*, *Lithocarpus*) – laurel (*Daphnogene*, *Neolitsea*) – myrtle (*Eugenia*, *Macclintockia*, *Rhodomyrtophyllum*) forests (Palamarev & Petkova 1994) existed in the region of the Rhodopes. Those three families were represented by three species each. The family *Fabaceae* was represented by two species and the other families by one species each (Table 1, Fig. 3).

In terms of NLR of the identified taxa, it could be assumed that they were fully related to the tropical and subtropical areas of the Earth, excluding the two cosmopolitan elements of *Cladium mariscus* and *Typha latifolia*. Distribution of these two recent species was related to the existence of water basins which, in turn, provided them with relatively steady ecological conditions and thus they were not determinant for the reconstruction of the paleoclimate. Of all other NLRs, the greatest number belonged to the Paleotropical Floristic Kingdom: nine. Present were two elements each of the Neotropical and Australian, as well as elements of mixed Paleotropical - Neotropical distribution. The elements of the latter type had NLR of two floristic kingdoms as follows: for *Dryophyllum dewalquei* those were *Trigonobalanus doichangensis* (A. Camus) Forman [subtropical Yunnan (SE

China) to N Thailand], *T. excelsa* Lozano, Hern. Cam. & Henao (endemic to Colombia), and *T. verticillata* Forman (tropical Indonesia and the Malayan Peninsula) (Palamarev & Petkova 1975); for *Cassiophyllum ambiguum*, as mentioned in the systematics section above, according to Palamarev & al. (1999a), the fossils of that type had many common characteristics with representatives of the *Sophoreae* tribe distributed in the tropical and subtropical regions of America and Asia.

Only one element had mixed Neotropical-Australian distribution. That was due to the fact that the fossil taxon *Rhodomyrtophyllum sinuatum* had four probable NLR: *Rhodomyrtus macrocarpa* Benth. (native to NE Australia, New Guinea and the Aru Islands), *R. psidioides* (Hook.) Benth. (native to E Australia), *Psidium cattleianum* Sab. (with native range restricted to the Amazonian Basin in Brazil), and *Lophostemon confertus* (R.Br.) P.G. Wilson & J.T. Waterh. (= *Tristania conferta* R.Br.) (with natural range in Australia, in NE New South Wales and coastal Queensland). All those recent species were evergreen shrubs or trees, which occur primarily in mesic tropical rainforest environments or other tropical areas with similar characteristics (Rüfle & Jähnichen 1976; Mai & Walther 1985).

Of all NLR to the species from the Orehovo paleoflora, most demanding to climatic conditions have been *Cinnamomum verum* (Paleotropical element) and *Melaleuca quinquenervia* (Australian element). Within the distribution range of the former, there are 2000-2500 mm of precipitation per annum, well-distributed across the year, and 1200–1400 mm of annual rainfalls for the latter. *Melaleuca quinquenervia* tolerates drought but both species are intolerant of frost. *Pinus lawsonii* (Neotropical element) has a high cold hardiness limit between -1°C and +4.4°C. That species is distributed in the tropical part of Mexico, in areas of 1300-2600 m a.s.l. and warm-temperate to temperate climate, with 600-1500 mm of annual precipitation and a dry season. Generally speaking, all NLR relate to high humidity, either owing to precipitation or to coastal habitats.

NLR of the here studied fossil species supported the assumption of Černjavska & al. (1988) that in the

**Table 3.** Climate characteristics of the fossil flora.

| Climatic parameters | MAT °C |      | CMMT °C |     | WMMT °C |      | MAP mm |      |
|---------------------|--------|------|---------|-----|---------|------|--------|------|
|                     | min    | max  | min     | max | min     | max  | min    | max  |
| Macroflora          | 13.4   | 18.5 | 6       | 7.7 | 23.8    | 28.1 | 1231   | 2336 |
| Microflora          | 16.8   | 18   | 7       | 8.5 | 24.7    | 27.2 | 1132   | 1742 |

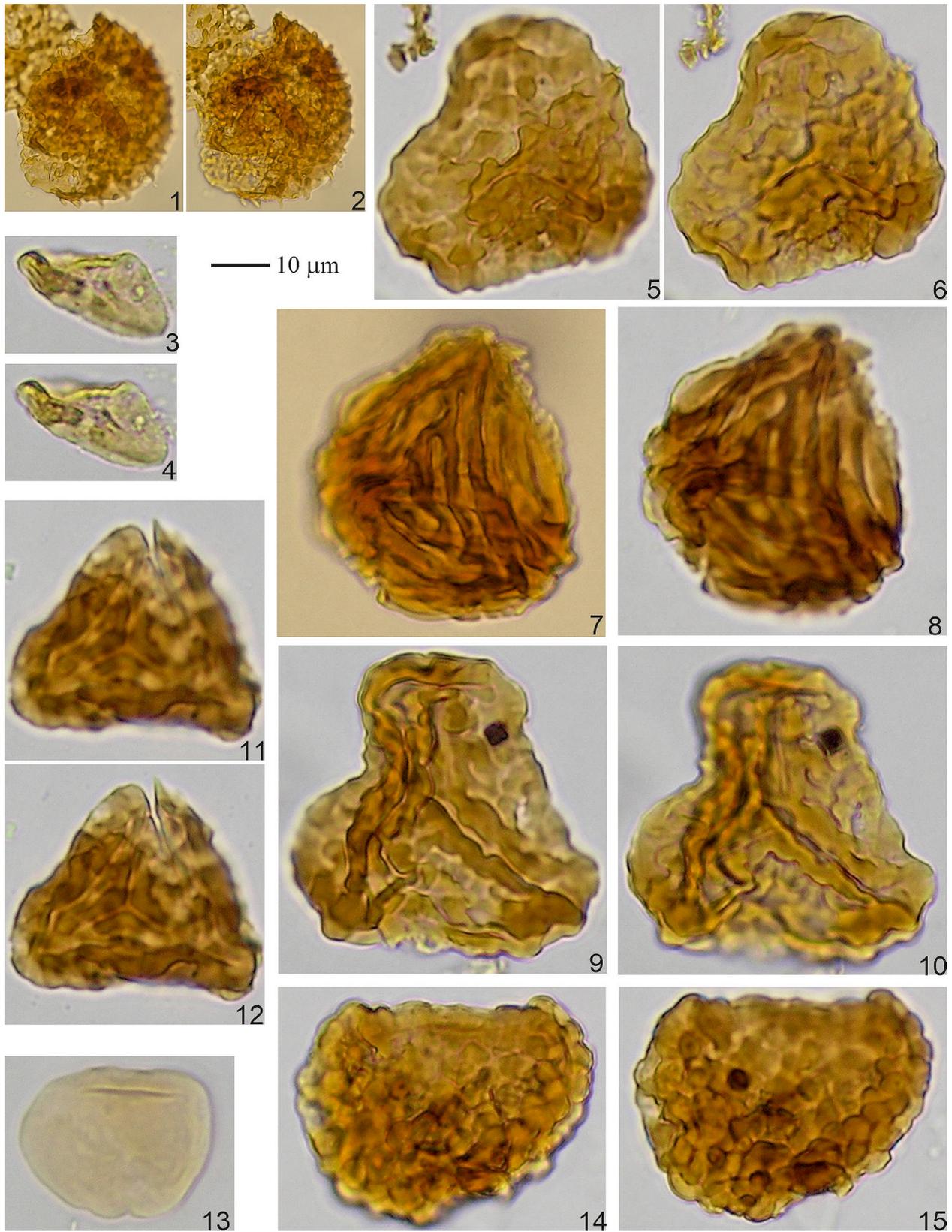
**Legend.** MAT – Mean Annual Temperature; CMMT – Coldest Month Mean Temperature; WMMT – Warmest Month Mean Temperature; MAP – Mean Annual Precipitation.

Hvoyna Basin, the main components of the paleo-landscape were woody mesic to subhumid communities containing species of the families *Lauraceae*, *Fagaceae*, *Sapindaceae*, *Myrtaceae*, and *Sapotaceae*. Species of the genera *Pinus* and *Doliosstrobos* participated as assectators in some habitats of the Basin. Other important components of these paleocommunities have been ferns. Representatives of the family *Fabaceae* were part to another paleocommunity – open xerophytic forest and shrub communities involving species of the genera *Cassiophyllum* and *Dalbergia*. The floristic composition and physiognomy of these paleocommunities related to the following recent vegetation formations in SE Asia: subtropical oak-laurel forest formations as those in Burma, Laos and Vietnam; subtropical evergreen sclerophyllous broad-leaved forest formations developed in the Chinese Yunnan Province; and subtropical montane rain forest formations of Taiwan (Černjavská & al. 1988).

Absence of Arcto-Tertiary elements in the Orehovo paleoflora, such as registered by Černjavská & al. (1988) in the other locations of the Hvoyna Basin, could be explained either by insufficient study material, or by location of the flora-bearing sediment on a lower stratigraphic level relating to the Upper Eocene. Owing to absence of representatives of the genera *Myrica*, *Nyssa*, *Acer*, *Platanus*, *Populus*, *Juglans*, *Pterocarya*, *Cyclocariya*, *Dodonaea*, *Sabal*, and *Palmophyllum* registered in the other locations of the Basin (Černjavská & al. 1988), it could be assumed that in the region of Orehovo no swamp and riparian communities had been present in the paleo-landscape. The specific microclimate conditions could explain the absence of such communities.

Twenty-three taxa of fossil spores and pollen were found in the composition of the microflora from Hvoyna. They belonged to 18 plant families (Table 2, Plates III-IV). The spore plants have been represented by nine species (39%), gymnosperms by four species (17%), and angiosperms by 10 species (44%). The fossil flora from the area of Hvoyna village has been enhanced with 14 new species, as compared to the available palynological data (Černjavská & al. 1988). The high percentage of spore plants testified to the ancient nature of the flora. That conclusion was also supported by the fact that most families and genera were represented by one species each, which was characteristic of the ancient polydominant paleocenoses. The family *Juglandaceae* displayed the highest taxonomic diversity: four species. Most palynomorphs referred to plants which were components of mesophytic forest paleocenoses. Presence of the representatives of marshy forests, riparian forests and aquatic plants testified to the existence of a water basin with marshy territories and a well-developed river network, which ran contrary to the flora and landscape in the area of Orehovo village (see above). In terms of geofloristic elements, the Hvoyna paleoflora was characterized by high participation of paleotropical elements (see Table 2, Fig. 4). Only five taxa belonged to the group of Arcto-Tertiary geofloristic elements, while representatives of A2 (cool temperate elements) have not been identified.

Stratigraphic analysis of the fossil microflora shows the presence of characteristic palynomorphs that can be used for age dating. The species *Plicapollis pseudo-excelsus* is characteristic of the Eocene, but according to some more recent data, it also occurs in the Early



**Plate III.** Photographs of microfossil material:

1-2. *Echinatisporis* cf. *cycloides*; 3-4. *Gleicheniidites* fsp.; 5-6. *Trilites multivalatus*; 7-8. *Cicatricosisporites chatensis* subsp. *chatensis*; 9-10. *Ischyosporites asolidus*; 11-12. *Polypodiaceoisporites gracillimus* subsp. *granoverrucatus*; 13. *Laevigatosporites* cf. *discordatus*; 14-15. *Verrucatosporites pseudoalienus*.



**Plate IV.** Photographs of microfossil material:

1-2. *Verrucatosporites* cf. *favus*; 3-4. *Inaperturopollenites hiatus*; 5-7. *Inaperturopollenites* fsp.; 8. *Pityosporites microalatus*; 9. *Podocarpidites libelus*; 10-11. cf. *Graminidites* fsp.; 12-13. *Sparganiaceapollenites* fsp.; 14. *Monocolpopollenites* fsp.; 15. *Tricolporopollenites* (*Castaneoidaeapollis*) *cingulum* subsp. *fuscus*; 16-17. *Caryapollenites* cf. *circulus*; 18. *Momipites* (*Engelhardtioipollenites*) *quietus*; 19. *Plicapollis pseudoexcelsus*; 20. *Pterocaryapollenites* fsp.; 21-22. *Bombacidites* cf. *palaeogenicus*; 23. *Tricolporopollenites* fsp.

Oligocene and even in the Middle Miocene. *Polypodiaceoisorites gracillimus* subsp. *granoverrucatus* is a typical representative of the Oligocene and Miocene floras of Central Europe. Prevalence of *Cicatricosporites chatensis* subsp. *chatensis* in Bulgaria pointed to the Oligocene – Middle Miocene. Distribution of the species *Bombacidites* cf. *palaeogenicus* Krutzsch is related to the Upper Eocene and that of *Caryapolenites* cf. *circulus* (Pfl.) Krutzsch is limited to the Upper Eocene – Lower Oligocene interval. Thus, the new palynological data confirmed the age of the sediments as Late Eocene – Early Oligocene.

Palamarev (2003) declared the Paleorhodopean Orogenic System as a region of exceptional importance for the evolution of the paleoflora in the Balkan Peninsula. He mentioned as an important element for that conclusion the high endemism characteristic of the paleoflora in that region. The new finds in the Orehovo paleoflora with its 18 fossil species supported that thesis, because two of the species, *Gleichenia rhodopaea* (Palamarev & Petkova 1990) and *Pinus palaeorhodopaensis* (*hoc loco*), were endemic and their percentage in regard to the other species was high (11.11%). That could be explained by the strong volcanic activity in the Rhodopes during the Paleogene (Boyanov & Goranov 2001), which presumed frequent changes of the boundaries of dry land. Hence, the possibility for isolation of some populations surrounded by water bodies and, subsequently, emergence of new taxa, as well as inset of new dry-land connections between Europe and Asia in the region of the contemporary Balkan Peninsula, which enabled migration. Identification of such species as *Daphnogene cinnamomea*, *Neolitsea palaeosericea* and *Dalbergia rectinervis*, both in the Paleogene of the Rhodopes and in the Upper Miocene of Georgia, was probably specifically related to migration of those species from the Balkan Peninsula along the southern coastline of the Eastern Paratethys to the Caucasus, where those species had found suitable conditions for their development into Pontian = Andalusian. In the Kodor Upper Miocene flora, the fossil taxon *Cladium mariscus* foss. (Kolakovski 1964) was identified, which corresponded to the here studied *Cyperacites chavannesii*. However,

as mentioned above, because of its belonging to the cosmopolitan floristic element, it was not of great importance for the determination or reconstruction of climatic conditions.

The paleoclimate quantification using the Coexistence Approach (based on Palaeoflora database Utescher & al. 2024) points to the persistence of warm temperate or subtropical climate conditions during the time-span regarded, with Mean Annual Temperature (MAT) derived by macrofloristic record between 13.4 - 18.5°C (Table 3). The results from the analysis of microflora shows a narrow temperature interval of 16.8 - 18.0°C. As regard the other paleoclimate parameters, the results are well in accordance and don't display strong differences: Coldest Month Mean Temperature (CMMT) is in the frame of 7-8 °C, and Warmest Month Mean Temperature (WMMT) displays an interval of 24-28°C. With a Mean Annual Precipitation (MAP) at 1200-2300 mm, the climate could be described as subtropical and humid, but some seasonality could be assumed as evidenced from species composition of fossil flora.

In terms of stratigraphic distribution of the fossil species in the Orehovo paleoflora, it could be said that only two of them registered changes. The species *Dalbergia rectinervis* and *Typha latissima* were identified for the first time in the Upper Eocene of the Rhodopes (Table 1). As mentioned above, as the NLR of *T. latissima* was tied down to water basins and its existence did not depend on such a limiting factor like humidity, it was only natural for it to have a wide stratigraphic range. In that sense, identification of that species in the Rhodopean Upper Eocene, as well as on the territory of Bulgaria was not a very important fact. The fossil species *Dalbergia rectinervis* was identified for the first time in the Upper Eocene of the Rhodopes, but it was also present in the Upper Eocene flora of Bersin (SW Bulgaria) (Bozukov & al. 2021). Another location of that species in SW Bulgaria dated to Late Oligocene – Early Miocene (Bozukov & al. 2009) has proved its distribution in the Paleogene of S Bulgaria in the Late Eocene – Late Oligocene interval. This makes registration of that species in the Orehovo paleoflora expected and absolutely acceptable.

## Conclusions

In the course of the present research, 14 new species have been found for the macropaleoflora of Orehovo, as well as 14 new species of palynomorphs for the flora of Hvoyna. Identification of those new species has been in accordance with the available data on the Paleogene flora of the Rhodopes, both ecologically and stratigraphically. Five of them are new for the macroflora of the Hvoyna Basin, but they do not change the total species composition of the paleoflora of the Rhodopes in the Upper Eocene - Lower Oligocene interval. The new data also confirm the high endemism, which is characteristic of the paleoflora of the Rhodopes. The species recorded for the Upper Miocene of Georgia, known from the Bulgarian Paleogene (and in particular from the paleoflora of Orehovo), such as *Daphnogene cinnamomea*, *Neolites palaeosericea* and *Dalbergia rectinervis*, supported the assumption that the species adapted to tropical and subtropical environmental conditions had migrated along the coastline of Eastern Paratethys, where subtropical climate still existed. That migration was triggered out by the global climate changes that occurred in Europe during the Late Oligocene and Miocene. Climate data obtained by the application of the Coexistence Approach method reveal a warm temperate or subtropical climate with MAT 16.8 - 18.0°C, and MAP of 1200-2300 mm. A further study of the paleoflora of Orehovo may reveal any differences in its composition with respect to the remaining deposits from the Hvoyna Basin and clarify its stratigraphic status. The stratigraphic interpretation of the new fossil data presented here confirmed the assumed Late Eocene to Early Oligocene dating.

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