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Eocene flora and trace fossils from the Hruby Regiel section in the Tatra Mountains (Poland): Taxonomic revision of the Wiktor Kuźniar fossil plant collection

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ABSTRACT:

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Latest Eocene plant macrofossils and trace fossils collected a century ago by Wiktor Kuźniar are revised and their stratigraphical and palaeoecological meaning is re-considered. They derive from marine limestones and marls cropping out on the northern slope of the Hruby Regiel mountain in the Western Tatra Mountains. Leaves belonging to the families Fagaceae and Lauraceae and fruits of the palm *Nypa* are recognized. The co-occurrence of the planktonic foraminifer taxa *Chiloguembelina* cf. *gracillima* and *Globigerinatheca* cf. *index* and fruits of *Nypa* suggests a latest Eocene age of the fossil flora. The plant assemblage is typical of paratropical or subtropical evergreen forests in a warm and humid subtropical climate, recent counterparts of which occur in southeast Asia. The presence of *Nypa* is characteristic of mangroves. The good state of preservation of the leaves suggests coastline proximity during sedimentation of the plant-bearing deposits.

Key words: Fossil leaves; Fossil fruits; Trace fossils; Foraminifera; Biostratigraphy; Palaeoecology; Palaeoclimate; Late Eocene; Western Carpathians.

INTRODUCTION

The Eocene, an important epoch in the evolution of the biosphere, is characterised by significant changes in the Earth climate. The warm and humid greenhouse climate of the Early and Middle Eocene changed to an icehouse climate through the Late Eocene (Zachos *et al*. 2001). The climatic deterioration led to dramatic changes in the Eocene flora and fauna and to a significant extinction within some groups of animals and plants (Boulter *et al*. 1988; Prothero 1994; Sepkoski 1996). During the greenhouse period, land areas of Europe were covered by paratropical rainforest vegetation (Mai 1995; Collinson and Hooker 2003).

Fossil remains of Eocene plants are known from many localities in Europe. One of them is Geiseltal near Halle, Germany, with excellently preserved plants and animals (Mai 1976; Wilde 1995; Mai and Walther 2000). In Poland, Eocene floras are rather scarce, represented mainly by assemblages of plant microfossils

yielded by borehole cores (Grabowska 1996a). Eocene plant macroremains in Poland are typically found in Baltic amber (Grabowska 1996b; Kosmowska-Ceranowicz 1996). However, amber in Poland is usually redeposited into Quaternary rocks from areas located to the north. Eocene plant macroremains in southern Poland were found in the Carpathians and almost exclusively in the Tatra Mountains. They are represented mostly by plant detritus, in some localities accompanied by remains of fossil leaves and exceptionally also by carpological remains (Głazek and Zastawniak 1999).

The first report on plant macroremains from the Eocene of the northern slopes of the Tatra Mountains was published by Raciborski (1892). In the "Turek valley" (territory of Slovakia), he found numerous horsetail remains, referred to as *Equisetum uhligi* Raciborski, accompanied by an oak leaf, some coniferous remains and other poorly preserved leaves (probably Myricaceae and Salicaceae). Kuźniar (1910) described abundant Eocene plant remains from the road-cutting on the northern slope of the Hruby Regiel mountain. This flora comprises almost exclusively impressions of leaves, with rare carpological remains. Szafer (1958) presented a new Eocene plant macroremains assem-
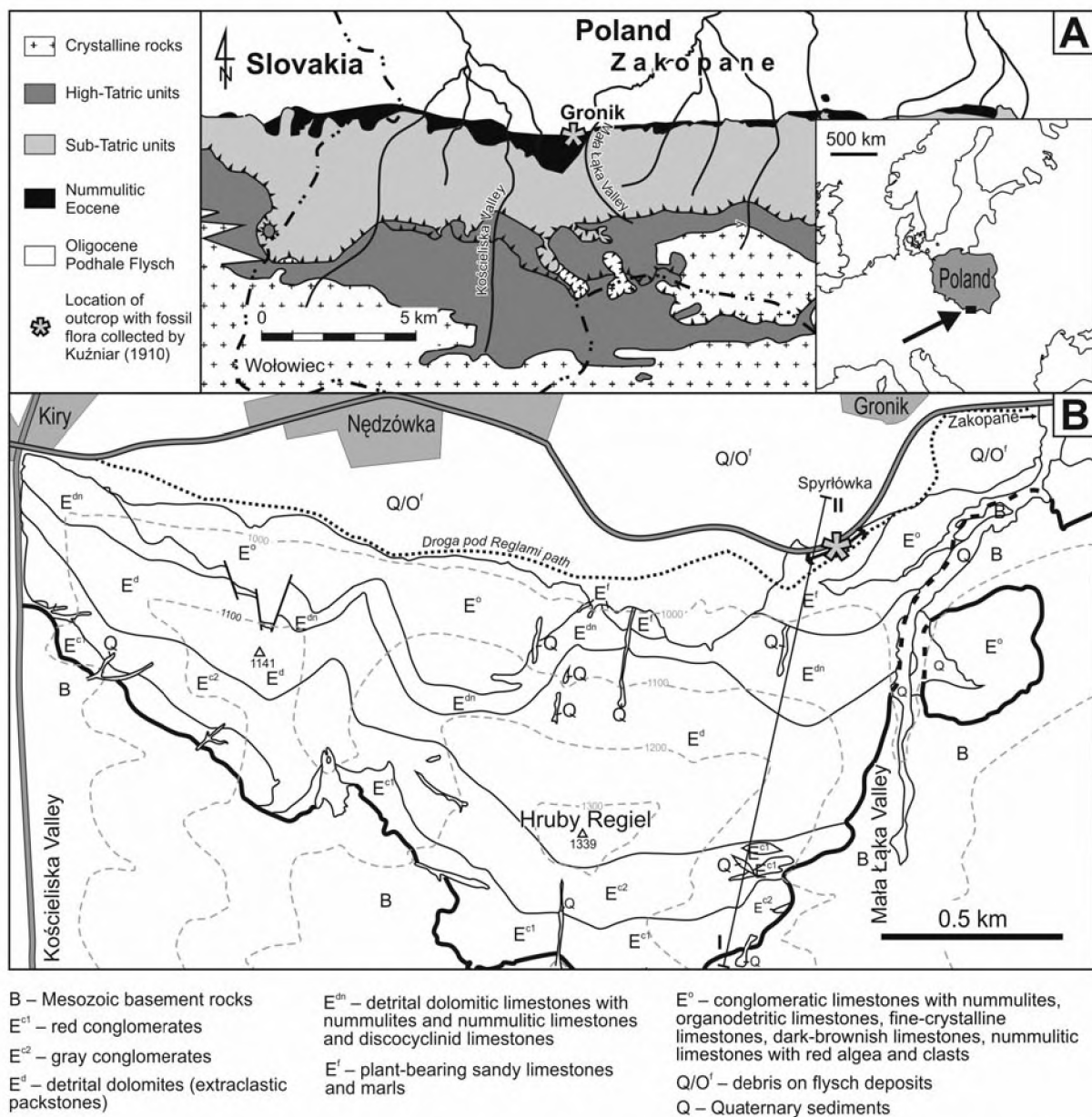

Text-fig. 1. Location maps. A – Geological sketch-map of the Polish part of the Tatra Mountains (after Bac-Moszaszwili *et al.* 1979, simplified). B – Detailed geological map of the Hruby Regiel Mountain with location of the study area (after Sokołowski 1959, modified)

blage from the quarry at Chłabówka. It is represented by leaves of Lauraceae (*Cinnamomum* sp.), Palmae, Myrtaceae, Cornaceae, and probably also Moraceae (*Ficus*), Myricaceae and Sterculiaceae. Zastawniak (in Passendorfer 1983) briefly revised Szafer's (1958) collection and ascribed these remains to *Sabalites*, *Daphnogene*, and presumably to Apocynaceae and Salicaceae. Subsequently, the material was revised by Głazek and Zastawniak (1999), who reported leaf remains of the fern *Acrostichum*, leaves of Lauraceae (*Daphnogene*), Araceae, palms (*Sabalites*) and an extinct member of Fagaceae, *Eotrigonobalanus furcinervis* Walther et Z. Kvaček. Starczewska-Koziołowa (1961) found some Eocene plant remains in the area of the Krokiew ski jump which were not subsequently investigated. The history of investigations of the Palaeogene plant macrofossils from the Tatra Mountains was summarised by Głazek and Zastawniak (1999).

The current investigation was aimed at a taxonomic revision of the plant macroremains of Kuźniar (1910) from the Eocene of the Hruby Regiel section, some of which appeared to be trace fossils. Most of the original plant determinations were revised and the entire material illustrated for the first time; Kuźniar (1910) did not illustrate his material. The study also revealed the presence of specimens never previously described. The revision enables reinterpretation of the taxonomic composition and palaeoecology of plant assemblages during the Eocene (Priabonian) in the Western Carpathians in relation to the palaeoclimate at that time.

GEOLOGICAL SETTING

The so-called Tatric or Nummulitic Eocene of the Tatra Mountains forms the lowermost part of the sedimentary succession of the Central Carpathian Palaeogene (Text-fig. 1; Bac-Moszaszwili *et al.* 1979). These deposits discordantly overlie the Variscan crystalline basement and its autochtonous and allochtonous Permo-Mesozoic sedimentary cover. They represent a transgressive sequence which starts with Lutetian and locally lowermost Bartonian terrigenous and littoral conglomerates composed of bedrock clasts (Text-fig. 2). These deposits are overlain by Lutetian–Bartonian littoral extraclastic carbonates represented by detrital dolomites and detrital dolomitic limestones with nummulites. Locally, in their uppermost part, nummulitic banks with large benthic foraminifera dominated by *Nummulites* sp. occur (Bieda 1963; Roniewicz 1969; Kulka 1985; Olszewska and Wieczorek 1998; Bartholdy *et al.* 1999; Jach and Machaniec 2014).
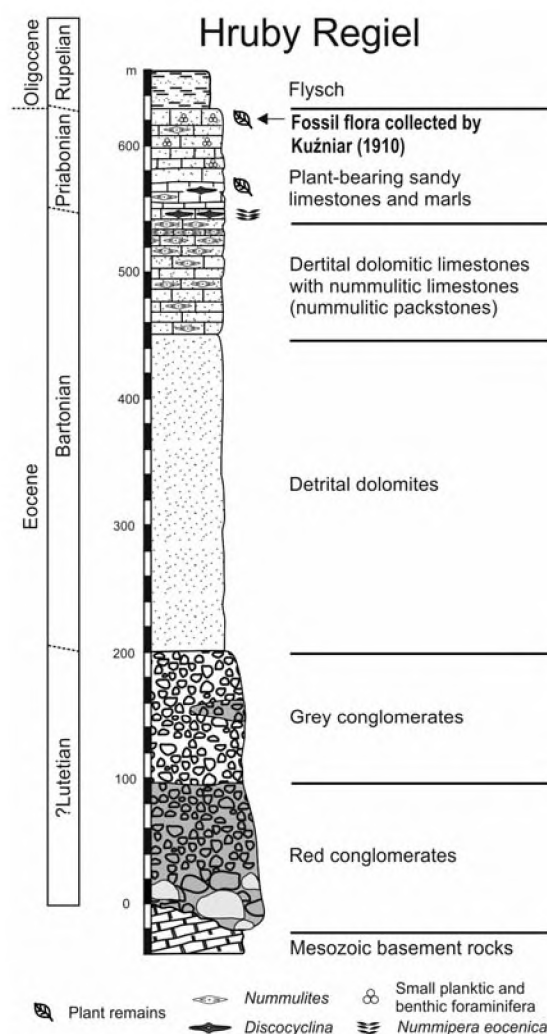
Text-fig. 2. Lithostratigraphical log of Eocene deposits in the Hruby Regiel section, Tatra Mountains (after Sokołowski 1959, modified)

The uppermost Bartonian through Priabonian carbonates are characterized by a distinct facies composition (Bieda 1963; Bartholdy *et al.* 1995; Machaniec *et al.* 2011; Jach *et al.* 2012). They are usually developed as limestones with abundant large benthic foraminifera and red algae, which are locally overlaid with carbonate conglomerates. Laterally, they are replaced with plant-bearing sandy limestones and marls. The latter, well-developed in the Hruby Regiel area, are about 70 m thick. These deposits were previously referred to as the "sandy limestones with fucoids" (Kuźniar 1910), "floral beds" (Sokołowski 1959) or "sandy limestones and shales with flora" (Guzik *et al.* 1958). In this area, the facies distribution was controlled by synsedimentary tectonics (Jach *et al.* 2009, 2012; Dąbrowska and Jurewicz 2013). The carbonates
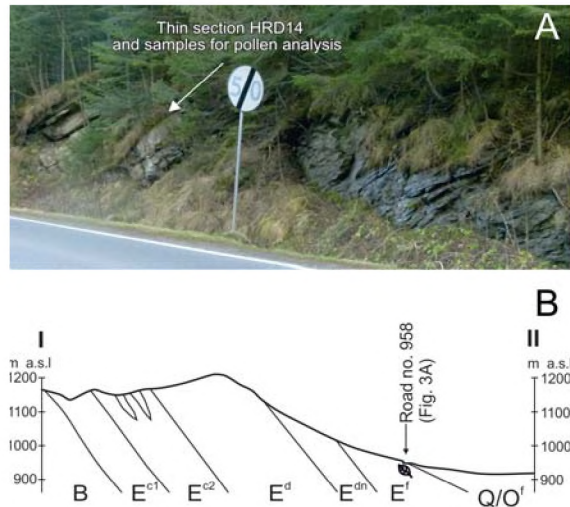
Text-fig. 3. Hruby Regiel section. A – View of the rock cliff with plant-bearing sandy limestones and marls, outcrop along the Zakopane–Witów road; B – Cross section I–II of the Hruby Regiel eastern slope as shown in Text-fig. 1 (after Sokołowski 1959, modified)

are succeeded by Oligocene turbiditic deposits, c. 2.5 km thick (e.g. Radomski 1959; Ludwiniak 2010).

The fossil flora described by Kuźniar (1910) was collected *ex situ* from the rock debris available during roadworks at the beginning of the 20th century. Based on Kuźniar's precise description, the locality is identified as a road-cutting along the Zakopane–Witów road (at present road no. 958), about 500 m towards the west from the Mała Łąka valley mouth, between the gullies running on the northern slope of Hruby Regiel (Text-figs 1, 3A, B). At present, there is a 3-m high cliff along the road (from N49°16.509′; E19°53.907′ to N49°16.465′; E19°53.807′), built of the uppermost part of Priabonian carbonates; their contact with the overlying flysch deposits is not exposed.

Cropping out in the cliff are sandy limestones and marls (extraclastic packstones) composed mainly of sharp-edged dolomite grains, quartz grains, limestone grains and bioclasts (Text-fig. 4A, B). These deposits reveal striking textural and mineralogical similarities to the samples collected by Kuźniar (1910) (Text-fig. 4C, D).
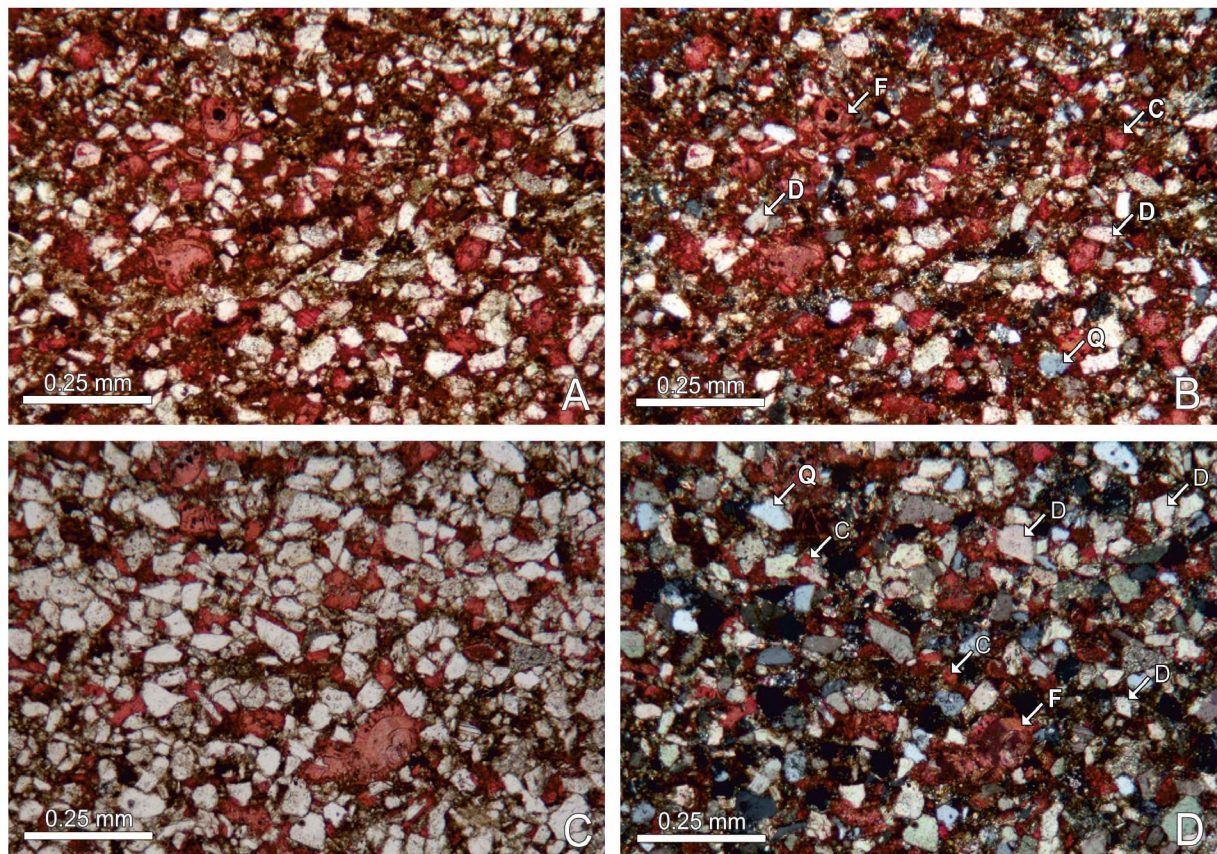
Text-fig. 4. Microfacies of plant-bearing sandy limestones and marls of Hruby Regiel section. Thin sections are stained with alizarin red S and ferricyanide potassium solution. Symbols: Q – quartz, D – dolomite, C – calcite, F –foraminifera. A – extraclastic packstone composed of sharp-edged dolomite grains, angular or moderately rounded quartz and calcitic bioclasts; sample HRD14, plane polarised light; B – sample HRD14, cross polarised light; C – extraclastic packstone composed of sharp-edged dolomite grains, angular or moderately rounded quartz and calcitic bioclasts mainly of foraminifera tests; sample 24/2013, plane polarised light; D – sample 24/2013, cross polarised light

MATERIALS AND METHODS

The collection of Wiktor Kuźniar is stored in the Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków. Unfortunately, Kuźniar (1910) did not put numbers directly on his specimens. In consequence, the loose labels accompanying the specimens are mixed and partially lost. Some of the specimens were added later by an unknown collector, as indicated by the label of one the specimens, with the note "1928". Barbara Kietlińska-Michalik (the Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków) found some previously uncatalogued and lost specimens from the collection. Most of the specimens were catalogued later and the catalogue prefix A-III-61 with the specimen number was added for each specimen. In total, the collection is composed of 50 specimens. All of them are re-catalogued here (No. 2013/1-50).

The plant macroremains (mainly leaves) are preserved mostly as impressions, one cast, and some coalified plant detritus, all in fine-grained limestones and marls. The state of preservation of the remains is usually good. However, the impressions of the network of the leaf venation are generally poorly preserved and only impressions of primary and some secondary veins are visible. The plant fossils were identified solely on the basis of macromorphology. Leaf descriptions follow mostly Ellis *et al.* (2009). The drawings were made under a Carl Zeiss stereomicroscope with a *camera lucida* attachment. Macrophotographs were taken using an Olympus E-PL1 digital camera.

Two samples for pollen analysis were taken from the outcrop (Text-fig. 3A). The material was processed in the laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. Each sample was divided into two parts. One part of the material was processed according to the modified Erdtman's acetolysis method (Moore *et al.* 1991), using hydrofluoric acid to remove mineral matter; and the second part was processed using heavy liquid ($ZnCl_2$ + HCl; density 2.2 g/cm^3). Additionally, half of the material from each sample was sieved at 5 μm on a nylon mesh. The microscope slides were made using glycerine as a mounting medium. The rock samples and palynological residues are stored in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. Both samples contained no sporomorphs. However, they were full of organic particles (sedimentary organic matter) allowing analysis of the palynological matter. Description of the sedimentary organic matter follows Tyson (1993, 1995) and Batten (1996). Microphotographs of palynofacies were taken using a NIKON Eclipse microscope fitted with a Canon digital camera.

Microfacies as well as the foraminifera were studied in thin sections [two thin sections from a sample collected by Kuźniar (1910; sample 24/2013) and 10 thin sections from the outcrop] under Carl Zeiss Axioskop and Nikon Eclipse E600 POL optical microscopes and a Nikon SMZ 1500 stereo microscope. Thin sections are stored at the Institute of Geological Sciences, Jagiellonian University in Kraków.

SYSTEMATIC PALAEOBOTANY

The classification of higher taxonomic categories follows Reveal (1996) and Takhtajan (2009) and author names of families follow APG III (2009).

Division: Magnoliophyta (Angiosperms) Cronquist, Takhtajan et Zimmermann ex Reveal 1996

Class: Magnoliopsida (Dicotyledons) Brongniart 1843

Family Lauraceae Jussieu 1789
Genus *Daphnogene* Unger 1845
cf. *Daphnogene* sp.
(Text-fig. 5A)

1910. *Daphnogene melastomacea* ? Unger; Kuźniar, p. 46.

MATERIAL: 8/2013 (A-III-61/5).

DESCRIPTION: One leaf, about 5 cm long and 4 cm wide, entire-margined, slightly asymmetric. Venation pinnate, secondary venation acrodromous.

REMARKS: The characteristic venation of the leaf remains allowed their identification as the fossil-taxon *Daphnogene* (synonym of *Cinnamomophyllum* and *Cinnamomum*). The generic name *Daphnogene* Unger is an artificial name given to fossil leaves from the family Lauraceae with acrodromous venation (triplinerved), similar to the recent genus *Cinnamomum* Schaeffer (Kvaček and Knobloch 1967; Mai and Walther 1978). In the opinion of Kvaček (1971), it is impossible to assign fossil leaf taxa of the family Lauraceae to an extant genus on the basis of either the morphology or the anatomy.

MODERN EQUIVALENTS: In respect of morphology, fossil leaves of *Daphnogene* could be compared to leaves of several extant genera of the Lauraceae, in-
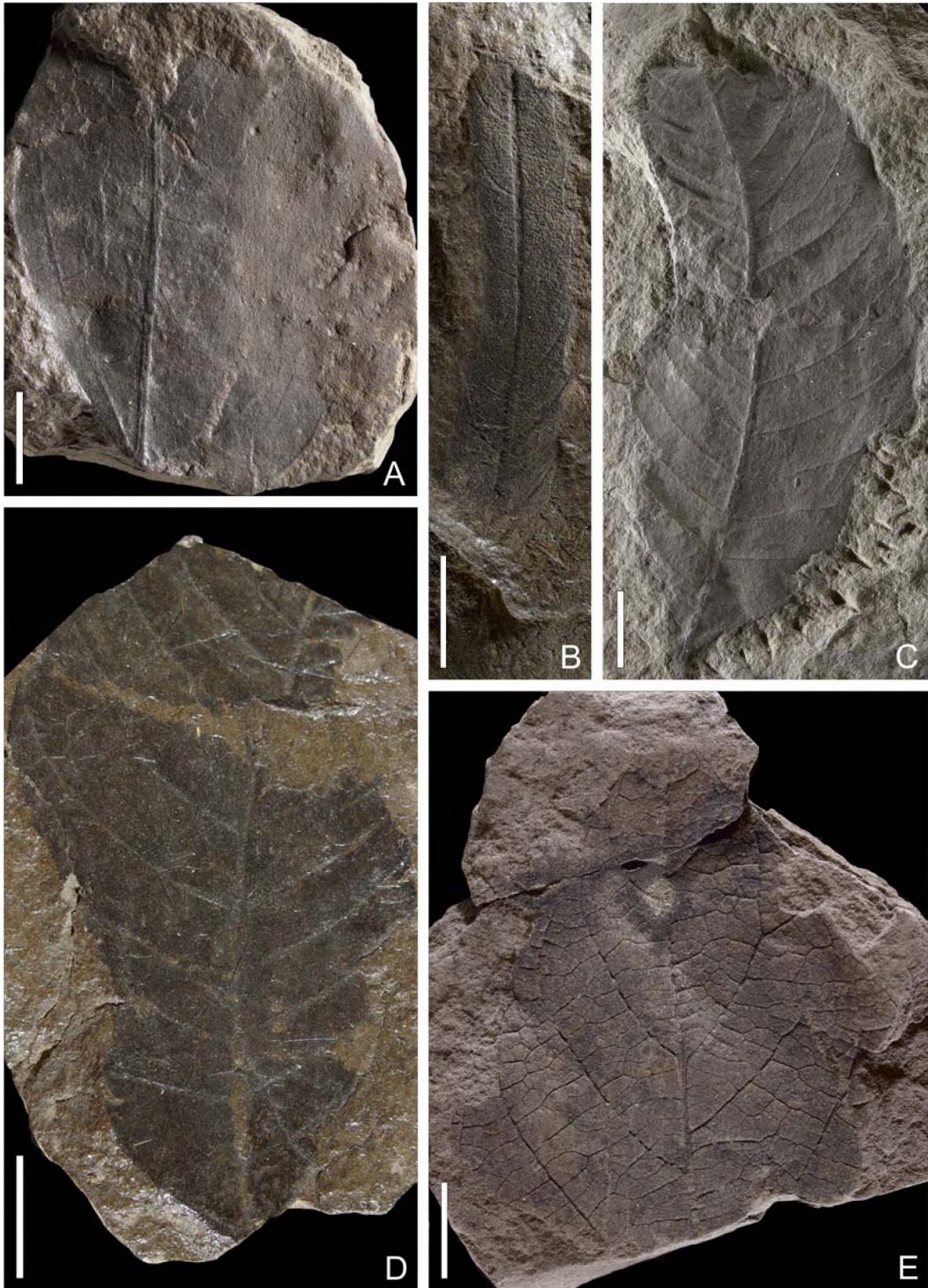
Text-fig. 5. Fossil plants from the Wiktor Kuźniar collection. A – cf. *Daphnogene* sp. (8/2013); B–D – *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček ssp. *furcinervis* 1989 (B: 19/2013, C: 42/2013, D: 7/2013); E – *Dicotylophyllum* cf. *juglandoides* (Rossmässler) Knobloch et Z. Kvaček 1996 (48/2013). Scale bar – 1 cm

cluding *Cryptocarya, Litsea, Lindera,* and *Neolitsea* (Kolakovskii 1958; Kvaček 1971). Acrodromous venation occurs in at least 11 genera of the family Lauraceae (Bannister *et al.* 2012).

ECOLOGY: *Daphnogene* represents a palaeotropical element and was a component of mesophytic and swamp vegetation.

OCCURRENCE: Leaves of *Daphnogene* are common in the fossil leaf assemblages of warm periods of the Palaeogene and Neogene of Europe (Mai 1995). In the territory of Poland, they are reported from Eocene and Miocene floras (Worobiec 2007).

Family Fagaceae Dumortier 1829
Genus *Eotrigonobalanus* Walther et Z. Kvaček 1989

Eotrigonobalanus furcinervis (Rossmässler) Walther et Z. Kvaček ssp. *furcinervis* 1989
[cf. *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček 1989]
(Text-figs 5B–D, 6A)

1840. *Phyllites furcinervis* Rossmässler, p. 33–34, pl. 6, fig. 25, pl. 7, figs 32–36.
1910. *Carpinus grandis* Unger; Kuźniar, p. 43
1989. *Eotrigonobalanus furcinervis* (Rossmässler); Walther et Z. Kvaček ssp. *furcinervis*, p. 583, figs 3–5, pl. 33, figs 1–6, pl. 38, fig. 3, pl. 39, fig. 1, pl. 40, figs 1–5, pl. 41, figs 1–4, pl. 42, figs 1–4, pl. 43, figs 1–6.

MATERIAL: 7/2013 (A-III-61/17), 19/2013 (A-III-61/6), 42/2013 (A-III-61/29), 2/2013 (cf. *Eotrigonobalanus furcinervis*).

DESCRIPTION: Leaf fragments, up to 7.6 cm long and 2–4 cm wide, one specimen with obtuse leaf base. Leaves both serrate and entire-margined, especially in basal part. Secondary veins and their branches terminate at tooth apex. Venation pinnate, primary vein straight or bent, usually rather thick. Secondary venation mixed: craspedodromous in serrate part of leaves and brochidodromous in entire-margined part. Up to 13 pairs of secondary veins are preserved. Secondaries curved upward, at intervals of 0.4–0.6 cm. Secondary veins form an angle of 50–70° with the primary vein.

REMARKS: Extinct member of the family Fagaceae. Serrate leaves are typical of this subspecies. A leaf of ?*Eotrigonobalanus furcinervis* was earlier reported from the Upper Eocene deposits of Chłabówka (Głazek and Zastawniak 1999). Kuźniar (1910) also probably reported it mistakenly as *Dryandroides angustifolia* ? Unger and *Quercus urophylla* Unger. It was not possible to find Kuźniar's (1910) taxonomic determinations of specimens 2/2013, 7/2013, and 19/2013.

MODERN EQUIVALENTS: Fossil-taxon related to recent members of the fagaceous genera *Castanopsis, Litocarpus* and *Trigonobalanus* (Denk *et al.* 2012).

ECOLOGY: *Eotrigonobalanus furcinervis* represents a palaeotropical element. This taxon was an important component of the European Palaeogene mesophytic to swamp forest vegetation (Mai 1995; Uhl *et al.* 2002; Denk *et al.* 2012; Hennig and Kunzmann 2013).

OCCURRENCE: *Eotrigonobalanus furcinervis* is reported from the Middle Eocene to Lower Miocene deposits of Europe (Mai 1995; Uhl *et al.* 2002; Denk *et al.* 2012; Hennig and Kunzmann 2013).
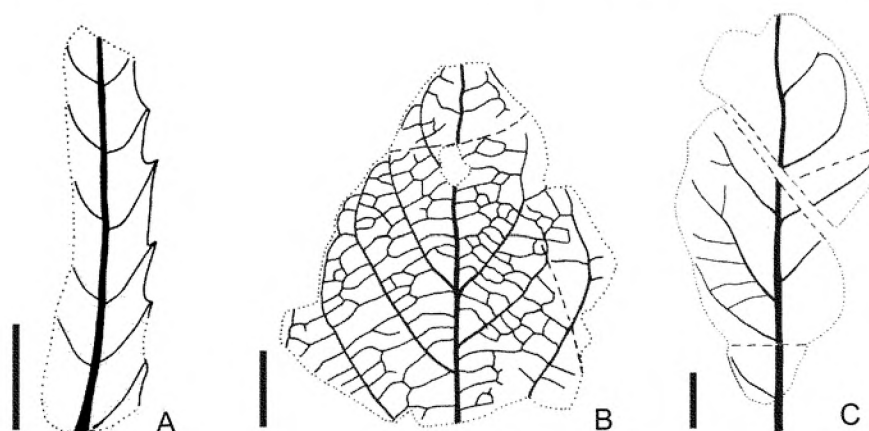
Text-fig. 6. Fossil plants from the Wiktor Kuźniar collection. A – *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček ssp. *furcinervis* 1989 (19/2013); B – *Dicotylophyllum* cf. *juglandoides* (Rossmässler) Knobloch et Z. Kvaček 1996 (48/2013); C – *Dicotylophyllum* sp. 5 (47/2013). Scale bar – 1 cm

Dicotyledones incertae sedis
Genus *Dicotylophyllum* Saporta 1894
Dicotylophyllum cf. *juglandoides* (Rossmässler)
Knobloch et Z. Kvaček 1996
(Text-figs 5E, 6B)

? 1840. *Phyllites juglandoides* Rossmässler, p. 29–30, pl. 4, fig. 16.

? 1996. *Dicotylophyllum juglandoides* (Rossmässler) Knobloch et Z. Kvaček; Knobloch *et al.*, p. 108–111, figs 53a–e, 54a–c, 55a–c, pl. 14, figs 2–3, pl. 20, figs 1–4, pl. 21, figs 1–3.

MATERIAL: 48/2013 (A-III-61/18).

DESCRIPTION: Leaf fragment, about 5 cm long and 5 cm wide, entire-margined. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation brochidodromous. Secondaries curved upward and interconnected in loops, distributed at intervals of 0.7–1.2 cm. Secondary veins form an angle of 40–50° with the primary vein. Tertiary venation distinctly percurrent. About 5 tertiary veins occur per 1 cm of secondary vein length. Higher-order venation reticulate.

REMARKS: The leaf shape and architecture of the leaf venation are similar to those in the fossil-species *Dicotylophyllum juglandoides* (Rossmässler) Knobloch et Z. Kvaček, a new combination erected on the basis of the Eocene leaf material from the locality Staré Sedlo in Czech Republic (Knobloch *et al.* 1996). It was not possible to find Kuźniar's (1910) taxonomic determination of this specimen.

MODERN EQUIVALENTS: Rossmässler (1840) compared discussed fossil with leaves of the Recent genera *Magnolia*, *Tetranthera*, *Persea* and *Visnea*.

Dicotylophyllum sp. 1
(Text-fig. 7A)

1910. *Eucaliptus oceanica* Unger; Kuźniar, p. 48–49.

MATERIAL: 6/2013 (A-III-61/32), 11/2013 (A-III-61/24).

DESCRIPTION: Leaf fragments, (specimen 11/2013: 6.6 cm long and 1.2 cm wide), entire-margined. Venation pinnate, primary vein straight, thick. Secondary veins curved upward.

REMARKS: The systematic position of these leaf fossil fragments remains unknown due to the absence of distinctive features and the poor state of preservation. The second specimen of *Dicotylophyllum* sp. 1, found in the collection of plant remains from Hruby Regiel and labelled "*Edocarpus eocenica* Unger", was not mentioned in the paper of Kuźniar (1910).

Dicotylophyllum sp. 2
(Text-fig. 7B)

MATERIAL: 18/2013 (A-III-61/21).

DESCRIPTION: Fragment of large leaf, about 13 cm long and 8 cm wide, entire-margined. Venation pinnate, primary vein straight, rather thick. Secondary veins distributed at intervals of about 2.5 cm, forming an angle of 40–50° with the primary vein.

REMARKS: The systematic position of this leaf fossil fragment remains unknown due to the absence of distinctive features and the poor state of preservation. It was not possible to find Kuźniar's (1910) taxonomic determination of this specimen.

Dicotylophyllum sp. 3
(Text-fig. 7C)

MATERIAL: 27/2013 (A-III-61/25).

DESCRIPTION: Fragment of probably coriaceous leaf, 5.2 cm long and 1.7 cm wide, entire-margined. Venation pinnate, primary vein straight, moderate thickness. Secondary venation brochidodromous. Secondary veins distributed at intervals of 0.7–1.1 cm, forming an angle of about 40° with the primary vein.

REMARKS: The systematic position of this leaf fossil fragment remains unknown due to the absence of distinctive features and the poor state of preservation. The specimen, found in the collection of plant remains from Hruby Regiel with the label "*Quercus daena* Heer", was not mentioned in the paper of Kuźniar (1910).

Dicotylophyllum sp. 4
(Text-fig. 7D)

1910. *Populus mutabilis repando-crenata* Heer; Kuźniar, p. 44–45.
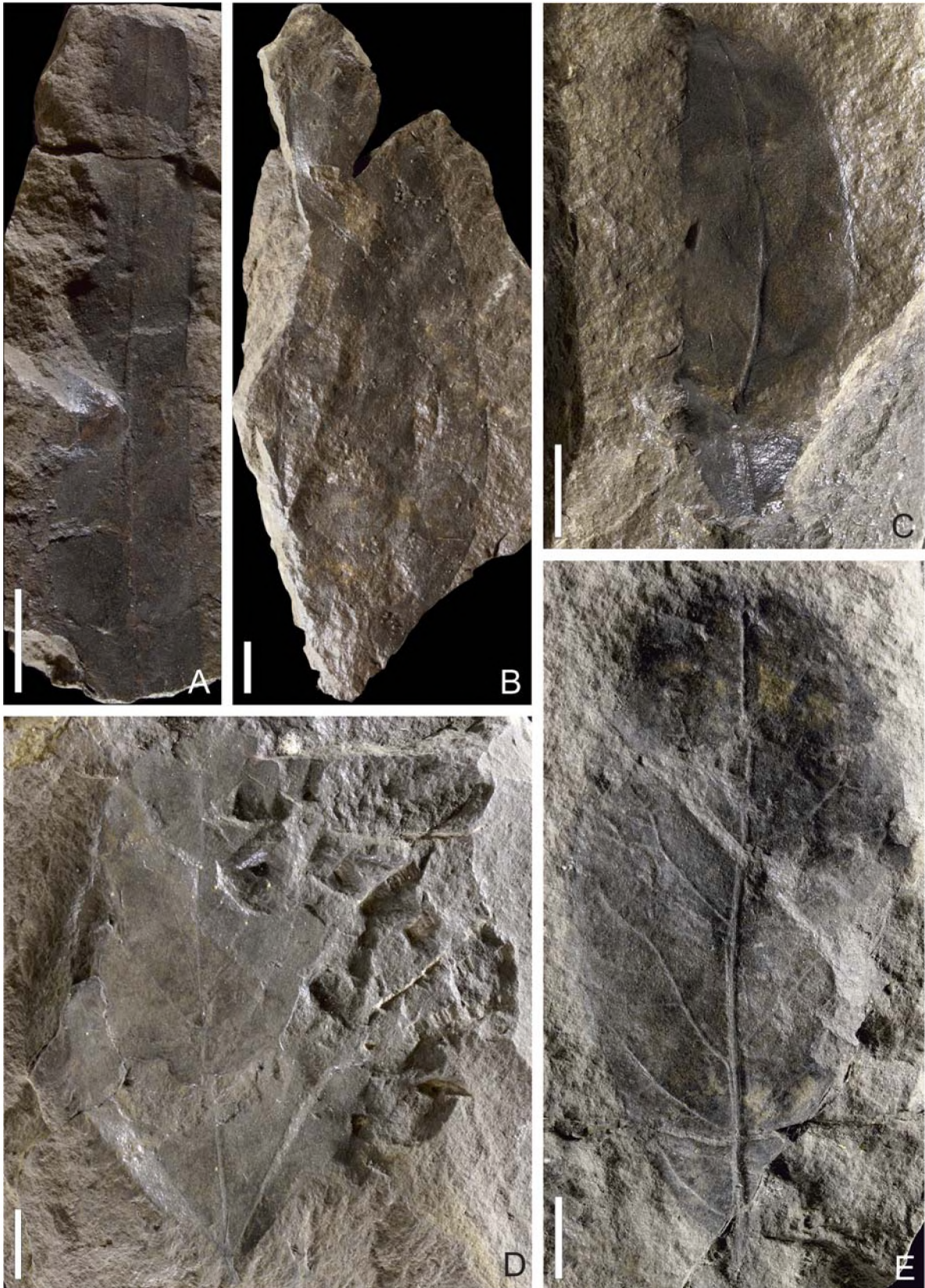
Text-fig. 7. Fossil plants from the Wiktor Kuźniar collection. A – *Dicotylophyllum* sp. 1 (11/2013); B – *Dicotylophyllum* sp. 2 (18/2013); C – *Dicotylophyllum* sp. 3 (27/2013); D – *Dicotylophyllum* sp. 4 (33/2013); E – *Dicotylophyllum* sp. 5 (47/2013). Scale bar – 1 cm

MATERIAL: 33/2013 (A-III-61/30), 34/2013 (A-III-61/14), 45/2013.

DESCRIPTION: Fragments of entire-margined leaves. Preserved leaf base more or less obtuse. Venation imperfectly acrodromous. Secondary veins form an angle of 50–60° with the midvein.

REMARKS: The systematic position of these leaf fossil fragments remains unknown due to the absence of distinctive features and the poor state of preservation. It was not possible to find Kuźniar's (1910) taxonomic determination of specimens 34/2013 and 45/2013.

Dicotylophyllum sp. 5
(Text-figs 6C, 7E)

1910. *Pyrus troglodytarum* Unger; Kuźniar, p. 49.

MATERIAL: 47/2013 (A-III-61/31).

DESCRIPTION: Fragment of entire-margined leaf, with obtuse leaf base. Venation pinnate, primary vein thick. Secondary venation camptodromous. Secondaries curved slightly upward and branched, distributed at intervals of 0.9–1.6 cm. Secondary veins form an angle of 40–55° with the primary vein.

REMARKS: The systematic position of this leaf fossil fragment remains unknown due to the absence of distinctive features and the poor state of preservation.

Dicotylophyllum sp. 6
(Text-fig. 8A)

1910. *Apocynophyllum lanceolatum* Unger; Kuźniar, p. 47.

MATERIAL: 36/2013 (A-III-61/33).

DESCRIPTION: Large coriaceous leaf, 17 cm long and 5 cm wide, entire-margined, margin revolute. Venation pinnate, secondary venation camptodromous. Secondaries curved slightly upward, distributed at intervals of about 1–2 cm. Secondary veins form an angle of about 50° with the primary vein.

REMARKS: The systematic position of this leaf fossil remains unknown due to the absence of distinctive features and the poor state of preservation

Dicotyledones incertae sedis = Dicotyledones indet.
(Text-fig. 8B, C)

1910. *Daphnogene melastomacea* Unger; Kuźniar, pro parte, p. 46 [only 30/2013].
1910. *Ficus morloti* Unger; Kuźniar, p. 44.
1910. *Laurus lalages* Unger; Kuźniar, pro parte, p. 45 [only 26/2013 and 28/2013].

MATERIAL: 5/2013, 17/2013 (A-III-61/26), 20/2013 (A-III-61/8), 21/2013, 22/2013, 24/2013, 25/2013 (A-III-61/19), 26/2013 (A-III-61/28), 28/2013, 30/2013 (A-III-61/10), 31/2013 (A-III-61/9), 32/2013 (A-III-61/13), 35/2013 (A-III-61/1), 40/2013 (A-III-61/7), 41/2013 (A-III-61/12), 43/2013 (A-III-61/11), 44/2013 (A-III-61/2).

REMARKS: The systematic position of these plant remains is unknown. Specimen found in collection from Hruby Regiel with the label "*Quercus chlorophylla* Unger", was not mentioned in Kuźniar (1910). It was not possible to find Kuźniar's (1910) taxonomic determination of specimens 20/2013, 21/2013, 22/2013, 24/2013, 25/2013, 31/2013, and 32/2013.

Class: Liliopsida (Monocotyledons)
Family: Arecaceae Bercht. et Presl. 1820
Genus *Nypa* Steck 1757
Nypa burtini (Brongniart) Ettingshausen 1879
(Text-fig. 8E, F)

1828. *Cocos burtini*; Brongniart, p. 121.
1849. *Nipadites burtini*; Brongniart, p. 88.
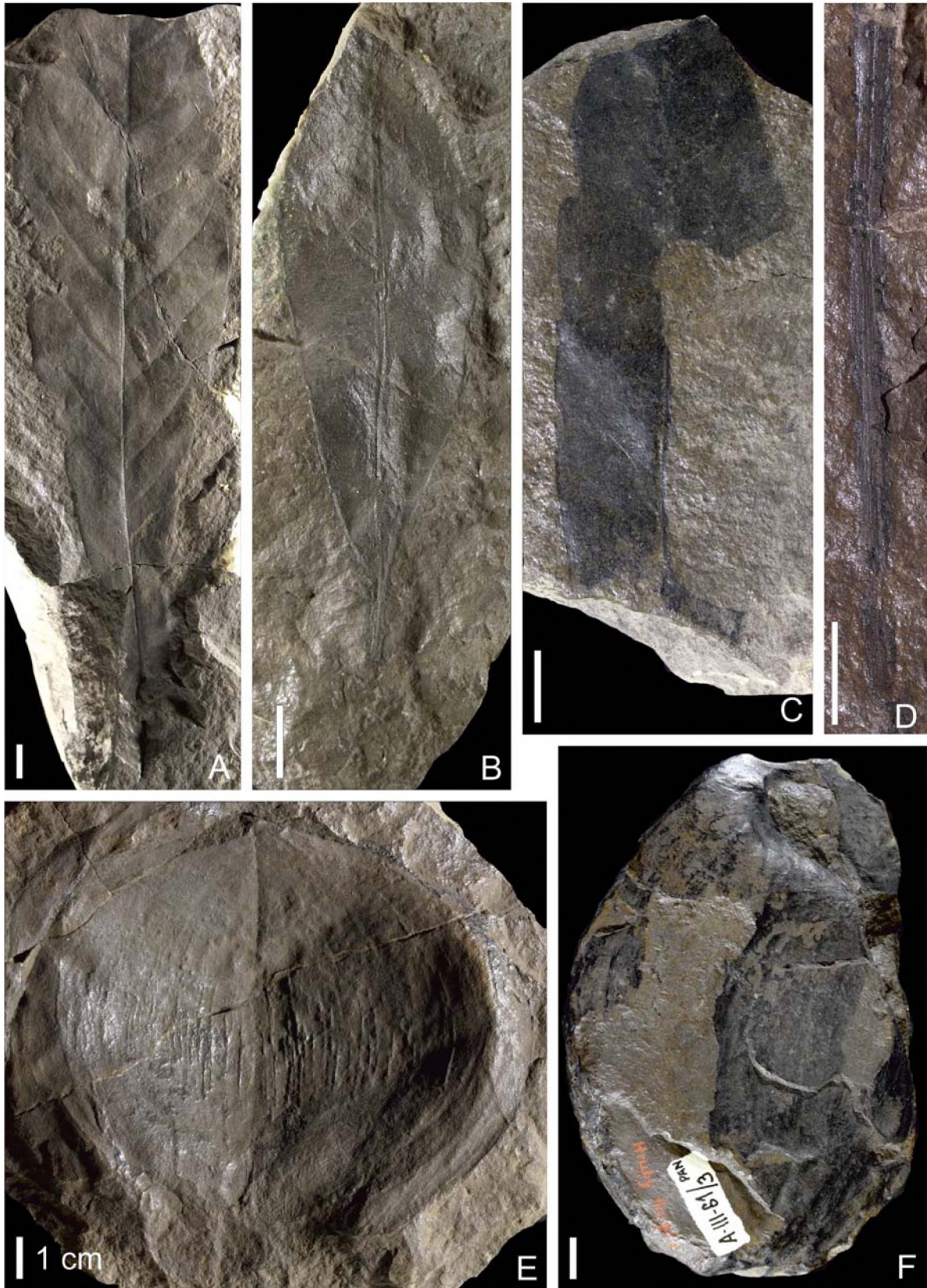1879. *Nipa burtini* Brongniart; Ettingshausen, p. 393.
1910. *Nipadites burtini* Brongniart; Kuźniar, p. 40–41.

MATERIAL: 15/2013 (A-III-61/34), 38/2013 (A-III-61/3).

DESCRIPTION: Two remains: impression and strongly compressed cast of fruit. Cast: 12.5 cm long, 8 cm wide, obovoid, with traces of longitudinal ridges and deformed umbo (about 2.3 cm in size). Impression: about 10 cm long and 11 cm wide, suborbicular, surface of impression with numerous impressions of longitudinal ridges.

REMARKS: The morphology of the remains, especially the obovoid shape and longitudinal ridges suggest an affinity with the genus *Nypa*. Fossil carpological remains comparable to *Nypa,* have been described under the genera *Burtinia, Castellinia, Fracastoria, Nipa, Nipadites,* and *Nypa* (Tralau 1964).

Text-fig. 8. Fossil plants from the Wiktor Kuźniar collection. A – *Dicotylophyllum* sp. 6 (36/2013); B, C – Dicotyledones incertae sedis = Dicotyledones indet. (B: 28/2013, C: 30/2013); D – Incertae sedis (11/2013); E, F – *Nypa burtini* (Brongniart) Ettingshausen 1879 (E: fruit impression, 15/2013, F: fruit cast, 38/2013). Scale bar – 1 cm

MODERN EQUIVALENTS: Today, *Nypa* is a mono-typic genus, with the species *N. fruticans* Wurmb., which is restricted to the tropical coast of southeast Asia and growing mostly in mangrove communities in a tropical, frost-free climate (Krutzsch 1989). *Nypa burtini* differs from the extant *N. fruticans* in seed morphology and anatomy, which is discussed broadly by El-Soughier *et al.* (2011).

ECOLOGY: *Nypa* represents a palaeotropical element. This taxon was a component of mangrove vegetation (Tsuji *et al.* 2011).

OCCURRENCE: *Nypa* is known from the beginning of the Cretaceous. In Europe it was common in Eocene floras (Belgium, France, Hungary, Poland, Spain, Ukraine, United Kingdom) and disappeared in the latest Eocene. Outside Europe, it was reported from the Late Cretaceous to Palaeocene of South America (Brazil, Colombia, Venezuela), the Eocene of North America, the Late Cretaceous to Middle Eocene of Africa (Cameroon, Egypt, Nigeria) and from the Late Cretaceous to Recent in many localities in southeast Asia and Australia (Krutzsch 1989; Gee 1990; Gray 1993; Gee 2001; Plaziat *et al.* 2001).

Incertae sedis
(Text-fig. 8D)

1910. *Quercus* sp.; Kuźniar, p. 43.
1910. *Poacites* sp.; Kuźniar, p. 40.

MATERIAL: 1/2013, 3/2013, 4/2013 (A-III-61/27 and A-III-61/24), 4/2013, 9/2013, 12/2013 (A-III-61/20), 16/2013, 23/2013, 29/2013, 37/2013, 39/2013, 46/2013, 49/2013 (A-III-61/15), 50/2013 (A-III-61/22).

REMARKS: Remains of uncertain origin. It was not possible to find Kuźniar's (1910) taxonomic determinations of specimens 1/2013, 4/2013, 10/2013, 12/2013, 13/2013, 16/2013, 23/2013, 29/2013, 37/2013, 39/2013, 46/2013, 49/2013, 50/2013, and 14/2013.

TRACE FOSSILS

Three specimens from the studied collection appeared to be trace fossils. Their original labels are missing. Moreover, small cylindrical burrows co-occur with leaves in a few specimens. The interpretation of trace fossils as plants was common throughout the 19th century and continued by some researchers at the beginning of 20th century (Baucon *et al.* 2012).

Ichnogenus *Gyrolithes* Saporta, 1884
?*Gyrolithes* isp.
(Text-fig. 9A, B)

MATERIAL: 10/2013.

DESCRIPTION: Fragments of horizontal to subhorizontal, arcuate, endichnial cylinders, 10–12 mm wide, elliptical in cross section, displaying a thin, knobby wall. The knobs, seen from the interior, are small, circular depressions, 0.5–1 mm wide, located 1–2 mm apart. Filling of the cylinders is the same as in the surrounding rock. The cylinders occur on the lower and upper surfaces and inside the specimen, which is a small, 32 mm thick slab. Their arrangement suggests a vertical, helical spiral pattern. The estimated whorl radius of the spiral can range from 15 to 40 mm for individual arcs.

REMARKS: The helical, vertical spiral is typical of *Gyrolithes* Saporta, 1884, however the fragmentary preservation of the described specimen does not allow its unequivocal determination. The knobby wall is known from *Gyrolithes marylandicus* (Mansfield, 1927) and *Gyrolithes nodosus* Mayoral and Muñiz, 1998, but the morphometric parameters (burrow width, whorl radius) does not fit these ichnospecies (see Uchman and Hanken 2013), being rather similar to those of the smooth-walled *G. saxonicus* (Häntzschel, 1934) or *G. cycloides* (Mikuláš and Pek, 1994). Larger *Gyrolithes* are burrows produced by crustaceans since the Permian (Uchman and Hanken 2013). Their monodominant ichnoassemblages are typical of brackish, shallow-marine deposits (e.g. Netto *et al.* 2007).

Ichnogenus *Ophiomorpha* Lundgren, 1891
Ophiomorpha isp.
(Text-fig. 9C)

MATERIAL: 13/2013.

DESCRIPTION: This trace fossil is preserved as a fragment of a horizontal to subhorizontal (toponomy of the specimen is unclear), endichnial cylinder, 11–13 mm in diameter, 145 mm long, circular in cross section, curved in a gentle arc. It displays a thin, knobby wall.
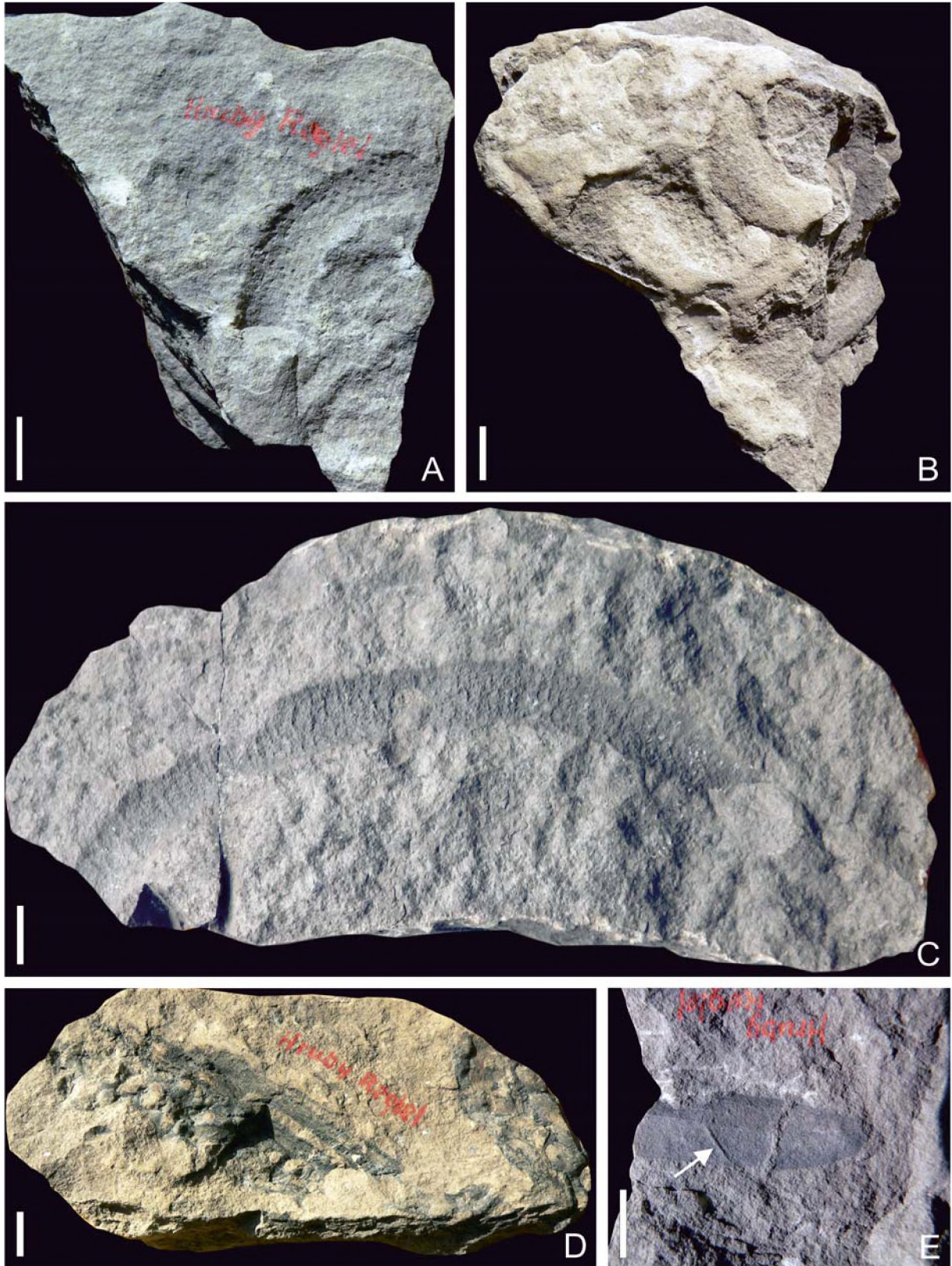
Text-fig. 9. Trace fossils. A, B – ?*Gyrolithes* isp. (10/2013), view from opposite surfaces; C – *Ophiomorpha* isp. (13/2013); D – *Teredolites clavatus* (14/2013); E – small cylindrical burrows (arrow) (32/2013)

The knobs, seen from the interior, are small, shallow, elliptical depressions, 2.5–3 mm long, 1–1.5 mm wide, the longer axes being perpendicular to the course of the cylinder. The knobs are arranged in rings. Filling of the cylinder is the same as in the surrounding rock.

REMARKS: The knobs in the wall, interpreted as agglutinated pellets, are typical of *Ophiomorpha* Lundgren, 1891. The perpendicular arrangement of the pellets and the diameter of the burrow are similar to *Ophiomorpha annulata* Książkiewicz, 1977 sensu Howard and Frey (1984) and Frey and Howard (1985), described from the Upper Cretaceous of the United States. However, the type material of *Ophiomorpha annulata* Książkiewicz, 1977 is different, showing mostly straight, commonly smooth, branched cylinders (Uchman 1995, 1998). *Ophiomorpha* is a crustacean, mostly decapod burrow, of which the type ichnospecies *O. nodosa* Lundgren, 1891 occurs mostly in shallow-marine sediments (Frey *et al.* 1978), while *Ophiomorpha annulata* Książkiewicz, 1977 is typical of flysch deposits (Uchman 1995, 1998).

Ichnogenus *Teredolites* Leymerie, 1842
Teredolites clavatus Leymerie, 1842
(Text-fig. 9D)

MATERIAL: 14/2013.

DESCRIPTION: *Teredolites clavatus* is visible as gregarious, tightly spaced clavate mounds in carbonized woody substrate, 2–6 mm in diameter, circular to irregularly oval in outline, showing sharp boundaries. Their length is difficult to estimate, because they are observed in cross section and many mounds are truncated by the specimen surface. They are perpendicular to oblique to the grain of the woody substrate. Some individual mounds are in contact with a mutual deformational adjustment.

REMARKS: *Teredolites* is a boring produced in woody (xylic) substrates (e.g. Kelly and Bromley 1984) by bivalves (Röder 1977) worldwide in shallow- to deep-marine environments (Kelly 1988). Recently, similar borings are produced by *Martesia* and in the fossil record by *Martesia* and *Opertochasma*. *T. clavatus*
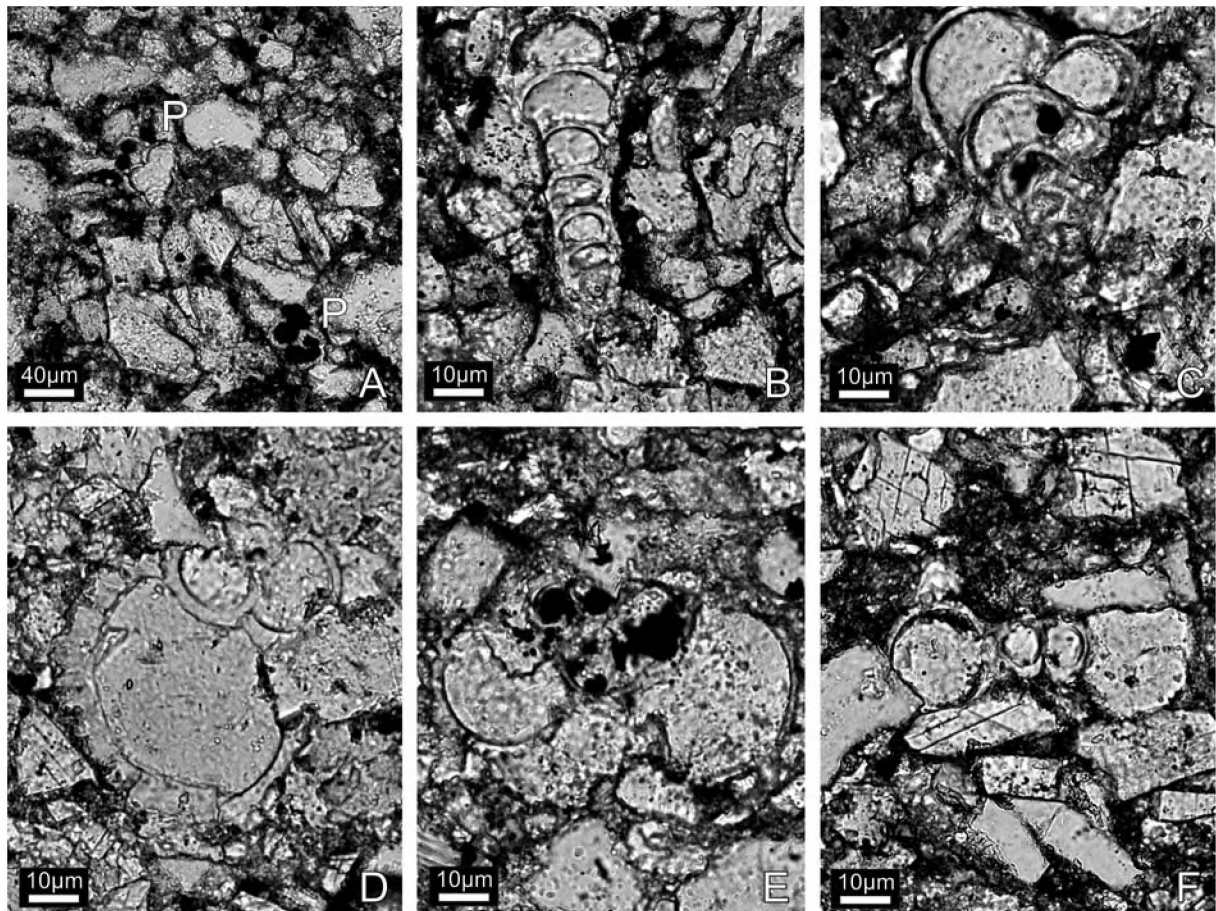
Text-fig. 10. Characteristic planktonic foraminifera from the sample of the Wiktor Kuźniar collection (24/2013). A – abundant *Chiloguembelina* cf. *gracillima* (Andreae) (P); B, C – *Chiloguembelina* cf. *gracillima* (Andreae); D – *Globigerinatheka* cf. *index* (Finlay); E, F – planktonic foraminifera

ranges from the Jurassic to Recent (Kelly and Bromley 1984). It is worth mentioning that the supposed palm fruits *Phoenix szaferi* described by Bąkowski (1967) from the Zakopane Beds, which overlie the study deposits, appeared to be *Teredolites* (Radwański 2009).

Small cylindrical burrows
(Text-fig. 9E)

MATERIAL: 32/2013.

DESCRIPTION: This trace fossil is preserved as a thin, almost straight ridge, 0.5 mm wide, running on the surface of the leaf blade of an incertae sedis dicotyledonous leaf and plunging into the surrounding sediments, where its visibility decreases greatly in a short distance from the leaf edge.

REMARKS: This is a burrow produced by unknown, small invertebrate. It resembles the category of "leaf underminings" being small burrows produced preferentially under leaves for food and protection (for sim-

ilar interpretation in fresh-water sediments see Uchman *et al.* 2004) and preserved preferentially as the leaf blade forms a stable "wall" preventing against rapid collapse in normal softground conditions.

RESULTS OF THE REVISION

The results of the revision are summarised in Tables 1 through 3.

FORAMINIFERA

Due to the validity of the Kuźniar collection only two thin sections were prepared from a part of a single rock sample (24/2013). Micropalaeontological analysis of the sections revealed foraminiferal assemblages dominated by planktonic species (Text-fig. 10). Tests of benthic symbiont-bearing taxa belonging mainly to the Nummulitidae occur sporadically and are usually damaged. Some small benthic calcareous forms can also occur.

Original name in Kuźniar (1910)	Current name
Amygdalus pereger Unger	specimen or original label missing
Apocynophyllum lanceolatum Unger	*Dicotylophyllum* sp. 6
Carpinus grandis Unger	*Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček ssp. *furcinervis*
Daphnogene melastomacea Unger	cf. *Daphnogene* sp.
Daphnogene melastomacea Unger	Dicotyledones incertae sedis
Daphnogene paradisiaca Unger	specimen or original label missing
Dryandroides angustifolia Unger	specimen or original label missing
Eucaliptus oceanica Unger	*Dicotylophyllum* sp. 1
Ficus morloti Unger	Dicotyledones incertae sedis
Laurus lalages Unger	Dicotyledones incertae sedis
Nipadites burtini Brongniart	*Nypa burtini* (Brongniart) Ettingshausen
Poacites sp.	Incertae sedis
Podocarpus eocenica Unger	specimen or original label missing
Populus mutabilis repando-crenata Heer	*Dicotylophyllum* sp. 4
Pyrus troglodytarum Unger	*Dicotylophyllum* sp. 5
Quercus sp.	Incertae sedis
Quercus urophylla Unger	specimen or original label missing
Sapotacites sideroxyloides Ettingshausen	specimen or original label missing

Table 1. Taxonomic determinations of plant remains from the Hruby Regiel section in Kuźniar (1910) and present determinations

Original name	Current name
Edocarpus eocenica Unger	*Dicotylophyllum* sp. 1
Quercus chlorophylla Unger	Dicotyledones incertae sedis
Quercus daena Heer	*Dicotylophyllum* sp. 3

Table 2. Labelled specimens found in collection of plant remains from the Hruby Regiel section, not mentioned in Kuźniar (1910) and their current taxonomical determinations

Current number	Number used by Museum of the Institute of Geological Sciences, PAS, Kraków	Original name in Kuźniar (1910)	Current name
1/2013			Incertae sedis
2/2013			cf. *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček
3/2013		*Quercus* sp.	Incertae sedis
4/2013	A-III-61/27	*Poacites* sp.	Incertae sedis
4/2013	A-III-61/24		Incertae sedis
5/2013			Dicotyledones incertae sedis
6/2013	A-III-61/32		*Dicotylophyllum* sp. 1
7/2013	A-III-61/17		*Eotrigonobalanus furcinervis (*Rossmässler) Walther et Z. Kvaček ssp. *furcinervis*
8/2013	A-III-61/5	*Daphnogene melastomacea* Unger	cf. *Daphnogene* sp.
9/2013			Incertae sedis
10/2013			?*Gyrolithes* isp.
11/2013	A-III-61/24	*Eucaliptus oceanica* Unger	*Dicotylophyllum* sp. 1
12/2013	A-III-61/20		Incertae sedis
13/2013			*Ophiomorpha* isp.
14/2013			*Teredolites clavatus*
15/2013	A-III-61/34	*Nipadites burtini* Brongniart	*Nypa burtini* (Brongniart) Ettingshausen
16/2013			Incertae sedis
17/2013	A-III-61/26		Dicotyledones incertae sedis
18/2013	A-III-61/21		*Dicotylophyllum* sp. 2
19/2013	A-III-61/6		*Eotrigonobalanus furcinervis (*Rossmässler) Walther et Z. Kvaček ssp. *furcinervis*
20/2013	A-III-61/8		Dicotyledones incertae sedis
21/2013			Dicotyledones incertae sedis
22/2013			Dicotyledones incertae sedis
23/2013			Incertae sedis
24/2013			Dicotyledones incertae sedis
25/2013	A-III-61/19		Dicotyledones incertae sedis
26/2013	A-III-61/28	*Laurus lalages* Unger	Dicotyledones incertae sedis
27/2013	A-III-61/25		*Dicotylophyllum* sp. 3
28/2013		*Laurus lalages* Unger	Dicotyledones incertae sedis
29/2013			Incertae sedis
30/2013	A-III-61/10	*Daphnogene melastomacea* Unger	Dicotyledones incertae sedis
31/2013	A-III-61/9		Dicotyledones incertae sedis
32/2013	A-III-61/13		Dicotyledones incertae sedis + trace fossil
33/2013	A-III-61/30	*Populus mutabilis repando-crenata* Heer	*Dicotylophyllum* sp. 4
34/2013	A-III-61/14		*Dicotylophyllum* sp. 4
35/2013	A-III-61/1	*Ficus morloti* Unger	Dicotyledones incertae sedis
36/2013	A-III-61/33	*Apocynophyllum lanceolatum* Unger	*Dicotylophyllum* sp. 6
37/2013			Incertae sedis
38/2013	A-III-61/3	*Nipadites burtini* Brongniart	*Nypa burtini* (Brongniart) Ettingshausen
39/2013			Incertae sedis
40/2013	A-III-61/7		Dicotyledones incertae sedis
41/2013	A-III-61/12		Dicotyledones incertae sedis
42/2013	A-III-61/29	*Carpinus grandis* Unger	*Eotrigonobalanus furcinervis (*Rossmässler) Walther et Z. Kvaček ssp. *furcinervis*
43/2013	A-III-61/11		Dicotyledones incertae sedis
44/2013	A-III-61/2		Dicotyledones incertae sedis
45/2013			*Dicotylophyllum* sp. 4
46/2013			Incertae sedis
47/2013	A-III-61/31	*Pyrus troglodytarum* Unger	*Dicotylophyllum* sp. 5
48/2013	A-III-61/18		*Dicotylophyllum* cf. *juglandoides* (Rossmässler) Knobloch et Z. Kvaček
49/2013	A-III-61/15		Incertae sedis
50/2013	A-III-61/22		Incertae sedis

BIOSTRATIGRAPHIC POSITION OF PLANT-BEARING DEPOSITS

The biostratigraphical determinations of the source of the plant-bearing deposits are based on the flora and foraminifera. *Eotrigonobalanus furcinervis* and *Nypa burtini* are typical plants of the European Palaeogene; *N. burtini* is restricted to the Eocene, disappearing by the end of this epoch (Gee 1990, 2001), whereas *E. furcinervis* is usually found in the Palaeogene, surviving in some localities until the Early Miocene (Denk *et al.* 2012).

The abundant planktonic foraminifera are dominated by *Chiloguembelina* cf. *gracillima* (Andreae) (Text-fig. 10A–C). This species indicates the standard planktonic foraminifer zones P16/17–P18, dated as latest Priabonian (Late Eocene) through to Rupelian (Early Oligocene) (see Berggren *et al.* 1995). Similarly, Samuel and Salaj (1968) noted *Ch. gracillima* in the uppermost part of the Eocene in the Slovak Carpathians. In addition, Olszewska (2009) reported this species from the Priabonian nummulitic deposits of the Tatra Mountains (localities Dolina Lejowa, Żleb Jaroniec, Dolina za Bramką, Suchy Żleb).

The foraminiferal assemblage also contains abundant, exclusively Late Eocene planktonic foraminifera, such as *Globigerinatheca* cf. *index* (Finlay) (Text-fig. 10D), and small benthic taxa, such as *Eponides* cf. *poligonus* of a Bartonian age and the Priabonian *Maslinella champani* Glaessner et Wade (Loeblich and Tappan 1988). The assemblage also includes rare, poorly preserved larger benthic foraminifera but they do not allow a precise dating of these deposits. However, the youngest Nummulitidae from the Tatric Eocene are dated as Priabonian (Bieda 1963; Machaniec *et al.* 2009; Jach and Machaniec 2014), more precisely to the SBZ 19–20 zones (see Serra-Kiel 1997). The co-occurrence of some planktonic (Text-fig. 10 E, F) and benthic forms of different ages suggests that the plant-bearing deposits may contain some recycled material.

The co-occurrence of *Chiloguembelina* cf. *gracillima* and other planktonic and benthic foraminifera (with ranges exclusively up to the Late Eocene) together with well preserved Eocene leaves and fruits limits the age of the plant-bearing deposits to the latest Priabonian.

## CHARACTERISTICS OF THE SEDIMENTARY ORGANIC MATTER

The organic particles in two samples from the plant-bearing deposits from the Hruby Regiel section include no structured organic matter (SOM), i.e. palynomorphs (plant sporomorphs, phytoplankton and zoomorphs) or structured phytoclasts (cuticles, wood tissues; Text-fig. 11A, B). Instead, highly homogeneous opaque and translucent phytoclasts with an admixture of amorphous organic matter (AOM) particles dominate. The AOM consists of both structureless grey fragments (derived from phytoplankton or degradation products of bacteria) and highly degraded plant tissues. The opaque phytoclasts are usually more or less equidimensional (O-Eq), angular, rarely roundish. Some of them are slightly translucent. They represent coalified or highly gelified structureless plant tissues corresponding to the vitrinite or inertinite maceral group. The sample dominated by coalified phytoclasts also contains roundish particles, most probably representing pyrite framboids. The presence of pyrite framboids was confirmed by means of the heavy liquid palynological procedure. After heavy liquid separation of the palynological matter from the residue, the roundish particles sank completely, confirming that they were heavier than the palynological matter, which is typical of pyrite. Pyrite framboids show a broad range of sizes (from ~ 2 μm to 30 μm) with mean diameters exceeding 5 μm. These framboid characters are typical of upper dysoxic depositional conditions (Wilkin *et al.* 1996; Bond *et al.* 2004; Zatoń *et al.* 2008) and indicate a possible dysoxic sedimentary environment during the deposition of the sediments of the Hruby Regiel section but not necessarily on the sea floor, as suggested by the absence of primary lamination and the occurrence of trace fossils. The absence of structured organic matter (palynomorphs and structured phytoclasts) could be due to a high rate of alteration of organic particles before and/or after burial in sediment. As a result, the palynomorphs and structured phytoclasts were highly degraded, homogenised and also coalified. This is confirmed by the dominance of highly gelified or coalified particles of plant origin.

PALAEOCLIMATIC CONSIDERATIONS BASED ON THE PLANT REMAINS AND FORAMINIFERA

Generally, there are two approaches to palaeoclimatic reconstructions using fossil leaf floras. The first one is the Nearest Living Relative method (NLR), based on an assumption that climatic tolerances of living relatives are similar to those of the fossil taxa (Mosbrugger and Utescher 1997). The quantitative method using NLR is the coexistence approach (CoA) as proposed by Mosbrugger and Utescher (1997). It

Table 3. The catalogue of plant taxa remains and trace fossils from the Hruby Regiel section
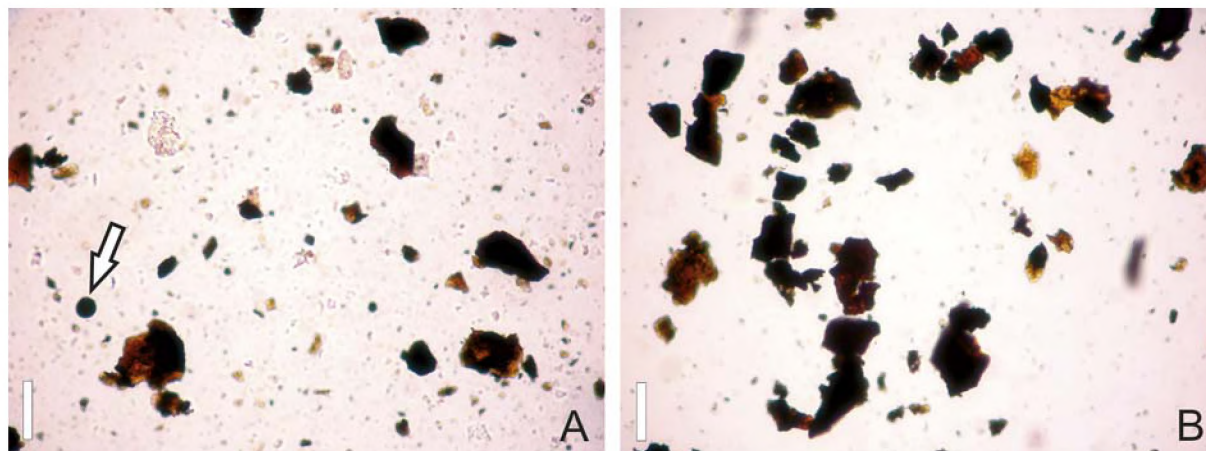
Text-fig. 11. Sedimentary organic matter from Hruby Regiel. Palynofacies dominated by highly homogeneous opaque and translucent phytoclasts. A – sample prepared without heavy liquid separation. Arrow indicates roundish pyrite framboid; B – sample prepared with heavy liquid separation. Visible concentrated SOM. Pyrite framboids completely absent. Scale bar – 50 μm

can be reliably used only for very young fossil plant assemblages, not older than Palaeogene. The second approach is based on correlation between climate and leaf physiognomy, i.e. the assumption that plant architecture (morphology of leaves) is modified by environmental conditions. Morphological characters used in this method include leaf margin architecture, size and shape of leaf, leaf thickness and the presence of special features, e.g. the drip tips (Spicer 1990). There are two methods for obtaining palaeoclimate proxies from leaf architecture: Leaf Margin Analysis (LMA) and the Climate Leaf Analysis Multivariate Program (CLAMP) using Canonical Correspondence Analysis (Bailey and Sinnott 1915, 1916; Wolfe 1971, 1978, 1993; Wing and Greenwood 1993). Compared with the NLR method, a palaeoclimatic approach based on leaf architecture has no time constraint and can be extended down to the Cretaceous extinct genera. Unfortunately, in the case of the leaf assemblage from the Hruby Regiel section, due to the rather small number of specimens (well below 100), a quantitative application of both NRL and leaf physiognomy methods (LMA + CLAMP) is not credible. Nonetheless, some considerations based on both approaches can be drawn.

Although the systematic position of most of the Eocene plant fossils from the Hruby Regiel section remains unclear, the leaves of *Eotrigonobalanus furcinervis* and *Daphnogene* sp. (Lauraceae) and the fruits of *Nypa burtini* could be related to extant nearest relatives. *Eotrigonobalanus furcinervis* is related to Recent members of the family Fagaceae belonging to the genera *Castanopsis*, *Lithocarpus* and *Trigonobalanus* (Denk *et al.* 2012). All of these three genera are restricted to areas of tropical to subtropical climate.

Daphnogene sp. shares morphological characters with at least eleven genera of the Lauraceae with acrodromous venation (Bannister *et al.* 2012). Like all members of the Lauraceae, these genera prefer warm climatic conditions. *Nypa fruticans,* a Recent relative of *Nypa burtini*, grows mostly in a tropical frost-free climate in mangrove communities of southeast Asia (Krutzsch 1989). It grows in areas with a warm and humid climate with a minimum temperature 20°C and more than 1,000 mm annual rainfall evenly distributed throughout the year (Lim 2012). *N. fruticans* is limited to tropical sea coasts with water temperatures above 20°C (Fechner 1988; Akgün 2013).

Among foraminifers occurring in the plant-bearing deposits the small, planktonic biserial forms of *Chiloguembelina* sp. predominate. Symbiont-bearing large benthic foraminifera, represented mainly by Nummulitidae, also occur. Most of their tests show evidence of damage. Large benthic foraminifera are limited to shallow, clear, oligotrophic, warm waters, with temperatures above 20°C in the photic zone (e.g. Hohenegger 2004). Planktonic chiloguembelinids required eutrophic water and are restricted to near-coastal environments (D'haenens *et al.* 2012). In the eutrophic waters of the depositional area, living conditions for large benthic foraminifera were unfavourable. In view of this and the damaged tests of the Nummulitidae, it is possible that the large foraminifera were redeposited from the shallower areas.

The occurrence of the fruits of *Nypa* in the deposits suggests proximity to the shoreline. Extant *N. fruticans* thrives only in brackish waters, rarely growing directly on the seashore, and is usually found in estuarine tidal floodplains (CABI 2014). It prefers fine-grained sub-

strates and avoids shores exposed to wave action and hypersaline conditions (Badve and Sakurkar 2003; Ellison *et al.* 2010; Lim 2012). The occurrence of *Nypa*, which is limited to coastlines with water temperatures above 20°C, suggests that the absence of large benthic foraminifers is not conditioned by temperature. It is probable that the increased supply of organic matter, clay minerals (marls) and detrital grains by river(s) were the main limiting factors. Consequently, it can be concluded that during the latest Eocene in the area of the Hruby Regiel section, a warm, subtropical to tropical climate prevailed on the adjacent lands.

Irrespective of the rather limited number (50) of specimens, some deductions in relation to the physiognomy of the studied Eocene leaves can be drawn. Almost all of the taxa, except for *E. furcinervis*, have leaves with an entire, rarely revolute margin, often with a coriaceous leaf blade. Some leaves are relatively large. These physiognomic characters are typical of extant plants in a subtropical to tropical humid climate (Bailey and Sinnott 1915; Wing and Greenwood 1993; Wiemann *et al.* 1998; Royer *et al.* 2005).

In conclusion, the nearest living relatives and the morphological characters of the studied fossil leaf taxa point to a warm and humid climate in the Western Carpathians during the latest Eocene.

PLANT PALAEOCOMMUNITIES

The Late Eocene in Europe is characterised by transitional changes in vegetation associated with climate cooling. Late Palaeocene to Middle Eocene paratropical evergreen forest vegetation changed stepwise to a broad-leaved, mixed, deciduous and evergreen forest in the Late Eocene, and then to a mixed mesophytic forest in the Oligocene (Collinson and Hooker 2003). The plant assemblage from the Hruby Regiel section represents vegetation similar to the paratropical or subtropical evergreen forests rather than to the broad-leaved mixed deciduous forests. *Eotrigonobalanus furcinervis*, Lauraceae, and numerous leaf remains of entire-margined, coriaceous taxa are typical of paratropical or subtropical evergreen forests. In the Late Eocene of Central Europe, similar vegetation existed in the Atlantic-Boreal, Western and Central Europe Bioprovince (Mai 1995) and is represented by floras of the Hordle-Zeitz Florenkomplex (floral assemblages sensu Mai and Walther 1978). The plant assemblages studied herein are most similar to those from the Staré Sedlo Formation in the Czech Republic (Knobloch *et al.* 1996; Kvaček and Walther 2003) and in the Weisselster Basin in Germany (Kunzmann and Walther

2002), which represent subtropical evergreen laurophyllous rainforest of a *Eotrigonobalanus-Quercus*-Lauraceae association dominated by members of the Fagaceae, Lauraceae, Magnoliaceae, Altingiaceae, Theaceae, Moraceae, Mastixiaceae, Myrsinaceae, Myrtaceae, Olacaceae, Sapindaceae, Saururaceae, Sterculiaceae and Symplocaceae (Mai 1995). Depending on the methods used, the mean annual temperature estimated for Staré Sedlo ranges between 16 and 24°C (Uhl *et al.* 2007). Kvaček (2010) classified this type of Eocene intrazonal vegetation as a broad-leaved evergreen riparian gallery forest with palms. The evergreen broad-leaved forests of southeast Asia (Box *et al.* 1991) may be regarded as its Recent counterpart. The Late Palaeocene and Eocene vegetation of Europe is also characterised by mangroves, which in the material studied are represented by fossil fruits of *Nypa burtini*. In the European Eocene, thermophilic and humid mangroves were associated with coastlines (Collinson and Hooker 2003). Therefore, the deposits studied accumulated in the proximity of the coast.

TAPHONOMY OF THE PLANT REMAINS

The plant macroremains are dispersed in fine-grained deposits. The flora is allochthonous, as indicated by the mixture of taxa characteristic of mangrove and mesophytic vegetation. The usually good state of preservation of leaves suggests a proximity to the source vegetation. However, most of the leaves are coriaceous. Therefore, they could survive some transportation in a marine environment. The fruits of *Nypa* could have been transported from more distant coasts.

CONCLUSIONS

The Kuźniar collection of macroflora from the Hruby Regiel section comprises 50 specimens of plant remains (mainly leaves, but also fruits of *Nypa* and some undetermined remains of plant bodies) and a few trace fossils. Both the flora and the foraminiferal assemblages are dated as latest Eocene. The plant assemblage represents paratropical or subtropical evergreen forests in a warm and humid subtropical climate. The occurrence of plants typical of mangroves is indicative of proximity to a shoreline.

Sedimentary organic particles from the Hruby Regiel section do not include any structured organic matter (SOM) such as palynomorphs and structured phytoclasts. A single sample dominated by coalified

phytoclasts also contains pyrite framboids showing characters indicating a possible dysoxic sedimentary environment during deposition of the sediments of the Hruby Regiel section but not necessarily on the sea floor, as suggested by the absence of primary lamination and the occurrence of trace fossils.

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