

COMPARATIVE MORPHOLOGY AND ANATOMY OF THE LEAVES OF *Ginkgo biloba* L. CULTIVARS

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Abstract. The article presents the results of research on the morphology and anatomy of the leaves of 21 cultivars (including 10 Polish cultivars) and two clones of *Ginkgo biloba*. Leaves from long shoots were collected at the Department of Dendrology and Nursery, Poznań University of Life Sciences, Poland. A light microscope and scanning electron microscope were used for observations. Eight morphological traits were analysed in the leaves, including the lamina and petiole. The research revealed that there were significant differences between the leaves of individual cultivars and that they differed in the length, width of the lamina and the length of petioles to a much greater extent than publications had described it so far. There were significant differences between the adaxial and abaxial epidermis of all the taxa, i.e. in the cuticle ornamentation, in the protrusive secondary sculpture (absence of papillae), the position and presence of stomata (occasionally on the adaxial leaf surface), the absence of the peristomatal ring and the thickness of the epidermis. Anatomical investigations revealed that the leaves of *Ginkgo* cultivars and clones under study were bifacial and the multi-layered mesophyll was diversified into spongy and palisade parenchyma. The research findings may be used for the identification of *Ginkgo biloba* cultivars, and the epicuticular traits may be useful for the identification and classification of fragments of fossil leaves. The article includes descriptions and illustrations of several new quantitative and qualitative characters of petiole and lamina which have not been published previously.

Key words: *Ginkgo*, anatomy, leaves, LM, macro- and micromorphology, SEM

INTRODUCTION

Ginkgo biloba is the only survivor of the Ginkgoaceae family. Due to its lineage, which dates back to the Jurassic period [Del Tredici 1989, Taylor and Taylor 1993, Zhou and Zheng 2003], it is often called a “living fossil” [Mohanta 2012, Rudall et al.

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2012]. The *Ginkgo* genus was widespread almost all over the world during the Jurassic, Cretaceous and early Tertiary [Tralau 1968, Hill and Carpenter 1999, Pole and Douglas 1999, Del Tredici 2000]. At present the only natural habitat of the *Ginkgo biloba* is in eastern China, in Zhejiang Province, on the west peak of Mount Tianmu [Liang 1993]. The original appearance of the ginkgo tree led to its gradual introduction on all continents.

According to the taxonomy, the ginkgo is classified as a representative of the Gymnospermae division, where it is the only plant with leaves rather than needles or husks. For this reason it is sometimes regarded as the missing link between deciduous and coniferous trees [Zhou and Zheng 2003]. However, contemporary molecular investigations point to its closer relationship to cycads [Hasebe 1997].

So far about 200 ginkgo cultivars have been selected and described. They differ from the species in the shape, size and colour of their leaves and, more rarely, in their crown habit (the number of cultivars was estimated according to the information provided by Santamour et al. [1983], Li et al. [2013] and on the basis of our own information – S.K.). However, there is no detailed characterisation of the cultivars in available publications.

Ginkgo leaves differ from each other depending on the shoots they grow on. Leaves grow individually on long shoots. They are wedge-shaped at the base and usually they have an indentation in the middle of the lamina (its depth depends on the age of the plant). There are usually 3–7 leaves on short shoots and they are fan-shaped (the author's observations – S.K.).

The literature does not provide much information about the morphology and anatomy of vegetative organs of *Ginkgo biloba* [Dallimore 1967, Batanouny 1992]. These are usually biometric and morphological data, which are very similar to each other. Leigh et al. [2011] compared selected morphological traits and the physiology of leaves from long and short shoots. Denk and Velitzelos [2002] described the traits of the epidermis of *G. biloba* and *G. adiantoides*, whereas Rudall et al. [2012] described the stomatal development and the distribution and structure of mature stomata in *G. biloba*. Toma and Rugina [1998], Cargo et al. [2000], Stan and Simeanu [2008], Bercu [2013] and Duarte et al. [2013] conducted research on the anatomical structure of ginkgo leaves.

The hypothesis of the present study is that the leaves of *Ginkgo biloba* cultivars and clones are more variable than it has been previously reported in literature. The main goal of this study was: 1) to describe variation in the leaf morphology of 21 cultivars of *G. biloba* and in two clones; 2) to describe and document the petiole and lamina anatomy and the lamina micromorphology.

MATERIAL AND METHODS

We collected *Ginkgo biloba* leaves from 21 cultivated ornamental plants (including 10 Polish cultivars) and one male and one female clone (tab. 1) from the collection of the Department of Dendrology and Nursery, Poznań University of Life Sciences. The trees did not differ in age, for about 20 years they had been cultivated in the soil, under similar habitat conditions.

Each specimen was represented by 30 randomly collected leaves in August 2013. We studied 8 morphological traits in the leaves (tab. 1). The length of the lamina was

measured from the base to the apex of the longest segment and the width was measured at the widest part of the lamina. The length of the petiole was measured up to the bases of the lamina and the width was measured at the base. We measured the area of the lamina by means of the SKWER program (Iksmodar). We calculated the arithmetic mean and standard deviation for each morphological trait mentioned (tab. 1) and analysed the biometric data statistically. Univariate analysis of variance (ANOVA) was used for each morphological trait to differentiate the means between the cultivars under study. If significant differences were noted, a multiple comparison was made by means of Tukey's test for equal sample size.

Completely dried leaves were investigated with an SEM. Micrographs were taken with an SEM, type EVO 40 (Carl Zeiss, Jena, Germany) at an accelerating voltage of 15kV, at the Confocal and the Electron Microscopy Laboratory, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland. Prior to observation the prepared material was sputtered (for 15 s) with gold by means of an SCB 050 ion sputter (Balzers AG Liechtenstein). Five leaves of individual taxa were examined for the following traits: adaxial and abaxial surfaces of the epidermis, the sculpture of wax and cuticle. The study was documented with ten microphotographs of each leaf. The photographs taken during the observation were magnified $\times 1000$ and $\times 20000$.

Living material was preserved in 70% alcohol for anatomical investigations. Transverse sections 50 μm thick were made with a microtome (Leitz). Twenty sections were taken from each petiole and lamina in the middle parts. All the sections were embedded in glycerine-gelatine and examined with an Olympus BX 43 light microscope with a camera lucida. Thus, slides were prepared and used to describe transverse sections (T.S.) and traits measured. The thickness of the petiole and lamina was measured between the adaxial and abaxial surface and in the lamina with and without veins. The epidermal thickness index (ETI) was calculated as the ratio between the adaxial and abaxial epidermis thickness.

The terminology of epicuticular waxes was applied according to Riederer [1989] and Barthlott et al. [1998].

RESULTS

The main morphological features of the taxa under investigation are shown in Table 1 and Figures 1–23. Selected SEM micrographs of the adaxial epidermis (figs 24–29, 53) and all micrographs of the abaxial epidermis (figs 30–52, 54) are shown. The anatomical characteristics of the petiole and lamina are shown in Table 2 and 3. Selected LM micrographs of the anatomical features of the petiole and lamina are shown in Figures 55–58.

General leaf morphology (figs 1–23, tab. 1)

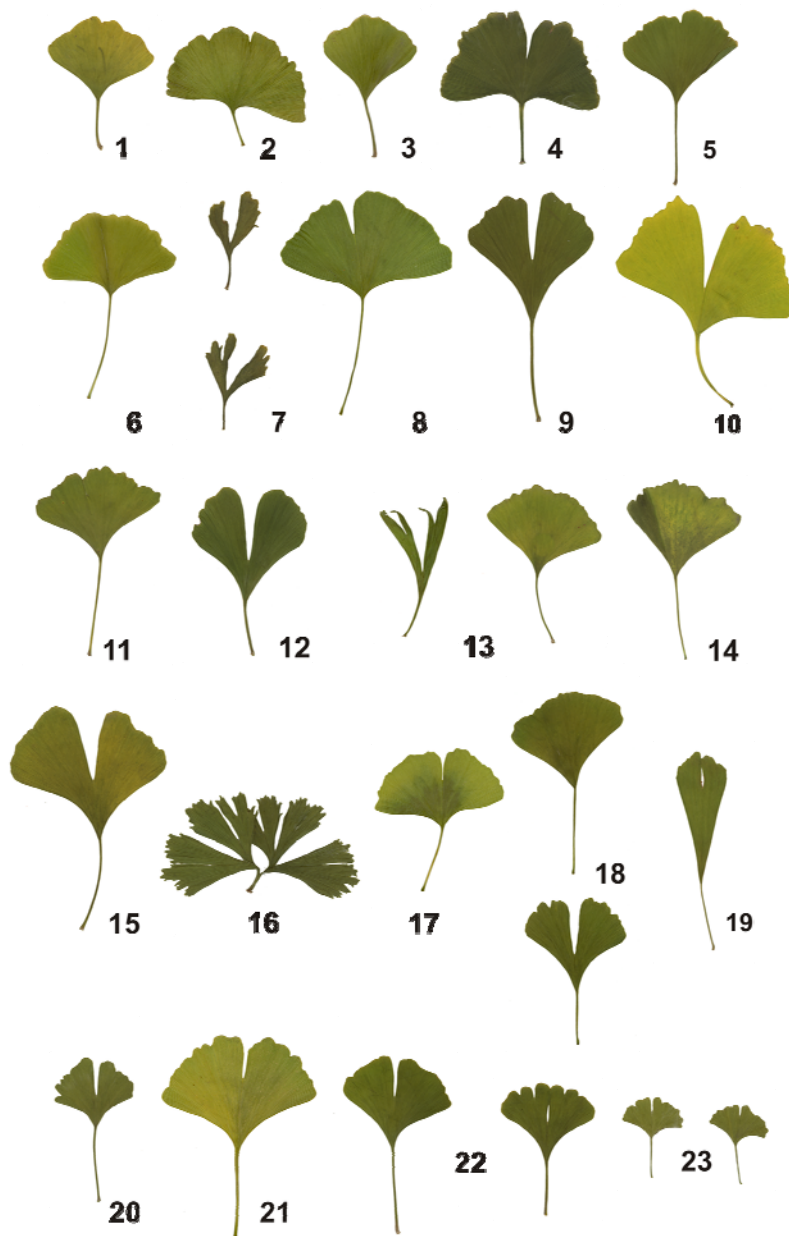
The leaves collected from the long shoots of the 23 taxa under study were characterised by high diversity both in shape and size (figs 1–23). The leaves were simple, entire, glabrous, flexible, deciduous, flabelliform, bilobate and lobulate. The longest laminae

Table 1. Mean values (\pm SD) and ranges (minimum-maximum) of the morphological features of the *Ginkgo biloba* leaf

<i>Ginkgo biloba</i> cultivars	Lamina			
	Length (mm)	Width (mm)	Depth of indentation (mm)	Area (cm ²)
10-98	66.9 \pm 5.8 g 53.1-81.8	79.4 \pm 16.0 c-f 46.7-108.7	12.5 \pm 7.5 abc 0.0-27.2	31.8 \pm 3.3 ij 23.2-36.2
Bolesław Chrobry	63.1 \pm 6.1 efg 52.1-77.4	94.8 \pm 9.1 i 75.1-113.1	19.9 \pm 10.9 c-f 0.0-39.7	41.5 \pm 1.8 m 38.2-44.2
DFS	62.3 \pm 4.6 efg 52.0-75.0	74.8 \pm 12.6 cd 54.9-103.1	14.6 \pm 7.8 bcd 0.0-29.8	27.9 \pm 1.7 fg 24.5-30.9
Fastigiata	63.4 \pm 10.9 efg 47.7-91.8	87.1 \pm 17.5 e-i 58.9-124.8	30.4 \pm 10.6 ghi 13.7-59.8	35.6 \pm 4.8 kl 25.0-44.9
Gui-Zhi	65.3 \pm 8.8 fg 44.2-82.5	77.4 \pm 17.6 c-f 48.9-108.5	18.0 \pm 7.6 b-e 0.0-31.1	30.3 \pm 2.9 hi 25.5-36.7
Hunan	48.6 \pm 4.8 b 39.4-60.4	74.3 \pm 12.9 c 47.5-101.0	10.8 \pm 6.7 ab 0.0-27.6	23.8 \pm 1.6 cd 21.0-26.6
Jadwiga	50.9 \pm 8.7 bc 34.9-71.4	44.4 \pm 9.7 b 28.2-71.2	28.7 \pm 6.0 fgh 17.3-40.5	12.9 \pm 0.6 b 11.9-13.8
Jagiello	62.7 \pm 7.3 efg 42.4-73.5	91.9 \pm 14.3 ghi 52.6-117.3	25.8 \pm 8.9 e-h 5.3-37.8	36.5 \pm 2.6 l 32.9-41.3
Jan III Sobieski	60.0 \pm 5.6 efg 48.7-69.0	87.1 \pm 8.2 e-i 71.4-99.7	4.3 \pm 6.5 a 0.0-16.1	31.9 \pm 4.6 ij 24.7-45.2
Kazimierz Wielki	57.2 \pm 8.0 cde 37.7-71.5	78.8 \pm 13.4 c-f 50.1-100.7	16.4 \pm 8.1 bcd 0.0-35.3	27.7 \pm 3.4 fg 20.1-32.8
male clone	62.8 \pm 5.5 efg 51.0-72.2	92.7 \pm 11.4 hi 65.4-119.7	14.1 \pm 10.7 bcd 0.0-38.8	37.6 \pm 1.5 l 35.4-40.7
female clone	61.5 \pm 6.3 efg 47.3-73.6	74.7 \pm 11.3 c 50.6-93.8	18.4 \pm 14.7 b-e 0.0-86.3	27.3 \pm 2.3 ef 23.8-32.0
Kořinek	48.2 \pm 10.0 b 29.2-70.2	25.1 \pm 18.1 a 4.3-63.0	16.8 \pm 11.1 bcd 0.0-45.1	very variable
Mieszko I	75.3 \pm 8.2 h 55.7-90.2	88.4 \pm 13.2 f-i 59.9-134.4	32.2 \pm 8.6 hi 15.6-53.2	37.5 \pm 3.0 l 33.9-45.4
Pendula (from Belgium)	60.0 \pm 8.5 efg 46.1-83.4	77.6 \pm 10.6 c-f 58.0-99.1	15.3 \pm 7.1 bcd 3.7-31.8	28.0 \pm 1.5 fgh 26.0-32.7
Pendula (from China)	58.5 \pm 7.1 def 38.6-73.4	86.6 \pm 13.4 d-i 48.9-115.7	38.1 \pm 9.3 i 14.7-61.6	33.6 \pm 3.2 jk 28.0-40.0
Profesor Łukasiewicz	64.9 \pm 5.1 fg 55.9-76.0	80.7 \pm 10.5 c-g 56.8-102.1	33.1 \pm 6.1 hi 15.6-47.1	29.7 \pm 1.5 ghi 27.6-33.0
Przemysław II	66.4 \pm 6.5 g 50.2-80.5	73.6 \pm 14.4 c 46.9-105.1	16.6 \pm 10.8 bcd 0.0-41.2	27.9 \pm 1.6 fg 24.6-32.9
Saratoga	81.8 \pm 12.3 h 64.7-129.2	53.8 \pm 12.0 b 37.0-91.3	30.8 \pm 18.7 hi 3.0-83.7	23.0 \pm 1.1 c 20.2-24.7
Stefan Batory	37.8 \pm 6.1 a 26.3-48.4	47.8 \pm 10.9 b 31.8-69.9	16.9 \pm 8.6 bcd 0.0-31.5	11.6 \pm 0.2 ab 11.2-12.0
Tabulaeformis	64.1 \pm 7.7 efg 44.6-83.4	82.3 \pm 10.4 c-h 60.1-104.3	12.3 \pm 7.7 abc 0.0-28.5	31.2 \pm 1.2 i 29.6-34.2
Variiegata	52.3 \pm 5.1 bcd 40.9-61.5	76.4 \pm 10.9 cde 55.1-105.2	21.8 \pm 7.2 d-g 9.7-41.5	25.4 \pm 0.8 de 23.5-26.7
Władysław Łokietek	32.1 \pm 7.9 a 20.9-60.2	44.9 \pm 7.5 b 34.7-63.9	15.9 \pm 5.5 bcd 6.0-30.3	9.7 \pm 0.2 a 9.1-10.1
ANOVA	F = 62.35 P < 0.01	F = 60.32 P < 0.01	F = 24.14 P < 0.01	F = 365.36 P < 0.01

<i>Ginkgo biloba</i> cultivars	Veins		Petiole	
	Number at the lamina base	Distance between the veins in the middle part of the lamina (mm)	Length (mm)	Width at the base (mm)
10-98	5.1 ±0.7 cde 4.0-6.0	0.8 ±0.1 a-d 0.7-1.0	68.9 ±11.4 l 32.8-91.2	2.1 ±0.2 f-i 1.7-2.5
Boleslaw Chrobry	5.7 ±0.8 d-g 5.0-8.0	1.3 ±0.1 i 1.1-1.7	36.8 ±10.1 abc 17.4-59.5	1.8 ±0.3 b-f 1.1-2.3
DFS	5.4 ±0.5 c-g 5.0-6.0	0.9 ±0.1 c-f 0.6-1.0	60.1 ±9.5 jkl 40.4-89.1	2.6 ±0.4 jk 2.1-3.6
Fastigiata	5.0 ±0.6 cd 4.0-6.0	1.0 ±0.1 h 0.8-1.1	58.0 ±19.3 i-l 28.6-99.4	2.2 ±0.5 hi 1.6-3.8
Gui-Zhi	5.5 ±0.8 c-g 4.0-7.0	0.9 ±0.1 b-e 0.6-1.0	63.3 ±8.6 kl 39.7-74.7	2.6 ±0.5 jk 1.8-3.8
Hunan	5.5 ±0.9 c-g 4.0-7.0	0.8 ±0.1 a-d 0.6-1.0	49.8 ±8.1 d-j 32.5-71.4	2.0 ±0.2 d-h 1.4-2.6
Jadwiga	4.1 ±0.3 ab 4.0-5.0	1.0 ±0.1 e-h 0.9-1.1	44.4 ±8.4 b-g 25.8-62.0	1.8 ±0.3 b-e 1.4-2.6
Jagiello	5.0 ±0.5 cd 4.0-6.0	0.9 ±0.1 cde 0.7-1.1	64.7 ±18.1 kl 27.2-91.0	1.7 ±0.2 b-e 1.3-2.1
Jan III Sobieski	7.0 ±1.1 j 5.0-9.0	0.8 ±0.04 ab 0.6-0.9	68.3 ±13.6 l 36.5-92.6	2.7 ±0.5 k 1.6-3.2
Kazimierz Wielki	5.3 ±1.2 c-f 4.0-8.0	0.7 ±0.1 a 0.5-0.9	42.5 ±9.9 a-e 20.9-63.5	1.8 ±0.3 b-g 1.2-2.4
male clone	5.3 ±0.7 cde 4.0-7.0	0.8 ±0.1 a-d 0.6-1.0	50.6 ±11.2 e-j 31.0-76.7	1.9 ±0.2 c-h 1.6-2.3
female clone	5.0 ±0.6 cd 4.0-6.0	0.8 ±0.1 abc 0.6-1.0	54.6 ±9.0 g-k 37.3-75.9	2.4 ±0.5 ij 1.8-3.8
Kořinek	4.3 ±0.5 ab 4.0-6.0	0.9 ±0.1 b-e 0.6-1.2	35.4 ±17.2 abc 8.6-66.2	1.8 ±0.3 b-e 1.1-2.2
Mieszko I	6.7 ±0.9 ij 5.0-9.0	0.8 ±0.1 ab 0.5-1.0	56.1 ±12.7 h-k 29.0-82.1	2.1 ±0.4 ghi 1.6-3.5
Pendula (from Belgium)	5.9 ±0.8 e-h 5.0-8.0	0.7 ±0.1 a 0.5-0.9	45.8 ±14.6 c-h 25.8-95.9	1.9 ±0.3 c-h 1.4-2.7
Pendula (from China)	5.3 ±0.7 cde 4.0-7.0	1.0 ±0.1 gh 0.7-1.2	39.2 ±9.5 a-d 20.4-54.2	1.8 ±0.3 b-e 1.3-2.6
Profesor Łukasiewicz	6.1 ±0.7 f-i 5.0-7.0	0.9 ±0.2 d-g 0.5-1.2	58.5 ±8.3 i-l 40.0-84.2	2.0 ±0.2 d-h 1.5-2.4
Przemyslaw II	6.5 ±1.1 hij 4.0-8.0	0.7 ±0.2 a 0.5-1.1	43.5 ±8.1 b-f 25.6-59.9	1.7 ±0.3 bcd 1.0-2.4
Saratoga	4.1 ±0.5 a 3.0-6.0	1.0 ±0.2 fgh 0.7-1.4	58.2 ±16.3 i-l 28.7-87.5	1.3 ±0.3 a 0.9-2.2
Stefan Batory	4.9 ±0.7 bc 4.0-6.0	0.7 ±0.1 a 0.6-1.0	32.1 ±5.0 a 21.1-42.4	2.0 ±0.4 e-h 1.3-3.1
Tabulaeformis	6.1 ±0.9 ghi 5.0-8.0	0.7 ±0.1 a 0.5-0.9	54.1 ±11.1 f-k 26.3-75.9	1.7 ±0.3 bc 1.2-2.4
Variiegata	5.2 ±0.7 cde 4.0-7.0	0.8 ±0.1 a-d 0.6-0.9	48.7 ±10.3 d-i 28.6-75.5	1.8 ±0.2 b-e 1.5-2.2
Władyslaw Łokietek	6.1 ±1.2 ghi 4.0-9.0	0.7 ±0.1 a 0.5-1.0	33.8 ±6.9 ab 21.5-54.1	1.6 ±0.3 ab 0.9-2.5
ANOVA	F = 27.88 P < 0.01	F = 44.18 P < 0.01	F = 26.51 P < 0.01	F = 33.57 P < 0.01

One way ANOVAs were performed separately for each feature to determine the differences among cultivars studied. Same letters indicate a lack of statistically significant differences between analyzed taxa according to Tukey's a posteriori test ($P < 0.05$)



Figs 1–23. Macroscopic characteristics of the *Ginkgo biloba* leaf: '10–98' (1), 'Bolesław Chrobry' (2), 'DFS' (3), 'Fastigiata' (4), 'Gui-Zhi' (5), 'Hunan' (6), 'Jadwiga' (7), 'Jagiełło' (8), 'Jan III Sobieski' (9), 'Kazimierz Wielki' (10), male clone (11), female clone (12), 'Kołinek' (13), 'Mieszko I' (13), 'Pendula' (from Belgium) (15), 'Pendula' (from China) (16), 'Profesor Łukasiewicz' (17), 'Przemysław II' (18), 'Saratoga' (19), 'Stefan Batory' (20), 'Tabulaeformis' (21), 'Variegata' (22), 'Władysław Łokietek' (23)

were observed in the American 'Saratoga' cultivar – on average 81.8 mm (max. 129.2 mm) and the Polish cultivar 'Mieszko I' – on average 75.2 mm (max. 90.2 mm). The shortest laminae were found in two Polish cultivars – 'Władysław Łokietek' (on average 32.1 mm) and 'Stefan Batory' (on average 37.8 mm). The length of the laminae was similar in the other taxa and ranged from about 50 to 65 mm on average.

The narrowest laminae (on average 25.1 mm) were observed in the 'Kofinek' cultivar. The laminae of the other taxa were two or even four times wider. The widest laminae were found in the following cultivars: 'Bolesław Chrobry' (on average 94.8 mm) and 'Jagiełło' (91.9 mm) and in the male clone (92.7 mm).

The smallest area of the lamina was observed in the following Polish cultivars with small leaves: 'Władysław Łokietek' (on average 9.7 cm²) and 'Stefan Batory' (on average 11.6 cm²). The small area of the lamina in the female 'Jadwiga' cultivar (on average 12.9 cm²) results from the structure of the leaves. They were deeply lobed and narrowly wedge-shaped at the base. The largest area of the lamina was observed in the 'Bolesław Chrobry' cultivar (on average 41.5 cm²). Its leaves were big and strongly corrugated.

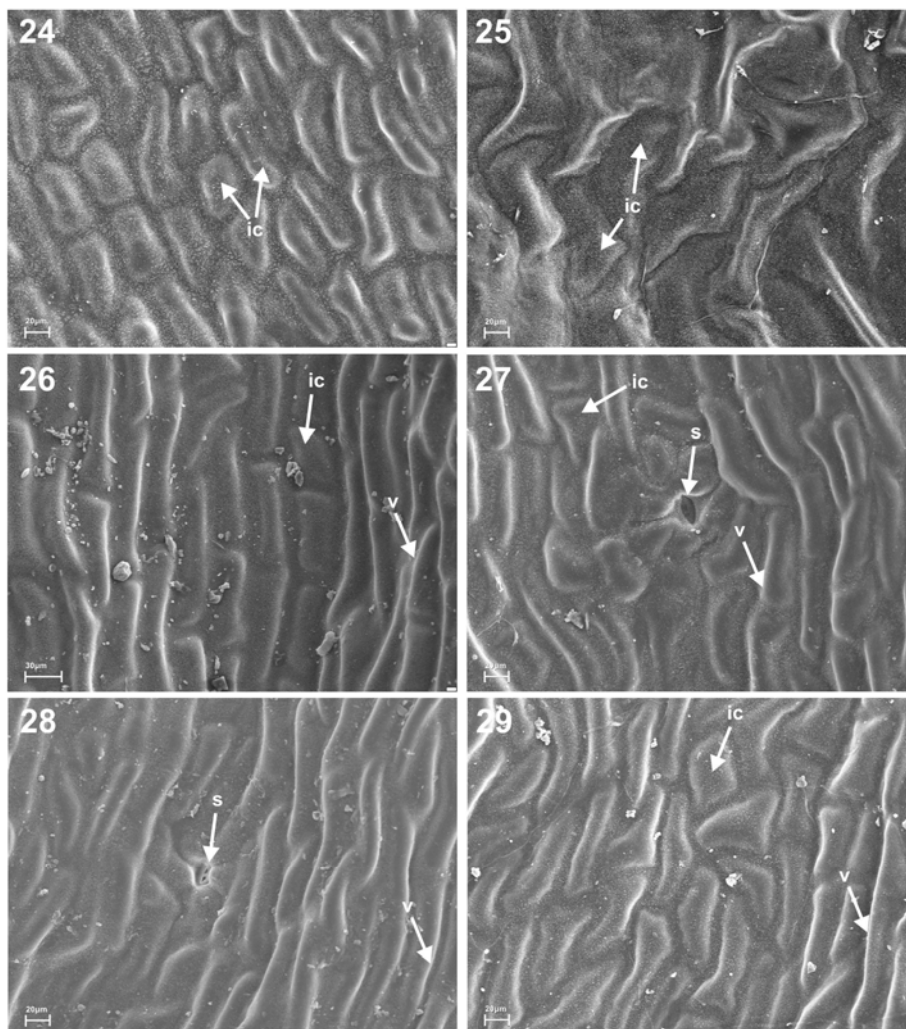
The notch in the lamina proves to be a very variable trait. Depending on the cultivar, it ranged from 0 to 6 cm in the 'Pendula' (from China) and 'Fastigiata' cultivars and up to 8 cm in the female clone and in the 'Saratoga' cultivar. The average distance between nerves, measured in the central part of the lamina, ranged from 0.7 to 1.3 mm. There were usually 4–9 nerves at the lamina base.

The ginkgo petiole length differed even within each taxon and ranged from about 2 cm to almost 10 cm. The '10–98' and 'Jan III Sobieski' cultivars had the longest petioles, whereas the 'Stefan Batory' and 'Władysław Łokietek' cultivars had the shortest petioles. The petiole width measured at the base ranged from 1.3 mm to 2.7 mm on average.

The results of the morphometrical features (tab. 1, figs 1–23) indicate that the differences were highly significant.

Lamina surface (figs 24–29 and 53, 54)

Adaxial epidermis. The epidermal cells above the veins were narrow and elongated with acute ends (figs 26, 28, 29). The anticlinal walls which formed a boundary between the epidermal cells were depressed below the outer tangential surfaces of the cells (figs 24–29). There were no stomata on the adaxial epidermis in most of the cultivars, except 'Jan III Sobieski' and the female clone, where a few stomata were found. The stomata surrounding five epidermal cells and subsidiary cells of these stomata had no papillae (figs 27–28). The periclinal cell walls of all the taxa were convex and smooth. However, in '10–98', 'Hunan' and 'Mieszko I', rare wart-like protrusions were found. The epidermal cells in the intercostal areas were irregularly polygonal or broad and rectangular (figs 24–27, 29). There were epicuticular wax deposits in the form of wax rodlets projecting outwards. Each wax rodlet was erect and tubular in shape (fig. 53). In all the taxa the cuticle ornamentation on the adaxial surface was smooth (figs 24, 26–29), except 'Bolesław Chrobry' (fig. 25). The description of the adaxial epidermis is the same for all the taxa under study.



Figs 24–29. SEM micrographs of the adaxial cuticle of *Ginkgo biloba*: ‘10–98’ (24), ‘Bolesław Chrobry’ (25), ‘Fastigiata’ (26), ‘Jan III Sobieski’ (27), female clone (28), ‘Saratoga’ (29); *ic* – intercostal area, *s* – stoma, *v* – vein area

Abaxial epidermis. The epidermal cells above the veins were elongated with acute or rectangular ends (figs 38–43, 45, 47, 48, 51). The epidermal cells in the intercostal areas were roundish, oval or polygonal (figs 30–52). The cell boundaries were similar to those in the adaxial surface. The periclinal cell walls were convex, often with one to three papillae. The stomata were randomly distributed (in the intercostal areas) and irregularly oriented, sunken and surrounded by a ring wall made up of fused convex subsidiary cells (figs 30, 32–52). There were papillae on the subsidiary cells of the stomata in all the taxa and their number ranged from (3) 4 to 6. Only in ‘Bolesław Chro-

bry' there were differences in the ring formation around the stomata and in the size of the papillae (fig. 31). There were some differences between the 'Pendula' cultivar from Belgium and the 'Pendula' from China in the density of the papillae on the periclinal cell walls (figs 44, 45). The cuticle ornamentation on the abaxial surface was smooth-striated in 'Bolesław Chrobry' (fig. 31), 'Jagiełło' (fig. 36), 'Jan III Sobieski' (fig. 38), the male clone (fig. 40), 'Košinec' (fig. 42), 'Mieszko I' (fig. 43), 'Pendula' (from Belgium) (fig. 44), 'Saratoga' (fig. 48), 'Stefan Batory' (fig. 49), 'Variegata' (fig. 51) and 'Władysław Łokietek' (fig. 52), and it was smooth in the other taxa. The ornamentation of the wax structure was the same as on the adaxial epidermis (fig. 54).

Petiole transverse section (T.S.) (tab. 2, figs 55–56)

Outline. The outline of petioles was hemispheric, adaxially flattened, slightly concave, straight or slightly undulate (fig. 55) and on the abaxial side it was rounded, straight or slightly undulate. The average petiole thickness in the median part ranged from 984.4 μm ('Stefan Batory') to 2321.3 μm ('Bolesław Chrobry').

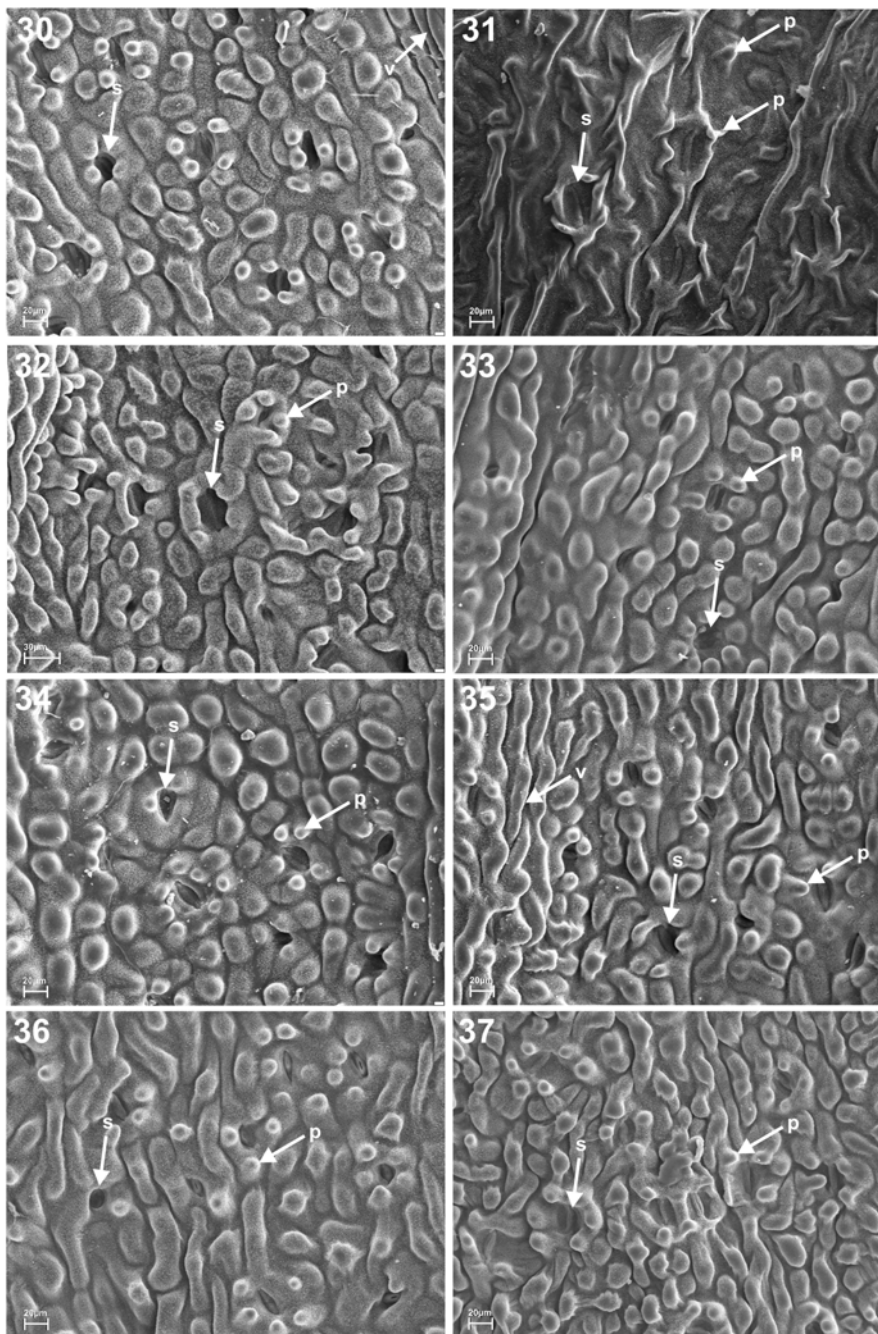
Cuticle: The epidermal cells were covered with a thick epicuticular layer. The average thickness of this layer ranged from 3.1 to 5.4 μm on the adaxial surface and from 2.9 to 5.9 μm on the abaxial surface (tab. 2).

Epidermis. The one-layered epidermis was made up of rounded, rectangular to square cells. The anticlinal cell walls were straight or slightly undulate and the outer periclinal cell walls on the adaxial surface were more or less convex and on the abaxial surface they were convex or papillate. The abaxial epidermis was thicker than the adaxial epidermis ($\text{ETI} > 1$) in 16 taxa and in the others it was reverse ($\text{ETI} < 1$). A few bicellular hairs could be found on the adaxial epidermis in seven cultivars (tab. 2, fig. 55). Sunken stomata with low frequency were distributed on the adaxial and lateral surface of the petiole.

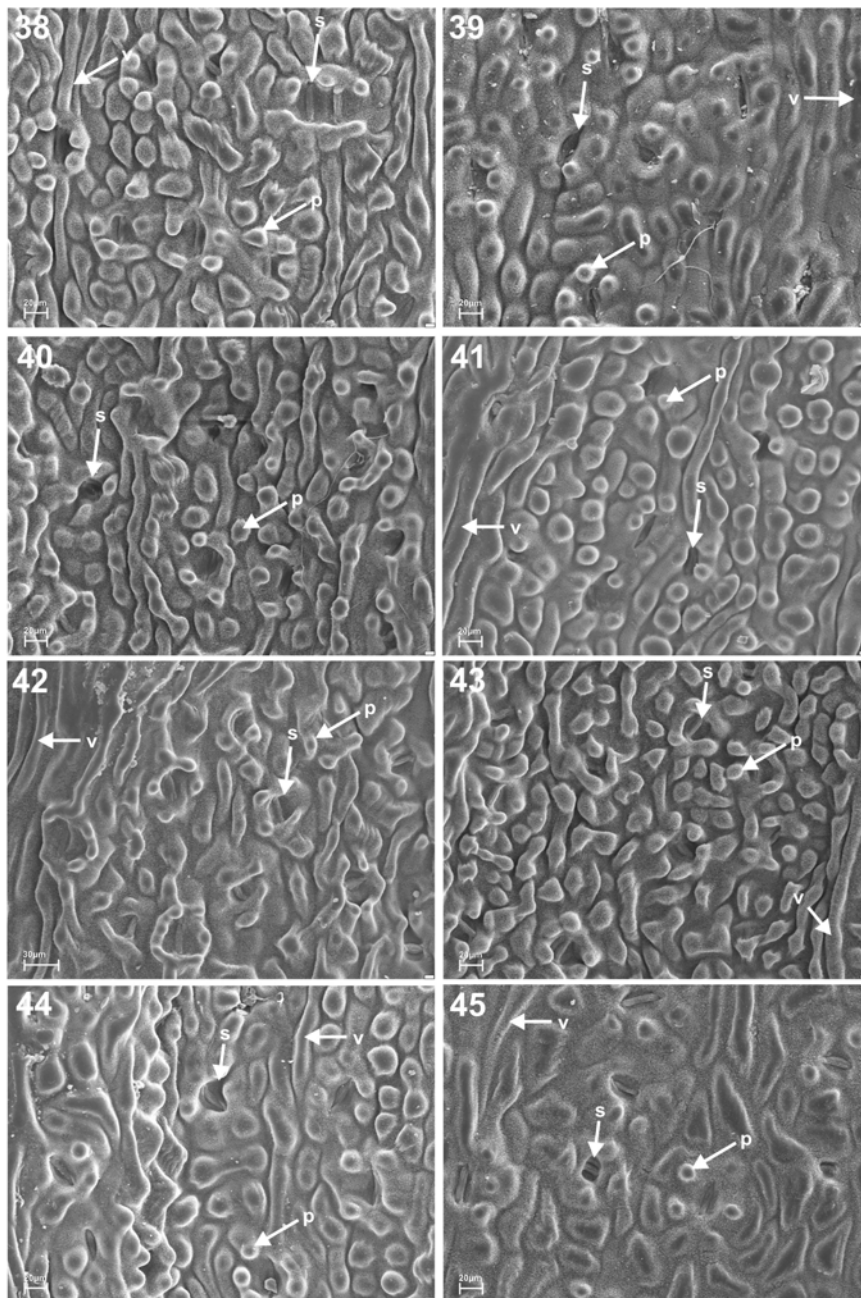
Hypodermis. A discontinuous hypodermis composed of 1–3 layers of thick-walled cells (sclerenchyma cells) alternating with thin-walled cells (chlorenchyma or parenchyma cells) and substomatal chamber was observed.

Mesophyll. The mesophyll was composed of 4–6 layers of the chlorenchyma tissue, generally isodiametric cells without intercellular air spaces. The parenchyma cells were multilayered.

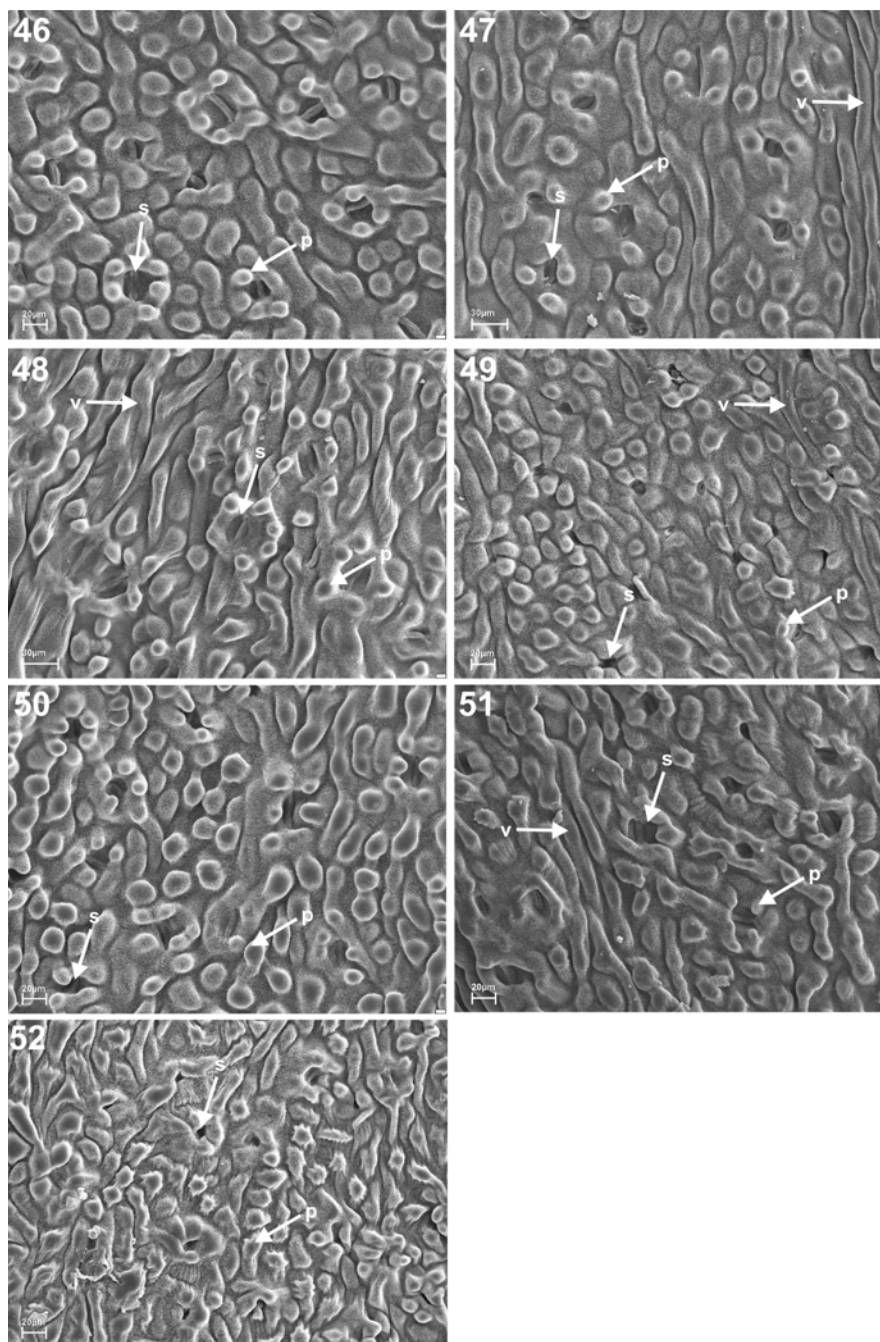
Vascular bundles. The centre of the petioles was occupied by two or four collaterally opened vascular bundles (tab. 2, fig. 55). The parenchymatic tissue separated the vascular bundles from one another. The xylem faced the adaxial petiole surface while the phloem faced the abaxial epidermis (figs 55–56). There were small calcium oxalate crystals sized 6.0–34.5 \times 4.5–35.1 μm in the vascular cambium. The vascular bundles were surrounded by a pericycle and a layer of endodermis. The transfusion tissue comprised parenchymatic cells and tracheids on the sides of the vascular bundles. There were spiral or reticulate thickenings on the transfusion tracheids (fig. 56). The cells in all the taxa contained calcium oxalate druses, irregularly dispersed in the chlorenchyma and in the parenchyma cells, sized 50.7–97.7 \times 42.5–89.75 μm . There were from one to seven schizogenic cavities sized 56.8–346.4 \times 43.3–279.15 μm in the chlorenchyma cells (tab. 2).



Figs 30–37. SEM micrographs of the abaxial cuticle of *Ginkgo biloba*: '10–98' (30), 'Bolesław Chrobry' (31), 'DFS' (32), 'Fastigiata' (33), 'Gui-Zhi' (34), 'Hunan' (35), 'Jadwiga' (36), 'Jagiello' (37); p – papillae, s – stoma, v – vein area



Figs 38–45. SEM micrographs of the abaxial cuticle of *Ginkgo biloba*: 'Jan III Sobieski' (38), 'Kazimierz Wielki' (39), male clone (40), female clone (41), 'Kořinek' (42), 'Mieszko I' (43), 'Pendula' (from Belgium) (44), 'Pendula' (from China) (45); *p* – papillae, *s* – stoma, *v* – vein area



Figs 46–52. SEM micrographs of the abaxial cuticle of *Ginkgo biloba*: 'Profesor Łukasiewicz' (46), 'Przemysław II' (47), 'Saratoga' (48), 'Stefan Batory' (49), 'Tabulaeformis' (50), 'Variegata' (51), 'Władysław Łokietek' (52); *p* – papillae, *s* – stoma, *v* – vein area

Table 2. A comparison of selected anatomical features in T.S. of the *Ginkgo biloba* petiole (*Ab* – abaxial epidermis, *Ad* – adaxial epidermis, ETI – epidermal thickness index, T.S. – transverse sections – absence of hairs + presence of hairs)

<i>Ginkgo biloba</i> cultivars	Characters								
	Petiole thickness (μm)	Epicuticular layer thickness (μm)		Petiole epidermis thickness (μm)		ETI	Number of vascular bundles	Number of schizogeni cavities	Hairs
		Ad	Ab	Ad	Ab				Ab
10–98	1352.0	3.3	3.6	19.3	19.0	1.01	2	2	–
Bolesław Chrobry	2321.3	4.4	4.2	25.5	21.5	1.18	2	5–6	–
DFS	1581.0	4.1	4.8	25.8	25.7	1.00	2	2–3	+
Fastigiata	1624.9	4.9	4.0	23.6	24.2	0.97	4	1–2	–
Gui-Zhi	1369.6	4.5	4.4	25.3	26.1	0.97	2	1–3	–
Hunan	1284.6	3.6	3.7	18.6	19.4	0.96	2–4	2	–
Jadwiga	1303.1	3.3	4.0	27.6	27.2	1.01	2	3–5	+
Jagiello	1448.7	3.7	3.4	22.7	18.8	1.20	2	2–3	–
Jan III Sobieski	1710.0	5.4	4.3	25.2	24.9	1.01	4	2–6	–
Kazimierz Wielki	1358.5	4.7	3.9	25.5	25.1	1.01	2	1	–
male clone	1392.1	3.3	3.7	25.2	23.1	1.09	2	1	–
female clone	1399.3	3.9	4.3	22.7	18.8	1.20	2	1–2	–
Kořinek	1293.4	4.3	4.9	27.2	28.6	0.95	2	4–5	+
Mieszko I	1430.6	3.1	3.0	20.4	21.0	0.97	2	1	+
Pendula (from Belgium)	1556.3	3.6	3.1	22.6	20.5	1.10	2	2–4	+
Pendula (from China)	1434.3	4.7	5.6	29.9	27.1	1.10	4	2	+
Profesor Łukasiewicz	1402.6	3.8	4.6	25.2	24.5	1.03	2	2	–
Przemysław II	1442.1	3.2	3.5	21.4	20.3	1.05	4	5–7	–
Saratoga	1322.1	3.6	3.2	20.4	22.4	0.91	2	1	–
Stefan Batory	984.4	3.1	2.9	15.8	16.4	0.96	2–4	3	–
Tabulaeformis	1760.8	4.8	4.5	25.2	25.2	1.00	4	5	–
Variegata	1254.8	3.1	3.2	23.3	21.3	1.09	2	3–5	–
Władysław Łokietek	1088.7	3.7	3.6	18.5	15.1	1.22	2	1	+

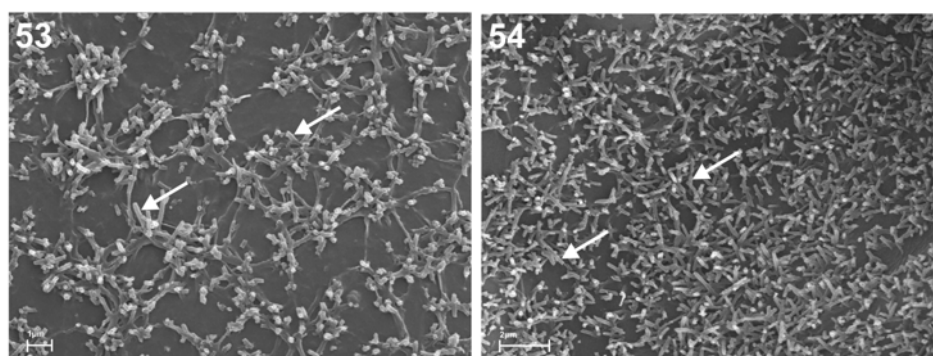
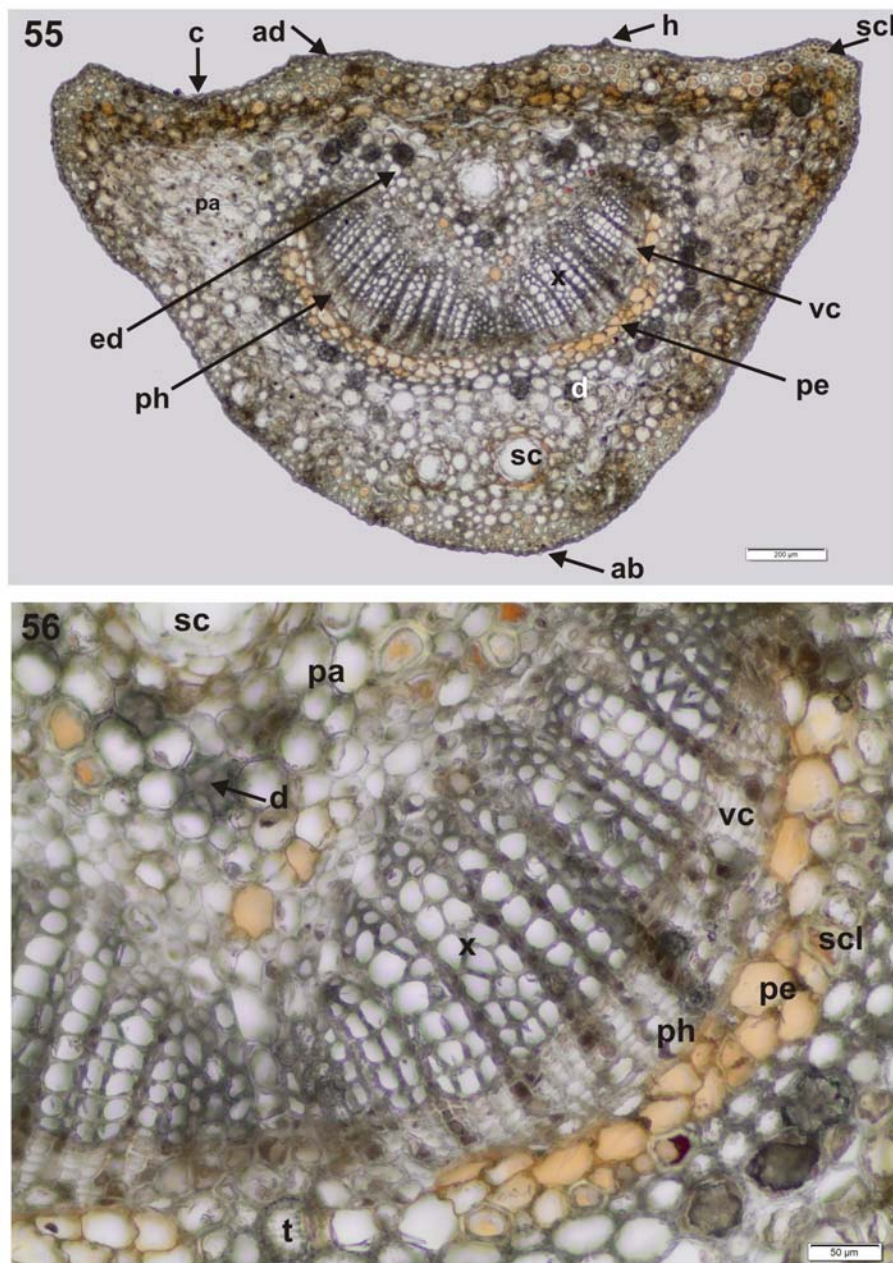
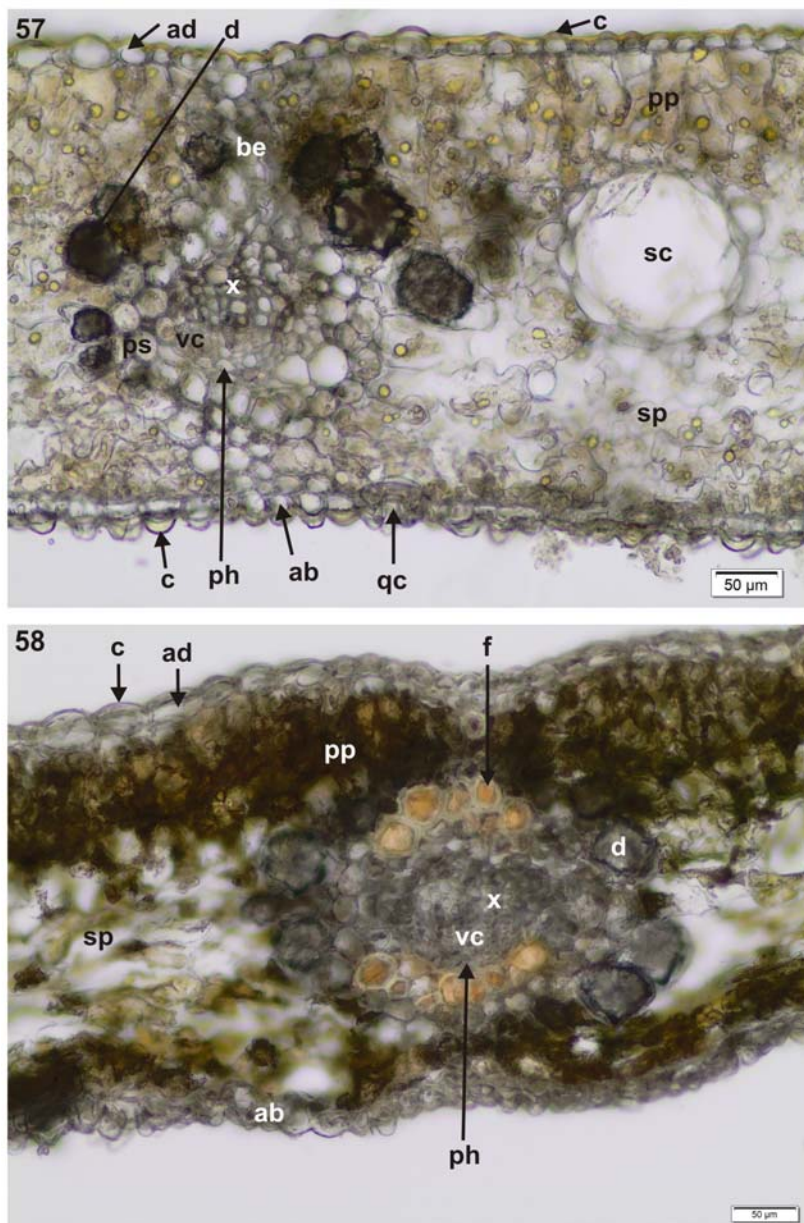
Figs 53–54. SEM micrographs of the wax ornamentation of *Ginkgo biloba*: 'Przemysław II' (53) adaxial leaf surface, 'Saratoga' (54) abaxial leaf surface

Table 3. A comparison of selected anatomical features in T.S. of the *Ginkgo biloba* lamina (*Ab* – abaxial epidermis, *Ad* – adaxial epidermis, ETI – epidermal thickness index, T.S. – transverse sections – absence of bundle sheath extensions on adaxial or abaxial surface)

<i>Ginkgo biloba</i> cultivars	Characters												
	Leaf vein thickness (µm)	Leaf lamina thickness (µm)	Epicuticular layer thickness (µm)		Leaf epidermis thickness (µm)		ETI	Width / height ratio of epidermal cells		Palisade mesophyll layer	Thickness spongy / palisade layer ratio	Presence of bundle sheath extension on adaxial (Ad) or abaxial (Ab) surface	
			Ad	Ab	Ad	Ab		Ad	Ab				
10–98	369.5	325.0	4.3	5.2	17.9	16.2	1.10	1.38	1.04	2	2.07	Ad + Ab	
Bolesław Chrobry	626.2	492.1	3.4	4.4	23.3	25.9	0.89	1.73	1.23	2	2.26	–	
DFS	440.9	351.5	4.6	4.5	19.1	19.9	0.96	1.79	1.24	2(-3)	2.44	Ad + Ab	
Fastigiata	427.1	405.1	4.5	4.7	19.9	21.3	0.93	1.66	1.06	1–2	2.51	Ab	
Gui-Zhi	429.8	361.1	5.3	5.6	18.1	16.5	1.09	1.66	1.10	2	2.81	Ad + Ab	
Hunan	366.5	327.6	4.1	4.6	19.2	14.5	1.32	1.44	1.48	2	1.84	Ab	
Jadwiga	611.8	420.3	3.7	4.8	25.5	22.1	1.15	1.18	1.35	2	2.83	–	
Jagiello	432.8	352.0	4.3	4.5	21.7	22.8	0.95	1.57	1.03	2	2.20	Ab	
Jan III Sobieski	491.1	434.7	4.2	5.7	17.4	21.8	0.79	1.59	0.75	1–2	3.79	Ab	
Kazimierz Wielki	442.5	409.4	4.5	5.8	16.7	17.7	0.94	1.47	1.15	2	2.57	–	
male clone	479.6	421.1	3.9	4.7	18.9	20.7	0.91	1.46	1.25	2	2.66	Ab	
female clone	484.3	472.6	4.2	6.5	20.4	22.1	0.92	1.47	1.05	2	2.49	Ab	
Kořinek	380.7	398.7	3.6	4.4	18.2	19.8	0.92	1.61	1.17	2(-3)	2.12	Ad + Ab	
Mieszko I	408.6	391.7	4.1	4.7	21.6	25.8	0.84	1.33	0.99	2	2.00	Ab	
Pendula (from Belgium)	415.4	410.2	4.3	5.5	20.7	18.9	1.09	1.48	1.21	2	1.91	Ab	
Pendula (from China)	426.5	379.9	4.1	5.7	17.5	23.2	0.75	1.82	1.23	1–2	2.13	Ab	
Profesor Łukasiewicz	393.0	337.6	4.2	5.4	21.5	21.2	1.01	1.50	0.98	2	2.82	Ab	
Przemysław II	329.6	316.1	3.9	4.5	15.9	21.3	0.75	1.65	1.28	1–3	3.78	Ad + Ab	
Saratoga	355.7	359.2	3.4	4.3	19.9	20.3	0.98	1.47	1.35	2	1.75	Ad + Ab	
Stefan Batory	395.8	350.7	4.1	5.1	23.3	19.1	1.22	1.57	1.18	1–2	2.95	–	
Tabulaeformis	459.5	437.7	4.4	6.2	18.5	17.2	1.07	1.36	1.33	2(-3)	2.18	Ab	
Variiegata	341.9	319.5	3.3	4.5	18.3	21.8	0.84	1.66	1.18	2	2.25	Ab	
Władysław Lokietek	355.7	347.8	3.6	4.2	18.8	18.4	1.02	1.49	1.06	2(-3)	2.04	–	



Figs 55–56. Petiole transverse sections (T.S.) of *Ginkgo biloba* ‘Košinec’: (55) T.S. of the petiole illustrating the general anatomy, (56) part of the vascular bundles at high magnification: *ab* – abaxial epidermis, *ad* – adaxial epidermis, *c* – cuticle, *d* – druse, *ed* – endodermis, *h* – hair, *pa* – parenchyma, *pe* – pericycle, *ph* – phloem, *sc* – schizogenic cavity, *scl* – sclerenchyma, *t* – transfusion tissue, *vc* – vascular cambium, *x* – xylem



Figs 57–58. Lamina transverse sections (T.S.) of *Ginkgo biloba* (LM): (57) ‘Kořinek’ – T.S. of the lamina illustrating the general anatomy, (58) ‘Jagiello’ – part of the lamina: *ab* – abaxial epidermis, *ad* – adaxial epidermis, *be* – bundle sheath extension, *c* – cuticle, *d* – druse, *f* – lignified fibre, *ph* – phloem, *pp* – palisade parenchyma, *ps* – parenchyma sheath, *qc* – sunken guard cells, *sc* – schizogenic cavity, *sp* – spongy parenchyma, *vc* – vascular cambium, *x* – xylem

Lamina transverse section (T.S.) (tab. 3, figs 57–58)

Cuticle. In all the taxa the cuticle on the abaxial epidermis was thicker than the cuticle on the adaxial surface (except ‘DFS’). The average thickness of the epicuticular layer ranged from 3.3 to 5.3 μm on the adaxial surface and from 4.2 to 6.5 μm on the abaxial surface.

Epidermis. In all the taxa the leaf epidermis consisted of single layers (figs 57, 58). The anticlinal walls were straight or straight and slightly repand, whereas the outer periclinal walls on the adaxial surface were more or less convex and papillate on the abaxial surface in all the cultivars (figs 57, 58). There were significant differences in the epidermal thickness in all the taxa. The average epidermal thickness varied from 15.9 μm (‘Przemysław II’) to 25.5 μm (‘Jadwiga’) on the adaxial surface and from 14.5 μm (‘Hunan’) to 25.9 μm (‘Bolesław Chrobry’) on the abaxial surface. The reciprocal proportion of the width and height in the epidermal cells ranged within the taxa from 1.18 to 1.82 on the adaxial epidermis and from 0.75 to 1.48 on the abaxial epidermis (tab. 3). The abaxial epidermis was thicker than the adaxial epidermis (ETI <1) in 14 taxa and ranged from 0.75 to 0.98 (tab. 3). The taxa differed in the leaf thickness and in the leaf epidermis thickness. There was no correlation between the epidermis thickness and the lamina thickness. The average lamina thickness between the vascular bundles ranged from 316.1 to 492.1 μm , where the vascular bundles ranged from 329.6 to 626.2 μm (tab. 3). The lamina surface in the T.S. was almost flat on both surfaces e.g. in ‘Korinek’ (fig. 57), more or less undulate in ‘Jagiełło’ (fig. 58) and ‘Bolesław Chrobry’, and very mounted on both surfaces in ‘Jadwiga’ and ‘Pendula’ (from China).

Mesophyll. The mesophyll was bifacial with a thicker spongy layer below the palisade. The palisade parenchyma was present in 1–2(-3) layers (tab. 3, fig. 57). The spongy parenchyma of elongate cells with undulate cell walls with small or without air spaces (figs 57, 58) was located close to the abaxial face. The reciprocal proportion of the thickness of the spongy parenchyma and the thickness of the palisade parenchyma ranged from 1.75 to 3.78 (tab. 3).

Vascular bundles. In T.S. of the lamina vascular bundles were collateral as in the petiole. The xylem faced the adaxial lamina surface while the phloem faced the abaxial epidermis (figs 57, 58). The sclerenchyma was represented only by the fibres. The vascular bundles had phloem and xylem fibre caps, and all fibre cells had thick lignified, secondary walls (fig. 58). Vascular cambium was found between the xylem and phloem (figs 57, 58). The vascular bundles were surrounded by a parenchymatous sheath (fig. 57) and accompanied by (0)3–6 large cluster crystals of calcium oxalate. The bundle sheath extended to the abaxial epidermis in 12 cultivars and to the adaxial and abaxial epidermis in six cultivars (tab. 3, fig. 57). Calcium oxalate crystals were represented by druses in all the taxa and they were present in the palisade and spongy parenchyma, sized 64.9–78.7 and 49.6–79.6 μm (respectively). Schizogenic cavities (resin ducts) were found in the leaves of all the cultivars under study (fig. 57) and their size was (45-)98.7–261.1 \times (48-)93–315 μm . The guard-cells were sunken on the abaxial surface in all the taxa under analysis.

DISCUSSION

We described the morphological and anatomical traits and detailed epidermal structures in *Ginkgo* cultivars and two clones (male and female) of leaves collected from long shoots. The findings showed that general leaf morphology is useful for the identification of individual cultivars. There were epidermal microcharacteristics and anatomical features in all the taxa, and they were diagnostic for the genus. The leaves of all the taxa were glabrous. There were hairs in the basal part and on the adaxial surface in the middle part of the petiole. Both surfaces of the leaves were covered with wax in the form of tubules [Riederer 1989, Barthlott et al. 1998]. This type of wax was found on the stem epidermis [Tomaszewski and Zieliński 2014]. The cuticle was smooth on the adaxial surface in all the taxa, whereas it could be smooth or smooth-striated on the abaxial surface of the lamina. However, Cargo et al. [2000] and Duarte et al. [2013] report that the cuticle was striated on the adaxial epidermis. The most conspicuous characteristics of the cuticle were prominent papillae on the subsidiary cells of the stomata and periclinal cell walls on the abaxial epidermis (figs 30–52) of the lamina in all the cultivars. According to Denk and Velitzelos [2002], the subsidiary cells may be with or without papillae. The presence of papillae is also a good diagnostic for the identification of fossil leaves [Denk and Velitzelos 2002].

In our study the anticlinal cell walls were usually straight, but they could be undulate [Cargo et al. 2000, Denk and Velitzelos 2002, Duarte et al. 2013]. Stan and Simeanu [2008] observed strongly sinuous anticlinal cell walls in the adaxial epidermis and slightly sinuous cell walls in the abaxial epidermis. Our study showed that sunken stomata were typically located on the abaxial surface (hypostomatic), except the ‘Jan III Sobieski’ and the female clone leaves (amphistomatic). Kanis and Karstens [1963] reported that they found amphistomatic leaves in the male tree. Denk and Velitzelos [2002] found amphistomatic leaves in *G. biloba* ‘Goethe-tree’, whereas Stan and Simeanu [2008] observed only hypostomatic leaves. The stomata in all the taxa were obscured by a ring of (3)4–6 blunt papillae on the surrounding cells. Our results are in agreement with the findings made by Rudall et al. [2012]. Denk and Velitzelos [2002] found that the subsidiary cells could be complete or incomplete amphycyclic. In our study we observed only complete subsidiary cells.

The abaxial lamina surface in *Ginkgo* provides more features of diagnostic value than the adaxial one, as was confirmed in previously published results. The *Ginkgo* lamina was bifacial, and the multi-layered mesophyll was differentiated into palisade and spongy parenchyma, but in young leaves the mesophyll was homogeneous [Cebret 2007]. So far the literature reports have described the *Ginkgo* lamina as isobilateral or bifacial with homogeneous mesophyll [Stan and Simeanu 2008, Bercu 2013].

Toma and Rugina [1998], Cargo et al. [2000], Stan and Simeanu [2008], Bercu [2013] and Duarte et al. [2013] presented the petiole anatomy. We also analysed the structure of petioles in a T.S. and it corresponded to the observations made in earlier studies conducted by the aforementioned authors. However, we observed a few differences, e.g. in the petiole epidermis thickness, number and size of schizogenic cavities and in the presence of the vascular cambium. Measurements of the cuticle thickness,

epidermis cell thickness, petiole and lamina thickness, palisade and spongy parenchyma thickness can be useful for identification of taxa.

Our results suggest that although some cultivated plants are morphologically well characterised by the size and shape of their leaves, they cannot be identified on the basis of the micromorphology of the epidermis because in all the taxa they were very similar and there were no absolute micromorphologic diagnostic characters between the taxa under study. Druse crystals and schizogenic cavities were found in all the taxa and they were typical of the *Ginkgo* genus. Stan and Simeanu [2008] reported the absence of calcium oxalate crystals in the leaf of *G. biloba*.

The micromorphology and anatomy of the leaves of some *Ginkgo* cultivars provided some important new data, e.g. wax rodlets and cuticle characteristics, petiole thickness and epidermis thickness, number and size of schizogenic cavities and the presence of hairs on the adaxial surface of petioles in some cultivars, lamina and epidermis thickness, the presence of bundle sheath extensions on the adaxial or adaxial and abaxial surfaces, the form of anticlinal walls and the presence of vascular cambium. We suggest that the outline of veins in the cross-section along the leaf lamina has high potential significance for the diagnosis of *Ginkgo* taxa. The epicuticular features may help to identify and classify dispersed fragments of the cuticle in fossil leaves, and therefore they can be used as an additional tool to identify this unique gymnosperm. Thus, this detailed analysis considerably broadened our knowledge of individual cultivars, and our research should be continued.

CONCLUSION

1. The leaves of the taxa under study were characterised by high variability of morphological traits in the size, shape and dissection of the apical leaf margin.

2. All the cultivars had bifacial leaves. In most of the taxa the leaves were hypostomatic and only two taxa *G. biloba* 'Jan III Sobieski' and the female clone had amphistomatic leaves.

3. The micromorphology and anatomy of the leaves of some *Ginkgo biloba* cultivars provided some important new data, e.g. wax rodlets and cuticle ornamentation, the presence of short hairs in the adaxial epidermis of petioles in some cultivars, petiole thickness and epidermis thickness, number and size of schizogenic cavities, lamina and epidermis thickness, presence of bundle sheath extensions on adaxial or abaxial surfaces, collaterally opened vascular bundles and form of anticlinal walls.

4. Measurements of the petiole and lamina anatomical features can be useful for identification of *Ginkgo* taxa. The abaxial leaf side in *Ginkgo* provided more features of diagnostic value than the adaxial one. Many micromorphological and anatomical traits were present in the leaves of all the taxa, and they may be typical of *Ginkgo biloba*.

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PORÓWNAWCZA MORFOLOGIA I ANATOMIA LIŚCI ODMIAN *Ginkgo biloba* L.

Streszczenie. W pracy przedstawiono wyniki badań nad morfologią i anatomią liści 21 odmian (w tym 10 polskiej hodowli) oraz dwóch klonów *Ginkgo biloba*. Liście z długopędów pochodziły z kolekcji Katedry Dendrologii i Szkółkarstwa Uniwersytetu Przyrodniczego w Poznaniu. Obserwacje prowadzono przy użyciu mikroskopu świetlnego i skaningowego. Liście analizowano pod względem 8 cech morfologicznych, uwzględniając blaszkę liściową i ogonek liściowy. Na podstawie tych badań stwierdzono, że liście poszczególnych odmian różnią się istotnie między sobą i wykazują większe zróżnicowanie w długości, szerokości blaszki liściowej i w długości ogonków niż dotychczas opisywano w literaturze. Cechy epidermy górnej i dolnej wszystkich taksonów różnią się istotnie, m.in. ornamentacją kutykuli, brakiem brodawek, położeniem i występowaniem szparek (sporadycznie na górnej powierzchni liścia), brakiem pierścienia wokółszparkowego i grubością epidermy. Na podstawie badań anatomicznych stwierdzono, że liście odmian i klonów miłorzębu są bifacjalne oraz mają zróżnicowany miękisz zieleniowy na palisadowy i gąbczasty. Prezentowane wyniki badań zmienności cech morfologicznych i anatomicznych mogą być wykorzystane w identyfikacji odmian *G. biloba*, a cechy epikutikularne przydatne w identyfikacji i klasyfikacji fragmentów liści kopalnych. Kilka cech opisanych i zilustrowanych w pracy jest nowych, dotychczas niepodawanych w literaturze.

Słowa kluczowe: *Ginkgo*, anatomia, liście, LM, mikro- i makromorfologia, SEM

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