

COMPARATIVE LEAF MORPHOLOGY AND ANATOMY OF SOME
NEOTROPICAL *PHILODENDRON* SCHOTT (ARACEAE) SPECIES

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(Received: April 03, 2014. Accepted: May 27, 2014)

ABSTRACT. A comparative morphological and anatomical study on the petioles and lamina of 22 taxa (species, subspecies and cultivars) of the genus *Philodendron* (subgenera *Meconostigma*, *Pteromischum* and *Philodendron*) has been made in order to investigate interspecific differences which may be useful in species identification. All species have bifacial leaves with petioles, amphistomatic with a strongly reduced density of stomata on the adaxial leaf surface. The species differ in the size and shape of their epidermal cells, the distribution and types of stomata and cuticle ornamentation in the lamina, thickness of epicuticular layer, presence or absence of hypodermis, structure of spongy mesophyll, thickness of palisade and spongy mesophyll layers, as well as types of raphides, and in the structure and forms of petioles. A combination of these characters may be useful in species identification. This study shows that there is some variation in petiole and leaf morphological and anatomical characters among the 22 taxa of *Philodendron*. However, many characters are present in all of them and may be typical of the genus. The study revealed several detailed interesting epidermal and anatomical features that have not previously been reported in the genus.

KEY WORDS: petiole, lamina, monocots, morphology, anatomy, *Philodendron* subgenera *Meconostigma*, *Pteromischum*, *Philodendron*

INTRODUCTION

With more than 700 species, the genus *Philodendron* is the second largest genus in the family Araceae after *Anthurium* Schott (CROAT 1997). This morphologically and ecologically diverse genus is strictly a New World genus, brought from northern Mexico to southern Uruguay (MAYO et al. 1997). The genus, has been initially divided into four subgenera: *Euphilodendron*, *Calostigma*, *Meconostigma* and *Sphinctrostigma* (SCHOTT 1832), and later into two subgenera *Euphilodendron* (= *Philodendron*) and *Meconostigma* (ENGLER 1899, KRAUSE 1913), is now subdivided into three subgenera. *Pteromischum* with 75 species (GRAYUM 1996), *Meconostigma* with 15 species (MAYO 1988, 1991, CROAT 1997) and *Philodendron* with more than 600 species (CROAT 1997) are accepted worldwide (MAYO 1988, GRAYUM 1990, 1996, MAYO et al. 1997,

CROAT 1997, SAKURAGUI et al. 2005). Two of them, i.e. *Meconostigma* and *Philodendron*, are morphologically well defined (MAYO 1990, 1991). Recently the subgenus *Meconostigma* has been revised (MAYO 1991, GONÇALVES & SALVIANI 2002) and partial revisions of the subgenera *Pteromischum* (GRAYUM 1996) and *Philodendron* (CROAT 1997) have been published. However, no complete revision of the genus has been undertaken since the classification of KRAUSE (1913), which included 222 species of *Philodendron*. Previous classifications were based on morphological characters mainly concerning the inflorescence, flower and leaf shape. As defined by morphological characters and based on molecular analyses [two ribosomal DNA nuclear markers, internal transcribed spacer (ITS) and external transcribed spacer (ETS), chloroplast intron *rpl16*] all the three subgenera are monophyletic (GAUTHIER et al. 2008). According to the results of

BARABÉ et al. (2002) and TAM et al. (2004), the genus *Philodendron* would be paraphyletic because the genus *Homalomena* Schott is nested within *Philodendron* (subgenus *Meconostigma*) in their phylogenetic analyses based on chloroplast DNA sequences. The genus *Homalomena* Schott is morphologically very similar to *Philodendron* (MAYO et al. 1997). *Philodendron* is a genus of outstanding horticultural importance and the subgenus *Meconostigma* includes some very well known ornamental species. *Philodendron bipinnatifidum* Schott ex Endl., one of the world's most ubiquitous houseplants, has provided a rich source of variation for breeding of different foliage forms. Most of the species popularly known as 'self-headers' belong to this subgenus. In cultivation other very common species also include *P. cordatum* (Vell) Kunth, *P. lacerum* (Jacq.) Schott, *P. hederaceum* (Jacq.) Schott from the subgenus *Philodendron* as well as other species and hybrids (MAYO et al. 1997). The purpose of this comparative study is to assess morphological and anatomical variations, potentially useful in species identification, as well as to test validity of the classification of the genus into subgenera and sections.

MATERIAL AND METHODS

For this study 18 species, one subspecies and three cultivars were examined. Samples were obtained from the greenhouses of the Botanical Garden in Poznań (Poland) (BG-AMU). We included taxa

from three subgenera of *Philodendron*. For the subgenus *Philodendron*, representatives from five of the nine sections recognised by CROAT (1997) were included (Table 1). For SEM studies mature air dried leaves were coated with gold and examined under a Philips 515 and Zeiss EVO 40 scanning electron microscope at the Electron Microscopy Laboratory, the Faculty of Biology, the Adam Mickiewicz University of Poznań. The sculpture of both surfaces of the lamina was studied with LM on permanent slides. For anatomical studies living material was stored protected in 70% alcohol. The anatomy of the lamina, midrib and petiole was studied. Transversal sections, 50 µm thick, were prepared with a microtome (Leitz). All sections were embedded in glycerin-gelatin. Slides thus prepared were used to describe transverse sections (T.S.) and measured characters (Tables 2–4). The epidermal thickness index (ETI) was calculated as the ratio of adaxial epidermis thickness to abaxial epidermis thickness (Table 4). All measurements were carried out under a light microscope (LM) (Olympus BX 43). Five leaves were examined from each species. The midrib outline was classified using the current terminology described in CROAT & BUNTING (1979). In this paper we followed KEATING (2002) for the description of stomata types, while the terminology of epidermis sculpturing follows BARTHOLOTT (1990). The classification of cells and tissues follows the nomenclature proposed by KEATING (2000, 2002) and raphides of calcium oxalate crys-

Table 1. *Philodendron* specimens used in this study

Taxa	Voucher information	Taxonomy	
		subgenus	section
<i>Philodendron bipinnatifidum</i> Schott ex Endl.	I-1005-005-0000-6991-4010	Meconostigma	
<i>P. surinamense</i> Schott ex Engl.	I-1005-002-0000-6995-2279	Pteromisium	Fruticosa
<i>P. crassinervium</i> Lindl	I-1005-002-0000-6990-2791	Philodendron	Baurisia
<i>P. melanochrysum</i> Linden et Andre	I-1005-002-0000-6994-3999	Philodendron	Philodendron
<i>P. ornatum</i> Schott	I-1005-002-0000-6964-0233	Philodendron	Philodendron
<i>P. hederaceum</i> (Jacq.) Schott var. <i>hederaceum</i>	I-1005-002-0000-6991-1687	Philodendron	Philodendron
<i>P. hederaceum</i> var. <i>oxycardium</i> (Schott) Croat	I-1005-002-0000-6002-3997	Philodendron	Philodendron
<i>P. bipennifolium</i> Schott	I-1005-002-0000-6991-0616	Philodendron	*Calostigma
<i>P. domesticum</i> G.S. Bunting	I-1005-002-0000-6998-2453	Philodendron	*Calostigma
<i>P. cordatum</i> Kunth ex Schott	I-1005-002-0000-6991-2609	Philodendron	*Calostigma
<i>P. erubescens</i> K. Koch et Augustin	I-1005-002-0000-6979-1543	Philodendron	*Calostigma
<i>P. erubescens</i> K. Koch et Augustin 'Burgundy'	I-1005-001-0000-6996-2326	Philodendron	*Calostigma
<i>P. imbe</i> Schott ex Endl.	I-1005-002-0000-6979-2234	Philodendron	*Calostigma
<i>P. martianum</i> Endl.	I-1005-002-0000-6960-2474	Philodendron	*Calostigma
<i>P. microstictum</i> Standl. et L.O. Williams	I-1005-002-0000-6993-2466	Philodendron	*Calostigma
<i>P. pedatum</i> (Hook) Schott.	I-1005-002-0000-6992-0784	Philodendron	Schizophyllum
<i>P. squamiferum</i> Poepp.	I-1009-002-0000-6979-2246	Philodendron	Schizophyllum
<i>P. angustisectum</i> Engl.	I-1007-002-0000-6996-2369	Philodendron	Polytomium
<i>P. lacerum</i> (Jacq.) Schott	I-1005-002-0000-6988-2577	Philodendron	Polytomium
<i>P. pinnatifidum</i> (Jacq.) Schott	I-1005-002-0000-6959-2440	Philodendron	Polytomium
<i>P. × corsinianum</i> Senoner	I-1005-005-0000-6992-2637		
<i>P.</i> 'Imperial Green'	I-1005-002-0000-6995-2256		

*Now called sec. *Macrobelyium* according to SAKURAGUI et al. 2005.

tals follows TURPIN (1836) and KEATING (2003, 2004 a). The interactions among quantitative features of stomata and lamina were tested using Pearson's correlation coefficient.

RESULTS

PETIOLE TRANSVERSE SECTION (T. S.) (TABLE 2, FIG. 1)

Outline: the outline varies from rounded in *Philodendron surinamense*, *P. cordatum*, *P. lacinatedum*, *P. angustisectum* and *P. lacerum*, oval in *P. crassinervium*, *P. bipennifolium* (Fig. 1 A), *P. pinnatifidum* and *P. × corsianum* with a small channel in *P. hederaceum* var. *hederaceum* (Fig. 1 B) or without a channel, hemicylindrical in *P. erubescens* 'Burgundy' (Fig. 1 C), D-shaped in *Philodendron* 'Imperial Green' and in *P. ornatum* (Fig. 1 D, G), flattened adaxially in *P. bipinnatifidum* (Fig. 1 E) *P. erubescens*, *P. martianum* to C-shaped in *P. melanochrysum*, *P. domesticum* (Fig. 1 I), *P. imbe* (Fig. 1 H) and *P. microstictum*. D-shaped petioles have their lateral margins weakly to prominently raised with the marginal rib either acute or obtuse and C-shaped broadly or narrowly sulcate adaxially with a sharply angled margin. Abaxial petiole rounding is observed in all the taxa.

Cuticle smooth and moderately thickened. **Epidermis** of small cells level or rounded on the surface and inner walls rounded to angular. Most species have a glabrous petiole surface, but there are conspicuous exceptions. Two species, *P. ornatum* and *P. squamiferum*, have "scaly petioles". In *P. ornatum* they are reduced to a small protuberance (Fig. 1 G), in *P. squamiferum* a small protuberance and trichome-like scales are found. **Hypodermis**: absent in seven species (Table 2) or present of 1–4 layers on adaxial side (Fig. 1 G, H, I). **Collenchyma**: beneath the epidermis or hypodermis as a continuous band of 3–13 angularly thickened layers (Fig. 1).

Chlorenchyma: beneath the epidermis or up to five rows of cells inside collenchyma (Fig. 1). Ground tissue of various sizes of parenchyma cells among numerous small to medium-sized air cavities. **Vascular bundles** numerous and scattered, mostly oriented with phloem facing perimeter (Fig. 1). Xylem of 1–3 protoxylem cells per bundle, with spiral to angular thickening and occasionally one metaxylem element. **Sclerenchyma**: fibers forming phloem cap usually not fully surrounding laterally. In *P. bipinnatifidum* and *P. martianum* fiber caps surrounding xylem and phloem. Calcium oxalate crystals are most frequently represented by druses (Fig. 1). Druses present subepidermally and in cells bordering air cavities. Small groups of prismatic crystals occur in ground

Table 2. Petiole characters of some *Philodendron* taxa

Taxa	Length of petiole (mm)	Width × thickness (mm)	Outline of the petiole in T.S.	Number of hypodermis layer	Number of collenchyma layer	Calcium oxalate crystals
<i>Philodendron bipinnatifidum</i>	32–102	14.0 × 12.0	flattened adaxially	–	12–18	R, S, D
<i>P. surinamense</i>	3–10	2.2	rounded	–	3–4	R, S, D
<i>P. crassinervium</i>	4–11	4.4 × 4.0	oval	–	3	S, D
<i>P. melanochrysum</i>	3–11	2.2 × 1.2	C-shaped	1–2	3–4	S, D, P
<i>P. ornatum</i>	12–35	4.6 × 3.8	irregular, flattened	1–2	(4)5–8	S, D, P
<i>P. hederaceum</i> var. <i>hederaceum</i>	3–8	5.0 × 3.5	rounded with small channel	2	3–4(5)	S, D, P
<i>P. hederaceum</i> var. <i>oxycardium</i>	3–14	2.2 × 2.0	slightly flattened	1–2	4	R, S, D, P
<i>P. bipennifolium</i>	5–22	4.4 × 4.6	oval	1	4–5	S, D
<i>P. domesticum</i>	14–23	6.0 × 7.0	C-shaped	2–3	3–4	R, S, D, P
<i>P. cordatum</i>	13–47	6.5	rounded	1	4–7	R, S, D
<i>P. erubescens</i>	8–40	7.0	flattened adaxially	–	4–5	S, D
<i>P. erubescens</i> 'Burgundy'	10–25	5.0 × 5.2	hemicylindrical	–	6–7	S, D, P
<i>P. imbe</i>	11–29	5.0 × 5.3	C-shaped	3–4	5–6	S, D
<i>P. martianum</i>	13–37	26.0 × 20.0	flattened adaxially	–	6–12	S, D
<i>P. microstictum</i>	2–12	3.4 × 2.4	C-shaped	2	4–5	R, S, D
<i>P. pedatum</i>	10–27	4.3	rounded	1	5–6	R, S, D, P
<i>P. squamiferum</i>	9–20	3.2	irregular, rounded	2–3	4–5	R, S, D, P
<i>P. angustisectum</i>	3–33	8.2	rounded	1	4–5	R, S, D
<i>P. lacerum</i>	12–35	8.0	rounded	1–2	3–8	S, D
<i>P. pinnatifidum</i>	27–75	13.0 × 12.0	oval	1	12–13	R, S, D, P
<i>P. × corsianum</i>	21–55	9.0 × 8.3	oval	2–3	10–12	R, S, D, P
<i>P. 'Imperial Green'</i>	6–27	11.5 × 8.2	D-shaped	–	4–7	R, S, D, P

“–” absence of hypodermis layer, R – raphide, S – styloid, D – druse, P – prism, T.S. – transverse section.

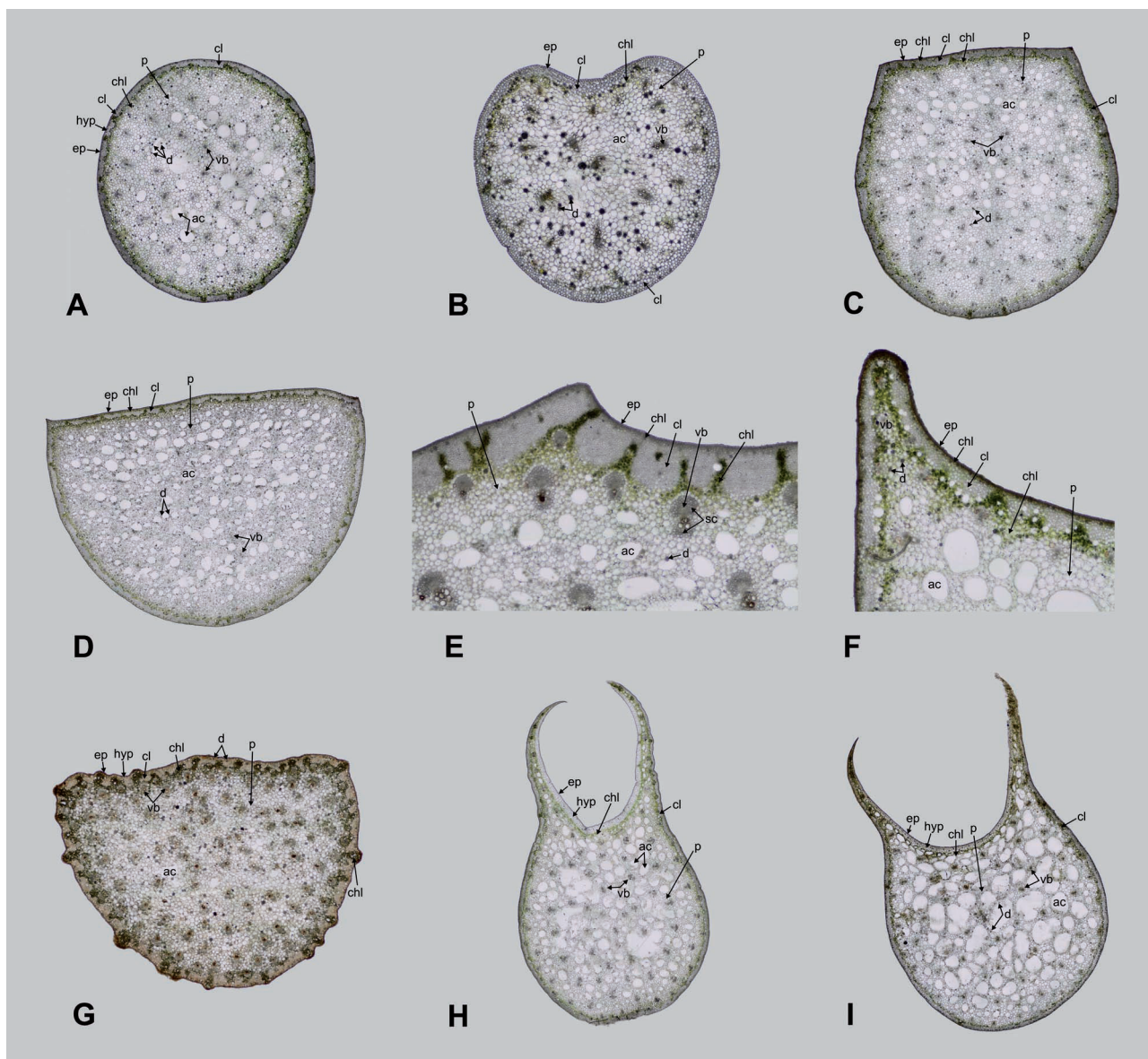


Fig. 1. Petiole transverse sections (T.S.) in some *Philodendron* taxa illustrating the forms and general anatomy. A – *P. bipennifolium*, B – *P. hederaceum* var. *hederaceum*, C – *P. erubescens* ‘Burgundy’, D – *P. ‘Imperial Green’*. E – *P. bipinnatifidum*. Part of marginal petiole on adaxial side, F – *P. martianum*. Part of marginal petiole on adaxial side, G – *P. ornatum*, H – *P. imbe*, I – *P. domesticum*; ep – epidermis, hyp – hypodermis, cl – collenchyma, chl – chlorenchyma, p – parenchyma, vb – vascular bundle, ac – air cavities, d – druses

tissue. Single styloids occur individually within cells. Raphides (one to several) that form in bundles are occasionally found in T.S. of petioles. Cell types may be idioblastic and become wide, spindle-shaped and biforine-shaped.

LAMINA SURFACE (TABLE 3, FIGS 2–5)

The shape of epidermal cells is similar on both surfaces. The cells are irregular or regularly polygonal (tetragonal, pentagonal and hexagonal), and more or less elongated on the midrib and margin, with straight or straight to slightly undulate, raised anticlinal walls and concave or convex periclinal walls. The anticlinal walls are thin or thick (Fig. 4

B, C, E). Stomata are found on both surfaces (Figs 2, 3, arrows), but at the adaxial surface restricted to the midrib and margins (Figs 2 A, C, E, G; 3 A, C, E). Because only a few stomata were present on the adaxial epidermis it was not possible to describe them in those taxa. The mean number of stomata per 1 mm² on the abaxial surface is variable among the taxa, ranging from 4.66 to 21.53. Stomata types (Fig. 4) observed mainly on the abaxial surface are: brachyparacytic (Fig. 4 A), brachypara-tetracytic (Fig. 4 C), brachyparahexacytic (Fig. 4 B, E), amphibrachy-paracytic (Fig. 4 D) and a rare anomocytic type in *P. imbe* (Fig. 4 F) and *P. erubescens* ‘Burgundy’. They are elliptical in shape, generally longer than wide. The main stomatal length varied from 21.24

Table 3. Comparison of selected abaxial epidermal features of some *Philodendron* taxa

Taxa	Characters					
	length of stomata (μm)	width of stomata (μm)	density of stomata (n/mm^2)	stomatal types	cuticular ornamentation on the subsidiary cells of stomata	cuticular ornamentation on the midrib
<i>Philodendron bipinnatifidum</i>	29.83	14.17	21.23	Bp	-	smooth
<i>P. surinamense</i>	28.80	12.96	9.06	Bh	-	smooth
<i>P. crassinervium</i>	27.99	11.47	13.86	Bp	-	smooth
<i>P. melanochrysum</i>	27.31	10.17	11.86	Bh	-	smooth/rugulate
<i>P. ornatum</i>	21.24	10.21	21.53	Ap, Bh	-	smooth
<i>P. hederaceum</i> var. <i>hederaceum</i>	24.61	12.69	4.66	Bh, Bt	-	smooth
<i>P. hederaceum</i> var. <i>oxycardium</i>	27.09	10.53	15.10	Ap, Bp	+	rugulate/striate
<i>P. bipennifolium</i>	23.67	8.19	17.00	Ap	+	rugulate
<i>P. domesticum</i>	25.56	9.36	9.70	Ap	+	smooth
<i>P. cordatum</i>	35.59	12.55	10.43	Ap, Bh	+	rugulate/striate
<i>P. erubescens</i>	27.13	9.18	14.40	Bh	+	rugulate/striate
<i>P. erubescens</i> 'Burgundy'	26.91	10.03	13.26	A	+	rugulate/striate
<i>P. imbe</i>	24.03	9.36	7.00	A, Ap	+	rugulate
<i>P. martianum</i>	29.56	8.37	9.93	Bh	-	smooth
<i>P. microstictum</i>	33.79	11.11	7.56	Ap	+	smooth
<i>P. pedatum</i>	23.44	8.32	12.83	Ap, Bh	+	smooth
<i>P. squamiferum</i>	26.46	9.67	16.96	Bh	+	smooth/rugulate
<i>P. angustisectum</i>	25.33	7.96	14.86	Ap	-	rugulate/striate
<i>P. lacinum</i>	28.75	11.92	9.76	Ap	+	smooth/rugulate
<i>P. pinnatifidum</i>	26.82	11.61	16.53	Bh	+	striate
<i>P. × corsinianum</i>	23.80	8.23	20.10	Ap, Bh	+	smooth
<i>P. 'Imperial Green'</i>	28.30	9.99	9.80	Bh	+	striate

A – anomocytic, Ap – amphibrachyparacytic, Bh – brachyparahexacitic, Bt – brachyparatetracitic, Bp – brachyparacitic, “-” – absence of cuticular ornamentation on the subsidiary cells of stomata, + – presence of cuticular ornamentation on the subsidiary cells of stomata.

μm to 33.79 μm and width from 7.96 μm to 14.17 μm . It results from the calculated Pearson's correlation coefficients that length of stomata is correlated with their width.

The epidermal cells are covered by cuticle. The cuticle of lamina is generally smooth. The striations are more or less irregular in orientation, radiating from guard cells (Figs 3 B; 4 C–F). In the midrib cuticular ornamentation is smooth (Fig. 5 A), rugulate (Fig. 5 B, C) or rugulate/striate (Fig. 5 D, arrows), or thickening of the smooth cuticle is observed on the elongated walls (Figs 2 G, H; 5 A, arrows). Cuticular, irregular protrusions and wart-like protrusions were found on the periclinal walls (Figs 2 C, D; 3 E, D). Epicuticular waxes on both epidermal cells are similar, forming platelets (Fig. 2 D), granules and flakes in *Philodendron* 'Imperial Green'.

LAMINA TRANSVERSE SECTION (T.S.) (TABLE 4, FIG. 6)

Cuticle: Cuticle in most taxa on the adaxial surface is thicker than the cuticle on the abaxial surface. In *P. crassinervium*, *P. domesticum*, and *P. microstictum* it is reverse and in *P. squamiferum* the cuticle on the adaxial surface is as thick as the cuticle on the abaxial surface. The average thickness of the epicuticular layer ranged from 2.5 to 5.3 μm on the adaxial surface

and from 2.1 to 5.7 μm on the abaxial surface. In *P. martianum* the cuticular layer is the thickest on the adaxial (Fig. 6 B) and abaxial surfaces.

Epidermis: In all taxa the leaf epidermis consists of a single layer (Fig. 6 A–E). The anticlinal walls are straight or straight and slightly repand (Fig. 6 D) and the outer periclinal walls are flat (Fig. 6 B, C, D) or convex (papillate), e.g. in *P. surinamense* (Fig. 6 F), *P. hederaceum* var. *oxycardium* and *P. melanochrysum* (Fig. 6 E). The epidermal cells are rectangular (Fig. 6 A–E) only in *P. lacinum*, while epidermal cells on the abaxial surface are square. The average thickness of anticlinal walls ranged from 0.81 μm to 3.24 μm on the adaxial epidermis and from 0.77 μm to 3.49 μm on the abaxial epidermis. Significant differences in some species are observed in the size (height) of epidermal cells with (Fig. 6 A, B) or without hypodermis (Fig. 6 C, D, E). The average height of epidermal cells with hypodermis ranged from 23.8 μm to 38 μm on the adaxial surface and from 17.7 μm to 36.9 μm on the abaxial surface. The average height of epidermal cells without hypodermis ranged from 17.1 μm to 82.3 μm on the adaxial surface and from 21.1 μm to 67.6 μm on the abaxial surface. Significant differences between the examined species are found in the shape of epidermal cells in T.S. The reciprocal proportion of the height and width in epidermal cells varies within examined species from 0.85 to 1.5 on

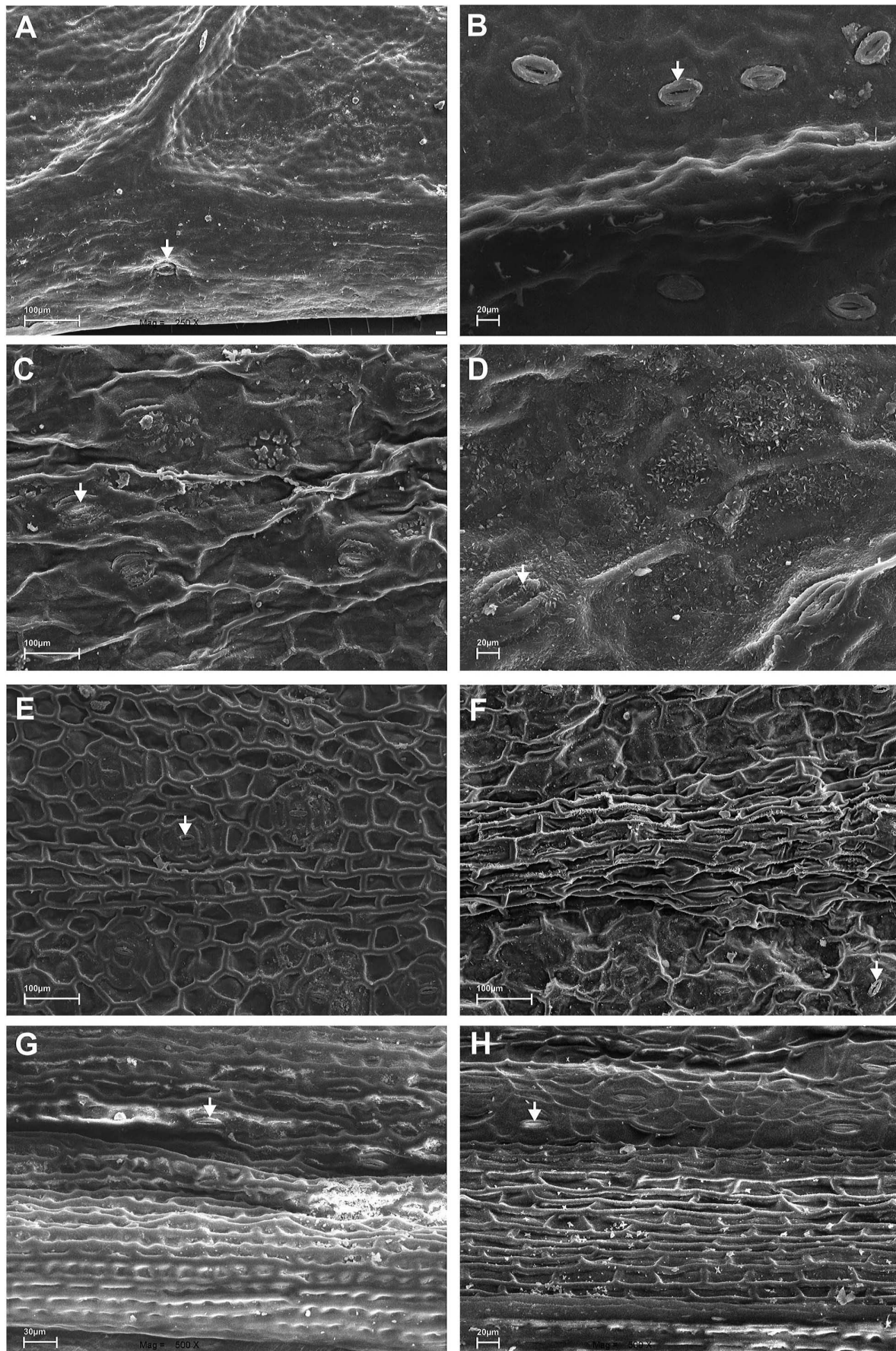


Fig. 2. SEM. Surface view of the adaxial (on the left) and abaxial (on the right) epidermis of *Philodendron*: A, B – *P. bippinatifidum*, C, D – *P. crassinervium*, E, F – *P. melanochrysum*, G, H – *P. bipennifolium* (note stomata arrows)

the adaxial epidermis and from 0.68 to 1.1 on the abaxial epidermis. The adaxial epidermis is thicker than the abaxial epidermis ($ETI > 1$) in most examined taxa, except for *P. bipinnatifidum*, *P. domesticum*, *P. erubescens* 'Burgundy', *P. martianum*, *P. imbe*, *P. angustisectum* and *Philodendron* 'Imperial Green', where $ETI < 1$. Guard cells are typically level with the other epidermal cells. Leaf thickness as well as leaf epidermis thickness differed significantly between the taxa. There is no correlation between epidermis thickness and leaf thickness. Leaf thickness of the lamina varied from 165.3 μm to 463.7 μm .

Hypodermis: absent (Fig. 6 C, D, E) or present beneath epidermis as 1-2 layers (Fig. 6 B) or 1-4 layer (Fig. 6 A) interrupted by palisade mesophyll on both surfaces or only on the abaxial surface.

Mesophyll: The mesophyll is bifacial, with a thicker spongy layer from 82.2 to 284 μm below the palisade (Fig. 6 A-E). The spongy mesophyll has a distinctive structure: with intercellular spaces (Fig. 6 C) and without them (Fig. 6 A, D, E). The palisade parenchyma is found in 1-3 rows in the adaxial part of the leaf blade. Most frequently palisade cells are 2-3 layers and their thickness varies from 36.4 to 79.9 μm .

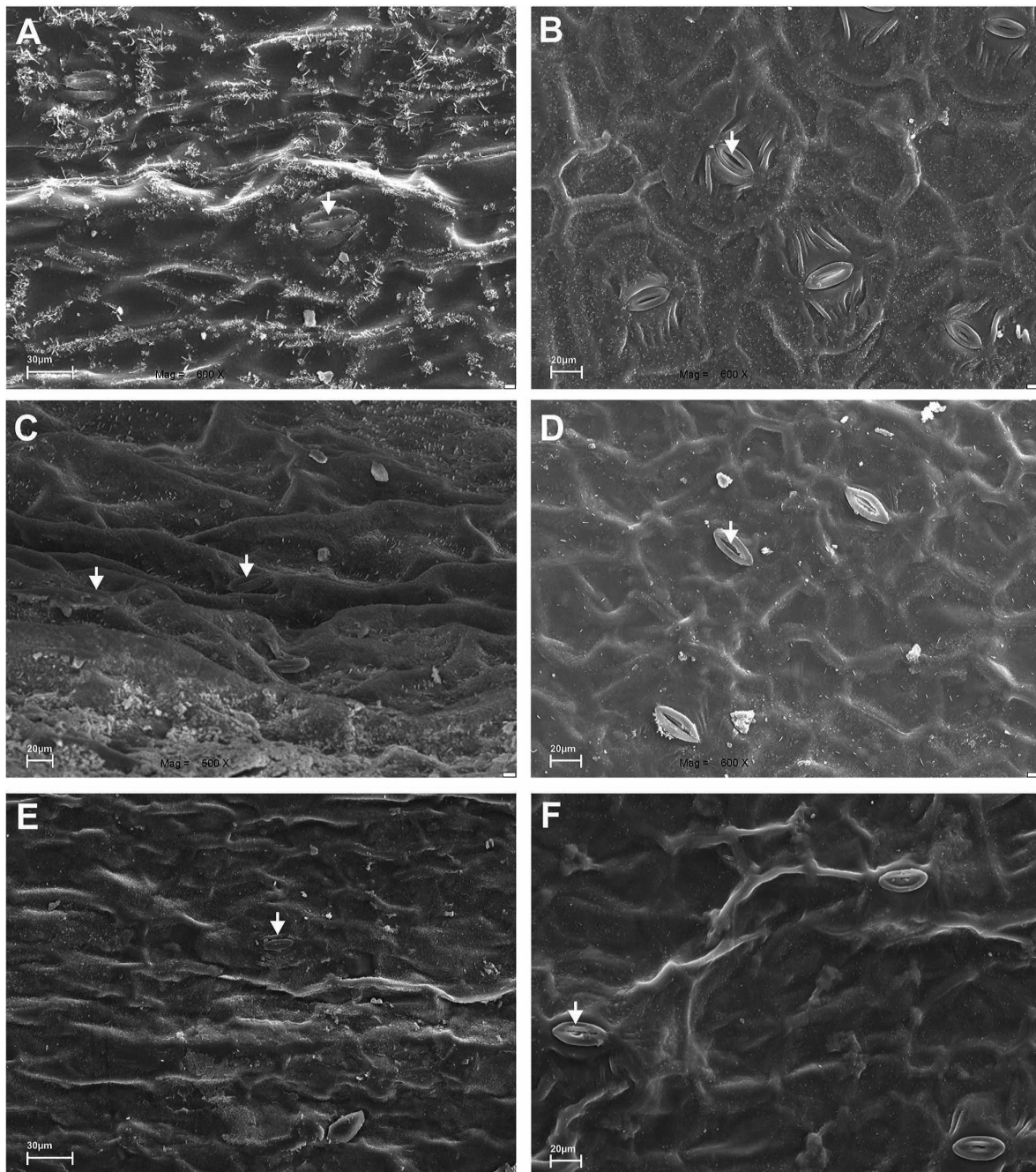


Fig. 3. SEM. Surface view of the abaxial (on the left) and abaxial (on the right) epidermis of *Philodendron*: A, B – *P. cordatum*, C, D – *P. imbe*, E, F – *P. squamiferum* (note stomata arrows)

Vascular bundle: In T.S. of lamina vascular bundles are collateral, more elliptic, with proto- and metaxylem with the fiber cap above phloem and xylem. The xylem faces towards the adaxial leaf surface, while the phloem faces the abaxial epidermis.

Midrib: The midrib outline of the lamina in T.S. varies from flat, slightly convex (Fig. 6 F, G) to slightly sunken (Fig. 6 H) on the adaxial surface. The abaxial midribs of *Philodendron* exhibit less variability varying from slight to highly convex. On the adaxial surface of the midrib the palisade parenchyma is usually interrupted by a hypodermis or collenchymatous

tissue (Fig. 6 G). However, typical apical collenchyma cells are found only in the abaxial region of the midrib (Fig. 6 F, G, H). In the midrib several vascular bundles are found. The large air cavities in the midrib are separated by uniseriate portions of ground tissue (Fig. 6 G).

Calcium oxalate crystals are represented by raphides, styloids, druses, prisms and crystal sand. The leaves of *Philodendron* demonstrate the presence of three distinctive raphide crystal types: thin-walled spindle-shaped cells (Sb), bifurcated (B) and wide cells (W). Druses are found more frequently in the pal-

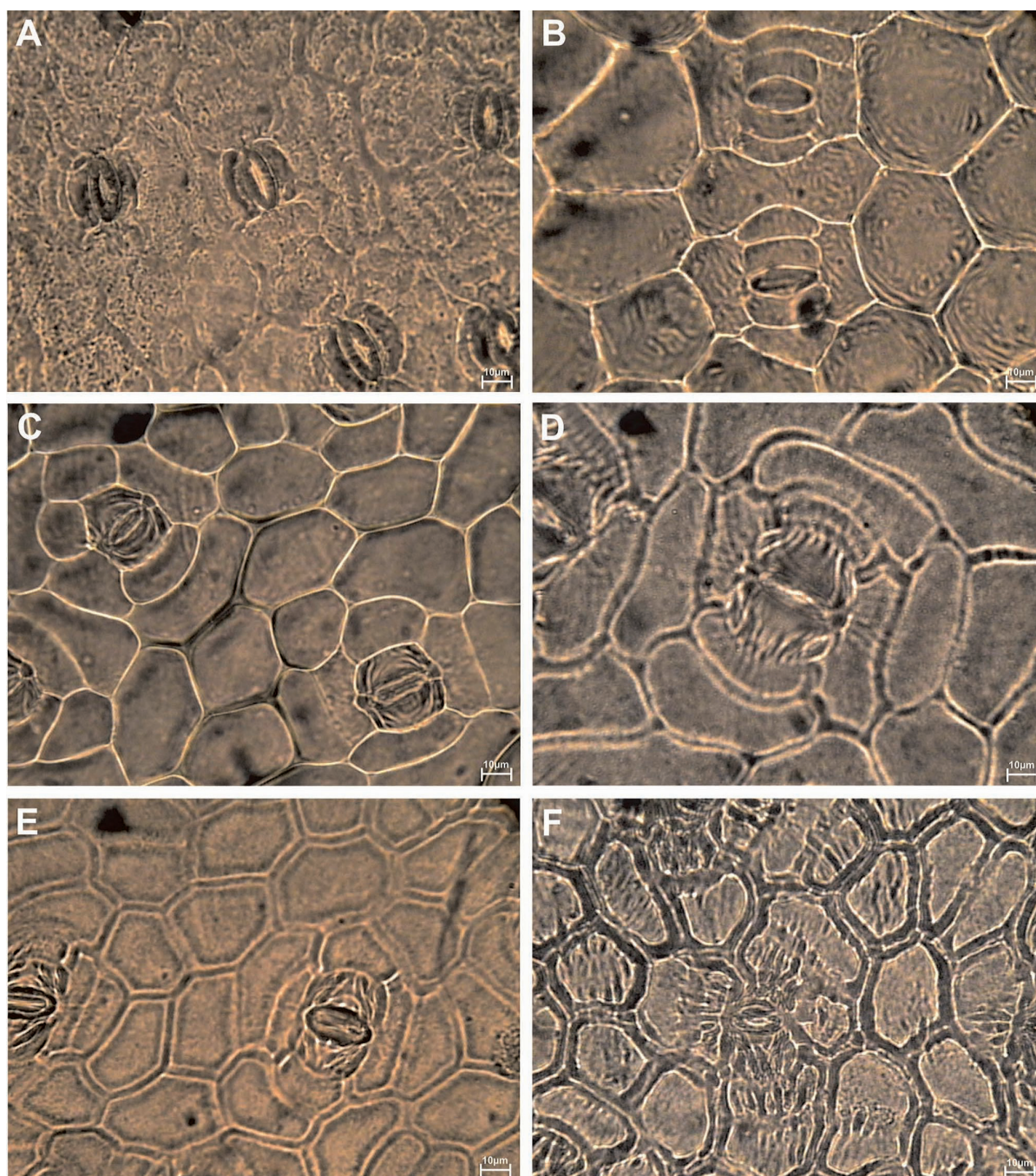


Fig. 4. LM. Surface view of the abaxial epidermis in some *Philodendron* species: A – *P. bipinatifidum*. Brachyparacytic stomata, B – *P. surinamense*. Brachyparahexacytic stomata, C – *P. hederaceum* var. *hederaceum*. Brachyparatetracytic stomata, D – *P. cordatum*. Amphibrachyparacytic stoma, E – *P. erubescens*. Brachyparahexacytic stomata, F – *P. imbe*. Anomocytic stoma

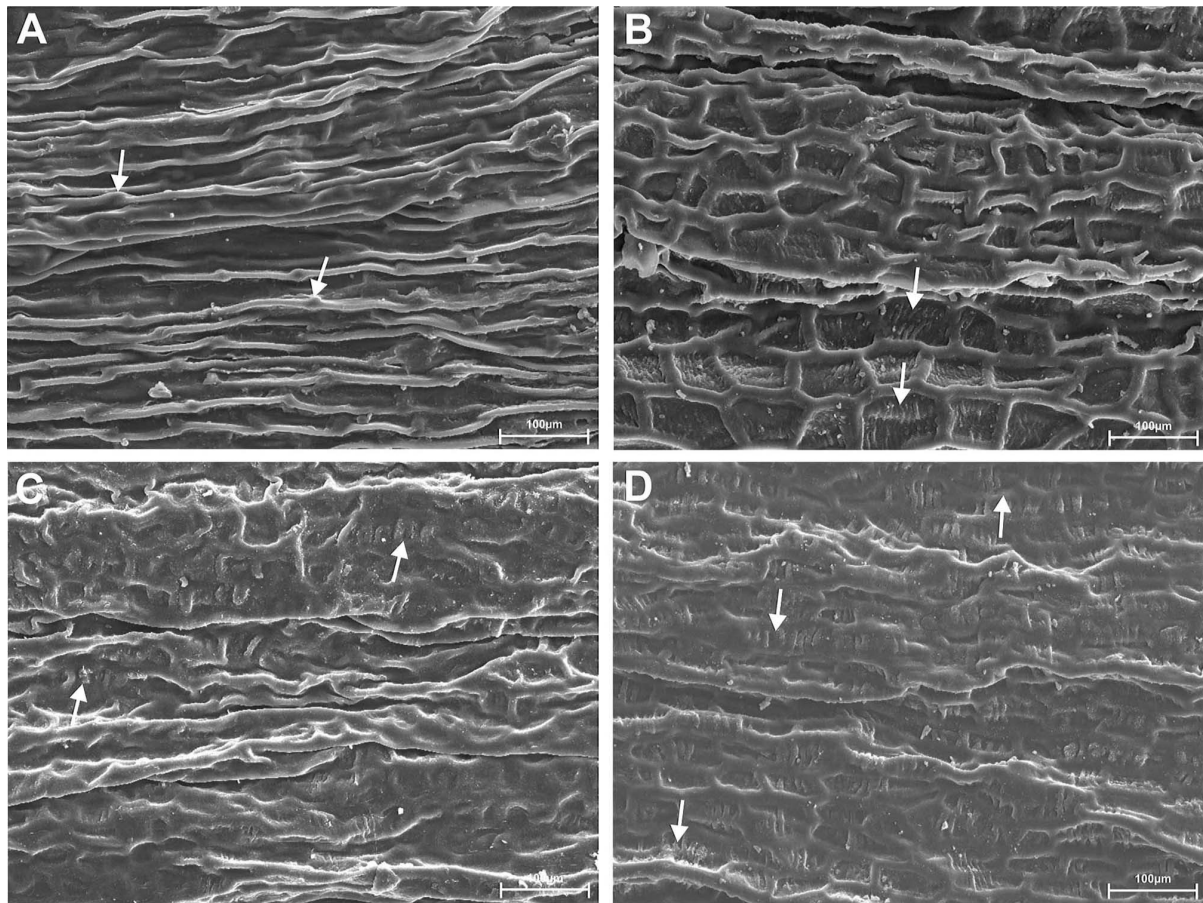


Fig. 5. SEM. Cuticular ornamentation on the midrib in *Philodendron* species: A – *P. crassinervium*. Cuticle smooth, thickening on elongated walls, B – *P. bipennifolium*, C – *P. imbe*. Cuticle rugulate, D – *P. angustisectum*. Cuticle rugulate/striate

isade mesophyll layer, hypodermis, collenchyma, ground tissue and rare in epidermis. Raphides are found more often in the spongy mesophyll and in aerenchyma tissue in the midrib. Crystals are found in the midrib in most taxa. Secretion (resin) canals are present in leaves of all species, being found in the mesophyll of lamina and in collenchyma of midribs. They consist of a schizogenous space. Hydathodes and laticifers are present, but detailed studies have not been conducted. Starch grains were not observed in the petiole or the midrib.

DISCUSSION

Here we showed that some morphological and anatomical characters of petioles and leaves are taxonomically useful for discriminating *Philodendron* taxa. Regarding *P. ornatum*, *P. squamiferum*, *P. erubescens* and *P. pinnatifidum* our results differ with those of GAUTHIER et al. (2008) in petiole outline. Cuticular features of the leaf surface cells proved to be of great diagnostic value. It should be noted in ornamentation patterns. Aroid species predominantly show smooth cuticles without ornamentation (KEATING 2002). The species analysed here have smooth cuticle on both surfaces of the lamina, but striped cuticular ornamentation was present on the subsidiary

cells of stomata. On the midrib of cuticular ornamentation on the periclinal walls is smooth, rugulate or rugulate/striate or thickening of the smooth cuticle on the elongated walls. In some taxa outer periclinal walls have small irregular protrusions or wart-like elevations. For the first time a detailed description of the surface epidermal leaf of *Philodendron* was made. Absolute micro morphological diagnostic characters of subgenera and sections levels are absent. The number and distribution of the subsidiary cells from the stomata vary significantly for the Araceae. KEATING (2002) reports brachyparacytic stomata and its variations and the rare type for the Araceae – anomocytic (GREAR 1973). The species analysed here have brachyparacytic, brachypara-tetra, hexacytic and amphibrachy-paracytic types. The anomocytic type was found in *P. imbe* and *P. erubescens* 'Burgundy'. The stomatal structure in species of the subgenus *Meconostigma* were studied by DILCHER & DAGHLIAN (1977) and GRAU (1983). DILCHER & DAGHLIAN (1977) reported that *Philodendron* of the subgenus *Meconostigma* leaves are amphistomatic and hypostomatic. GRAU (1983) found that *P. bipinnatifidum* (subgenus *Meconostigma*) had hypostomatic leaves with the paracytic stomata. In the subgenus *Pteromischum* (*P. surinamense*) leaves are hypostomatic with paracytic stomata (GRAYUM 1996). According to CROAT (1997), in the subgenus

Table 4. Comparison of selected anatomical features of some *Philodendron* taxa

Taxa	Characters												
	leaf thickness (μm) lamina	epicuticular layer thickness (μm)		ETI	height/width ratio of epidermal cells		hypodermis layer		palisade mesophyll layer	spongy mesophyll layer	raphide type	druse	styloid
		Ad	Ab		Ad	Ab	Ad	Ab					
<i>Philodendron bipinnatifidum</i>	165.3	5.3	3.8	0.97	0.96	0.77	Ih2-4	Ih1	1-2	6-8	B	+	+
<i>P. surinamense</i>	229.1	2.7	2.2	1.16	1.03	0.79	-	-	2-3	5-6	Sb	+	+
<i>P. crassinervium</i>	234.0	2.7	3.4	1.09	1.06	0.96	-	-	2	7	Sb	+	+
<i>P. melanochrysum</i>	256.1	3.8	3.1	1.13	1.06	0.85	-	-	1-2	4-5	B	+	+
<i>P. ornatum</i>	216.2	3.5	2.9	1.33	1.09	0.94	-	-	2-3	5-6	B	+	+
<i>P. hederaceum</i> var. <i>hederaceum</i>	277.8	4.3	3.0	1.21	1.36	1.05	-	-	1-2	4-5	W	+	+
<i>P. hederaceum</i> var. <i>oxycardium</i>	242.3	2.5	2.1	1.35	0.97	0.86	-	Ih 1	2-3	5-6	B	+	+
<i>P. bipennifolium</i>	272.0	3.1	2.6	1.56	1.46	0.85	-	Ih1	2-3	6-8	B, W	+	+
<i>P. domesticum</i>	259.2	3.3	4.3	0.90	0.99	0.93	-	Ih 1	2-3	8	B, Sb	+	+
<i>P. cordatum</i>	208.0	5.3	4.4	1.34	1.08	0.75	-	-	2-3	6-7	B	+	+
<i>P. erubescens</i>	264.7	4.8	3.9	1.11	0.94	0.83	Ih1	Ih1	1-2	5-6	B	+	+
<i>P. erubescens</i> 'Burgundy'	306.0	4.8	3.8	0.96	0.94	0.88	Ih1-2	Ih1	1-2	8-10	B, Sb	+	+
<i>P. imbe</i>	426.9	3.6	3.7	0.83	0.85	0.75	1-2	Ih1	2-3	10	B, Sb	+	+
<i>P. martianum</i>	463.7	9.3	5.8	0.79	1.16	0.87	1-2	1-2	2-3	6	B	+	+
<i>P. microstictum</i>	444.0	5.3	5.7	1.21	1.32	1.12	-	-	2-3	7-8	B, Sb, W	+	+
<i>P. pedatum</i>	197.8	3.0	2.9	1.41	1.33	1.00	-	Ih1	2-3	6	B	+	+
<i>P. squamiferum</i>	244.3	2.9	2.9	1.07	1.15	0.90	-	-	2-3	5-6	B	+	+
<i>P. angustisectum</i>	187.8	2.8	2.2	0.89	1.13	1.09	-	-	2-3	5-6	B	+	+
<i>P. lacerum</i>	218.6	2.5	2.2	1.52	1.12	0.88	-	-	1-2	5-6	B	+	+
<i>P. pinnatifidum</i>	176.9	3.5	3.6	1.38	0.95	0.65	-	Ih1	2-3	6-7	B	+	+
<i>P. × corsinianum</i>	182.4	3.5	2.5	1.56	0.87	0.68	Ih1-2	-	1-2	6	B	+	+
<i>P. 'Imperial Green'</i>	302.2	4.1	3.9	0.97	0.84	0.88	Ih1-2	Ih1	2-3	8-10	B	+	+

Ad – adaxial epidermis, Ab – abaxial epidermis, ETI – epidermal thickness index, Ih1 – one, interrupted hypodermis layer, “-” – absence of hypodermis layer, + – presence of druses and styloids, B – biforine, Sb – thin-walled, spindle raphide cells, W – wide cells.

Philodendron stomata are abaxial, randomly oriented, brachyparacytic to brachyparahexacytic. Our studies show that the species of three subgenera of *Philodendron* have amphistomatic leaves with a strongly reduced density of stomata on the adaxial leaf surface. This conclusion is true and documented with SEM photographs. In T.S. the stomata were positioned at the same level of epidermal cells in all taxa. Significant differences are observed in the density of stomata. In the subgenus *Meconostigma* the mean density of stomata was 21 (per mm^2), and in *Pteromisium* it was about 10. A much greater variation in this characteristic was recorded in the species from the subgenus *Philodendron* ranging from 4 to 21.5. KEATING (2002) reported several useful leaf anatomical characters for diagnostic use in 380 species and 105 genera of Araceae. The same author classifies the epidermal cell walls in the paradermal view as straight, undulate or extremely sinuous. In the *Philodendron* specimens analysed here straight and straight-slightly undulate cell walls were observed. KEATING (2002) stated that in some aroid genera the outline of the periclinal wall of the epidermal cells, as well as their height/width proportion, have diagnostic value for taxonomy. In most *Philodendron* taxa studied here the outer periclinal cell walls in both surfaces were flat, but in *P. surinamense* (subgenus *Pteromisium*), *P.*

melanochrysum and *P. hederaceum* var. *oxycardium* (subgenus *Philodendron*) the outer periclinal walls were convex (papillate). Measurements of the thickness of the epidermis appeared to be useful for distinguishing *Philodendron* species. The general organisation of mesophyll tissue in vegetative organs has not been investigated in the subgenus *Pteromisium* (GRAYUM 1996) and *Meconostigma* (MAYO 1991). The overall structure of the leaves is described in the subgenus *Philodendron* by CROAT (1997). The mesophyll of Araceae is predominantly bifacial with a thicker spongy layer below the palisade. The spongy mesophyll in *Philodendron* has a distinctive structure in leaves with compacted cells and with air spaces (ENGLER 1920, SOLEREDER & MAYER 1928, BUNTING 1968). Air spaces in spongy mesophyll were irregular in most species, but large cavities are observed in the midrib and in petioles. The palisade parenchyma cells were generally short. Our conclusions are identical. Measurements of leaf blade thickness appeared to be useful for distinguishing *Philodendron* species. In the *Philodendron* species studied the presence or absence of hypodermis could be a diagnostic character. Raphide and druse crystals are typical of the family Araceae. KEATING (2003, 2004 a) for all the family described eight raphide types and in *Philodendron* five. In our study we found three types of raphides. One, two or

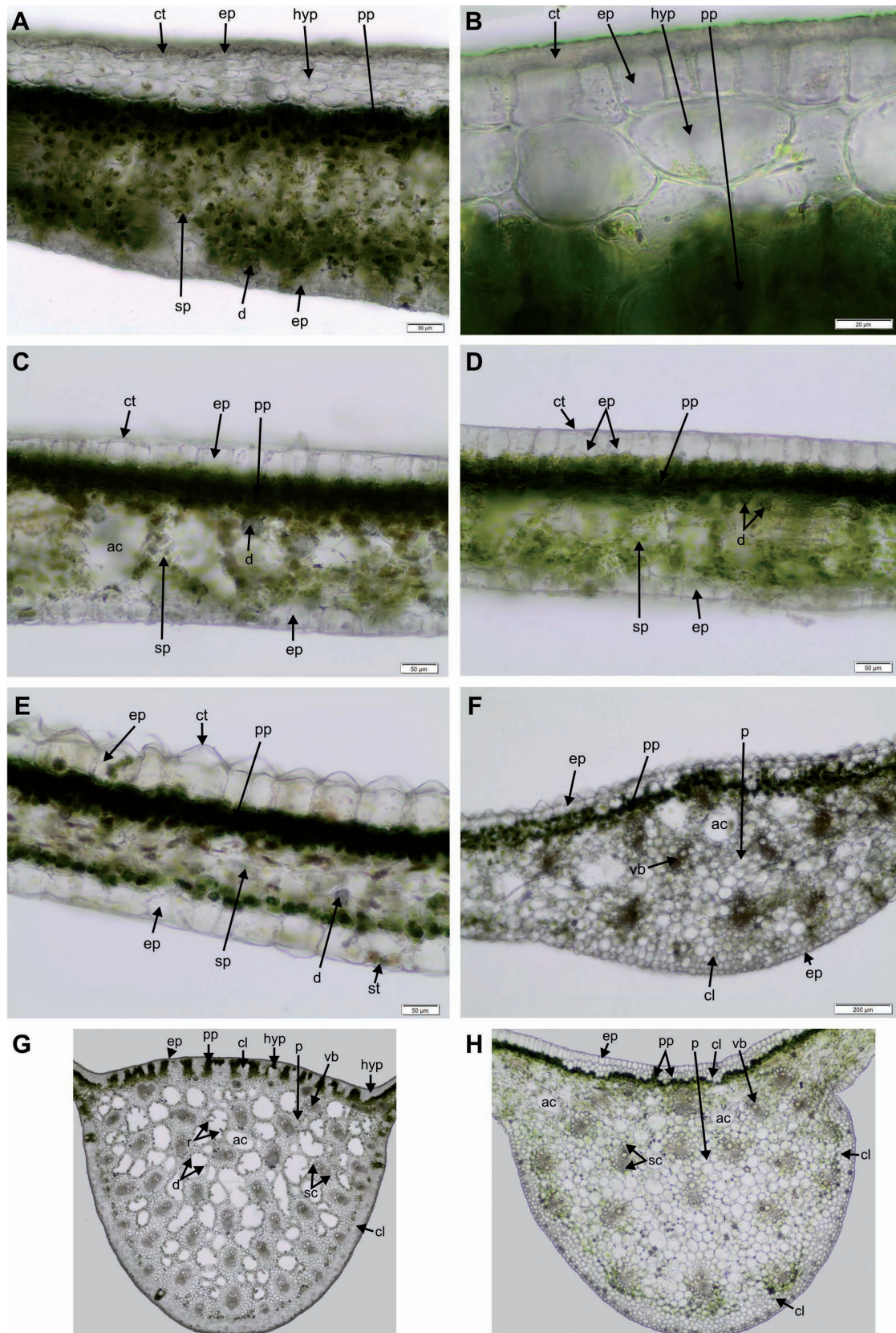


Fig. 6. Transverse section (T.S.) of lamina (A–E) and midrib (F–H) in some *Philodendron* taxa: A – *P. bipinatifidum*. The hypodermis has elongated cells, B – *P. martianum*. Detail of the epidermis with a thick cuticle, C – *P. cordatum*. Spongy mesophyll layer with air cavities, D – *P. angustisectum*, E – *P. melanochrysum*. Papillose adaxial epidermis, F – *P. surinamense*. Papillose adaxial epidermis on the midrib, G – *P. bipinatifidum*, H – *P. lacinatedum*. Vascular bundles with fiber phloem and xylem caps; ct – cuticle, ep – epidermis, hyp – hypodermis, pp – palisade mesophyll, sp – spongy mesophyll, d – druse, ac – air cavities, st – stoma, p – parenchyma, vb – vascular bundle, cl – colenchyma, sc – sclerenchyma, r – raphides

three types of raphides can be found simultaneously on a single plant. The results of the occurrence, type and location of calcium oxalate crystals will be published separately. In *Philodendron* the outline of the petiole and the midrib on the adaxial surface, epidermis and lamina structure, mesophyll, sclerenchymatous cells, collenchyma and raphide crystals are of potential use as character states in phylogenetic analysis and may be potentially informative characters of systematic importance. The presence of raphides and leaves bifacial with petiole and lamina are proposed as plesiomorphs of the Araceae (MAYO et al. 1997). The results slightly support the classification of the genus *Philodendron* into three subgenera. The species from different subgenera and sections have some very similar characters. The present research suggests stem anatomy to be very useful in delimitation of the infrageneric taxa of the genus (TENORIO et al. 2012). In petioles and laminae many characters are present in all of them and may be typical of the genus. More morphological/anatomical and molecular data are needed to confirm the sectional affiliation of certain species.

ACKNOWLEDGEMENTS

We are grateful to Ilona Wysakowska for technical assistance and to Wojciech Klimko for assistance with computer data recording.

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