Roczniki Akademii Rolniczej w Poznaniu CCCLXXXVII

Botanika – Steciana

12, 2008, 117-127

www.au.poznan.pl/steciana

ISSN 1896-1908

SCANNING ELECTRON MICROSCOPIC STUDIES OF LEAF SURFACE IN TAXA OF GENUS *DRACAENA* L. (DRACAENACEAE)

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(Received: March 20, 2008. Accepted: April 29, 2008)

ABSTRACT. Foliar micromorphology of 38 taxa (species, varieties, and cultivars) of the genus *Dracaena* was investigated by scanning electron microscopy (SEM). The study has revealed several interesting foliar features that were not previously reported in this genus. Leaves are characterized by anomocytic stomata and have no trichomes. Leaves are amphistomatic in 21 species, except for *Dracaena ellenbeckiana*, *D. reflexa* and *D. reflexa* 'Song of Jamaica', which have hypostomatic leaves, and 14 other taxa with nearly hypostomatic leaves (a strongly reduced density of stomata on the adaxial surface). Differences are especially prominent in the position and distribution of stomata, and the type of cuticle and wax. Among the studied dracaenas, only stomata of *D. draco*, *D. cinnabari*, *D. schizantha*, *D. ombet* and *D. ellenbeckiana* are surrounded by a cuticular flange, which is characteristic of xerophytes, similarly as a thick cuticle with a wax layer and a high density of stomata on both sides (except for *D. ellenbeckiana*).

KEY WORDS: *Dracaena*, micromorphology, leaf, SEM

INTRODUCTION

The family Dracaenaceae was first described in 1866 by Salisbury (Bos 1998). Depending on the taxonomic classification, it contains either two genera, i.e. *Dracaena* L. and *Sansevieria* Thunb. (Dahlgren et al. 1985), or only one – *Dracaena* (Bos 1998). In the past one more genus was distinguished, i.e. *Pleomele* Salisb. (Brown 1914), which was included in the synonymy of *Dracaena* (Bos 1998). The first described species of this genus was *Dracaena draco* (L.) L., assigned by Linnaeus to the genus *Asparagus* L. due to the similarity of their flowers (Bos 1998, Walker 1999). The taxonomy of species belonging to this family is still not completely clarified. Depending on the author, the number of species it comprises is defined as 100 for the whole family (Bos 1998), 50 (Dahlgren et al. 1985) or 70 species for *Sansevieria* (Koller and Rost 1988), and between 50 and 150 species for *Dracaena* (Palmer and Pitman 1972, Bos 1984, Dahlgren et al. 1985, Marrero et al. 1998, Walker 1999).

The geographical range of the family Dracaenaceae is contained in the tropical zone with the exception of South America. In the subtropical climate only *D. draco* and *D. tamaranae* A. Marrero, R.S. Almeida & M. Gonzales-Martin are found in the Mediterranean area (Marrero et al. 1998), as well as *D. aletriformis* (Haw.) Bos in the subtropical zone in the Cape Province, South Africa (Bos 1998). The preferred habitats are rainforests (shrubby dracaenas) or semi-deserts (dragon tree). Some species are adapted to living in other habitats, such as the ecotone between a forest and the seashore, or beds of periodical rivers (Bos 1998).

Due to their ornamental leaves, *Dracaena* species are among the most important ornamental foliage plants in Europe, North America (Bos 1984), Asia and Africa. The most frequently grown species are *D. fragrans* (L.) Ker Gawler, *D. marginata* Lam. Hort., *D. deremensis* Engl., *D. reflexa* Lam. and *D. sanderiana* Sander.

The medicinal application has resulted in the interest in chemical compounds found in dracaenas. Such studies concern primarily species producing red resin, i.e. *D. cochinchinensis* (Lour.) S.C. Chen (Zheng et al. 2004), *D. cinnabari* Balf. (Himmelreich et al. 1995, Masaoud et al. 1995 a, b, c, Veselá et al. 2002), *D. draco* (Mimaki et al. 1999 , González et al. 2004, Hernández et al. 2004), *D. tamaranae* Marrero, Almeida & Gonzáles-Martin (González et al. 2004), but also many others, e.g. *D. concinna* Kunth (Mimaki et al. 1998) and *D. loureiri* Gagnepain (Masaoud et al. 1995 b). Dracaenas contain steroidal saponins (Dahlgren et al. 1985). *Dracaena aubryana* (E. Morren) and *D. marginata* were included in DNA studies and their data were used to revise the taxonomic classification of the order Asparagales (Bogler and Simpson 1996, Rudall et al. 2000).

The main objectives of this study were: (1) to analyse in detail the sculpture of the leaf epidermis of *Dracaena* taxa; and (2) to identify the characters that are of diagnostic value for the differentiation of species and their cultivars in the vegetative stage.

MATERIAL AND METHODS

The study is based on 38 taxa of *Dracaena* (25 species, five varieties and eight cultivars). Plant material was obtained from the Botanical Garden (BG) in Berlin, Royal Botanic Gardens (RBG) Kew, the Botanical Garden of the Adam Mickiewicz University (BG-AMU) in Poznań (Poland), the Museum of Berlin-Dahlem (B) in Berlin (Germany), and the herbarium (POZG) (Table 1). The leaves were fixed with AFE (acetic acid – formalin-ethanol). Voucher specimens are deposited at the Department of Botany, the Agricultural University of Poznań.

The adaxial and abaxial surfaces between the midvein and the leaf margin were observed under a Philips FEN 515 and Zeiss Evo 40 Scanning Electron Microscope.

Table 1. Voucher information of materials used for study

No	Taxon	Collection
1.	*Dracaena aletriformis* (Haw.) Bos	cul. BG (140-29-74-83), Germany
2.	*D. americana* Donn. Sm.	Martinez, 103/2005-20 (B), Mexico; Croat 213425 (KRAM), Panama
3.	*D. arborea* (Willd.) Link	cul. BG (054-68-74-83), Germany; RGB (1982-5108), Kew
4.	*D. aubryana* C.J. Morren	cul. BG (138-20-00-70; 020-99-74-83), Germany
5.	*D. aurea* Mann	Degener, Degener, 103/2005-19 (B), Hawaii
6.	*D. cambodiana* Piere ex Gagnep.	Haw, 103/2005-28 (B), Haiwan
7.	*D. camerooniana* Baker	cul. BG (107-06-79-83), Germany
8.	*D. cinnabari* Balf. f.	cul. BG (175-01-96-20), Germany; RGB (1979-4242), Kew
9.	*D. conferta* Ridl.	Kadiw, 103/2005-21 (B), North Borneo
10.	*D. deremensis* Engl.	cul. BG (054-67-74-83), Germany; BG-AMU, Poland
11.	*D. deremensis* 'Bausei'	cul. BG (140-21-74-83), Germany; BG-AMU, Poland
12.	*D. deremensis* 'Compacta'	cul. BG (140-23-74-83), Germany; BG-AMU, Poland
13.	*D. deremensis* 'Green Stripe '	cul. BG-AMU, Poland
14.	*D. deremensis* 'Warneckii'	cul. BG (136-03-74-83), Germany; BG-AMU, Poland
15.	*D. draco* (L.) L.	cul. BG (066-49-00-10), Germany; BG-AMU, Poland; Baranowski, 150 (POZG), Teneryfa
16.	*D. ellenbeckiana* Engl.	Bos, 103/2005-38 (B), Kenya; cul. BG-AMU, Poland; RGB (1982-5108), Kew
17.	*D. elliptica* Thunb. & Dalm	Humbert, 103/2005-22 (B), Madagascar
18.	*D. fernaldii* St. John	Degener, 103/2005-32 (B), Hawaii
19.	*D. forbesii* Degener	Hatheway, Morton & Yasuda, 103/2005-29 (B), Hawaii
20.	*D. fragrans* (L.) Ker Gawler	Wiland, Mboya, 167 (POZG), Tanzania, cul. BG-AMU, Poland
21.	*D. fragrans* 'Lindenii'	cul. BG-AMU, Poland
22.	*D. fragrans* 'Massangeana'	cul. BG-AMU, Poland
23.	*D. hawaiiensis* Deg. & Deg.	Degener, Degener, 103/2005-33 (B), Hawaii
24.	*D. mannii* Baker	Bos, 103/2005-17 (B), Tanzania
25.	*D. marginata* Lam.	cul. BG-AMU, Poland
26.	*D. multiflora* Werbg.	De Mesa, Viliamii, 103/2005-44 (B), Philippines
27.	*D. ombet* Kotschy & Peyr.	Fris et al., 10741 (RGB), Ethiopia
28.	*D. pendula* Peyr.	Chaon, 103/2005-40 (B), Malaya
29.	*D. reflexa* Lam.	Viguier, Humbert, 103/2005-16 (B), Madagascar; Wiland, Mboya 165 (POZG), Tanzania
30.	*D. reflexa* var. *angustifolia* Bak.	Humbert, 103/2005-23 (B), Madagascar
31.	*D. reflexa* var. *lanceolata* Pers.	Humbert, 103/2005-24 (B), Madagascar
32.	*D. reflexa* var. *linearifolia* Bak.	Humbert, 103/2005-25 (B), Madagascar
33.	*D. reflexa* 'Song of India'	cul. BG-AMU, Poland
34.	*D. reflexa* 'Song of Jamaica'	cul. BG-AMU, Poland
35.	*D. schizantha* Baker	cul. RBG (1979-4242), Kew
36.	*D. steudneri* Engl.	Wiland, Mboya, 63 (POZG), Tanzania; cul. RGB (1970-1666), Kew
37.	*D. surculosa* Lindl. var. *maculata*	cul. BG-AMU, Poland
38.	*D. surculosa* Lindl. var. *surculosa*	cul. BG (029-98-74-83), Germany; BG-AMU, Poland

The investigated microscopic qualitative features included the shape of epidermal cells, wall cuticular and wax patterns, the location and distribution of stomata, as well as the shape of cuticular thickenings of stomata.

RESULTS AND DISCUSSION

Despite intensive phytochemical research on dracaenas, no information is available on its foliar micromorphology (this information was orally confirmed in 2002 by J.J. Bos), although the epidermal morphology is well documented in the botanical literature for several other groups of angiosperms (Stace 1965, Barthlott and Ehler 1977, Jeffree 1986, Petroncini et al. 2003, Sonibare et al. 2005, Klimko and Truchan 2006, Aliero et al. 2006, etc.).

The characters of structures are grouped into three categories: (1) primary sculpture (shape of cells); (2) secondary sculpture, superimposed on primary sculpture (relief of outer cell walls, caused mainly by cuticular ornamentation); and (3) tertiary sculpture, of epicuticular secretions, mainly wax (Barthlott 1989, 1990).

So far, in Floras of China, Zimbabwe, and North America, keys to the identification of species and monographs, only morphological leaf characteristics were taken into account, e.g. size, shape and colour (Bos 1984, John 1985, Bos and Cullen 1986, Venter 1996, Yee 2000, Mbugua and Beentje 2001, Watson and Dallwitz 2006, etc.).

Among the studied taxa, 27 have completely green leaf blades (26 species and only one cultivar, *D. deremensis* 'Compacta'). Yellow or white stripe variegation is observed in seven cultivars of *D. deremensis*, *D. fragrans* and *D. reflexa*. In contrast, *D. marginata* has only red margins, while in *D. draco* leaf margins are yellow or red. Spotted variegation is also found in *Dracaena surculosa* Lindl. var. *maculata* and var. *surculosa*. *D. surculosa* is the only species in which varieties are recognized (Bos 1984).

Our observations showed that leaf surface in most taxa is smooth and shiny, except for *D. surculosa* (smooth and slightly rough), and *D. draco*, *D. cinnabari*, *D. ombet* Kotschy & Peyr. and *D. schizantha* (rough and dull). The leaf blade can be straight or slightly undulate (*D. fragrans*, *D. camerooniana* Baker).

The foliar micromorphology of *Dracaena* taxa is presented in Figs 1-8.

EPIDERMAL CELLS

In all taxa investigated, the leaf epidermis consists of a single cell layer and has no trichomes. Epidermal cells on the adaxial and abaxial leaf surface vary considerably in size and shape. They are regularly or irregularly elongated, with straight and either straight or slightly undulate walls.

The characteristics of the leaf epidermis in *Dracaena* sp. are of particular taxonomic as well as phylogenetic interest, because they differ conspicuously between species. The size and shape of epidermal cells may be considered as good diagnostic features for the identification of species on the basis of foliar anatomy (Klimko and Wiland, unpubl. data).

CUTICULAR AND WAX ORNAMENTATION

Details of the outer cuticle structure, such as thickness and ornamentation, vary in some species and also depending on the side of the leaf surfaces. The highest variability in the cuticle between the adaxial and abaxial surfaces was observed in six species: e.g. *D. arborea* (Willd.) Link (Figs. 1A, 2A), *D. aubryana* (Figs 1B, 2B), *D. deremensis* (Figs 1C, 2C), *D. fragrans* 'Lindenii' (Figs 1D, 2D), and *D. surculosa* (Fig. 3). However, differences in leaf sculpture were not detected in *D. draco* (Figs 1F, 2F, 5), *D. cinnabari* (Fig. 6), *D. schizantha* (Fig. 7), *D. ombet* (Fig. 8), *D. camerooniana*, *D. deremensis* 'Warneckii', *D. marginata* and *D. reflexa* var. *lanceolata*.

Details of the structure of the outer cuticle, particularly its sculpture, attest to variation between species. The cuticle can be either undulate on the abaxial and adaxial epidermis (Figs 1E, 2E) or only adaxially (Fig. 2D), due to long protuberances; either verrucose abaxially, with large (Figs 2A, 3B) or small verrucae (Figs 3D, 4C); or smooth (Figs 1F, 2F, 4B, 4F); or mixed, i.e. composed of several types of structures, more or less homogenous.

On both surfaces in *D. americana* Donn. Sm., *D. cinnabari*, *D. deremensis* 'Warneckii' and *D. cambodiana*, rounded cuticular outgrowths are quite regular, markedly elevated above the surface of the leaf blade, but in *D. aubryana* only on the abaxial surface (Fig. 2B).

The leaf epidermal characters, such as cuticular ornamentation, are constant in some species and variable in others, and thus of great significance in understanding the relationships between and within species. The leaf cuticle is one of the most characteristic features of epidermal phenotype (Martin and Juniper 1970).

Tertiary sculpture concerns wax, which shows remarkable variation in the studied dracaenas. Detailed SEM observations of both surfaces showed that the wax layer is usually granulate (in 21 taxa), e.g. in *D. arborea* (Figs 1A, 2A), *D. fragrans* 'Massangeana' (Figs 1E, 2E) and 'Lindenii' (Figs 1D, 2D); but it forms flakes in *D. draco* (Figs 1F, 2F, 5), *D. ellenbeckiana* Engl. (Fig. 4D), *D. cinnabari* (Fig. 6) and *D. schizantha* (Fig. 7), *D. ombet* (Fig. 8), while rodlets in *D. deremensis* (Fig. 2C), both flakes and granules in *D. aubryana* (Figs 1B, 2B), both rodlets and granules in *D. surculosa* var. *maculata* (Fig. 3A), or both crust and granules.

In detail, the micromorphology of these crystalloids shows an extraordinary diversity of high systematic significance.

STOMATAL APPARATUS

The types and features of stomata are often considered helpful in defining taxa. Stomata in all species of the genus *Dracaena* are always anomocytic (the ranunculaceous type), without any subsidiary cells. In the opinion of numerous authors, the stomatal complexes

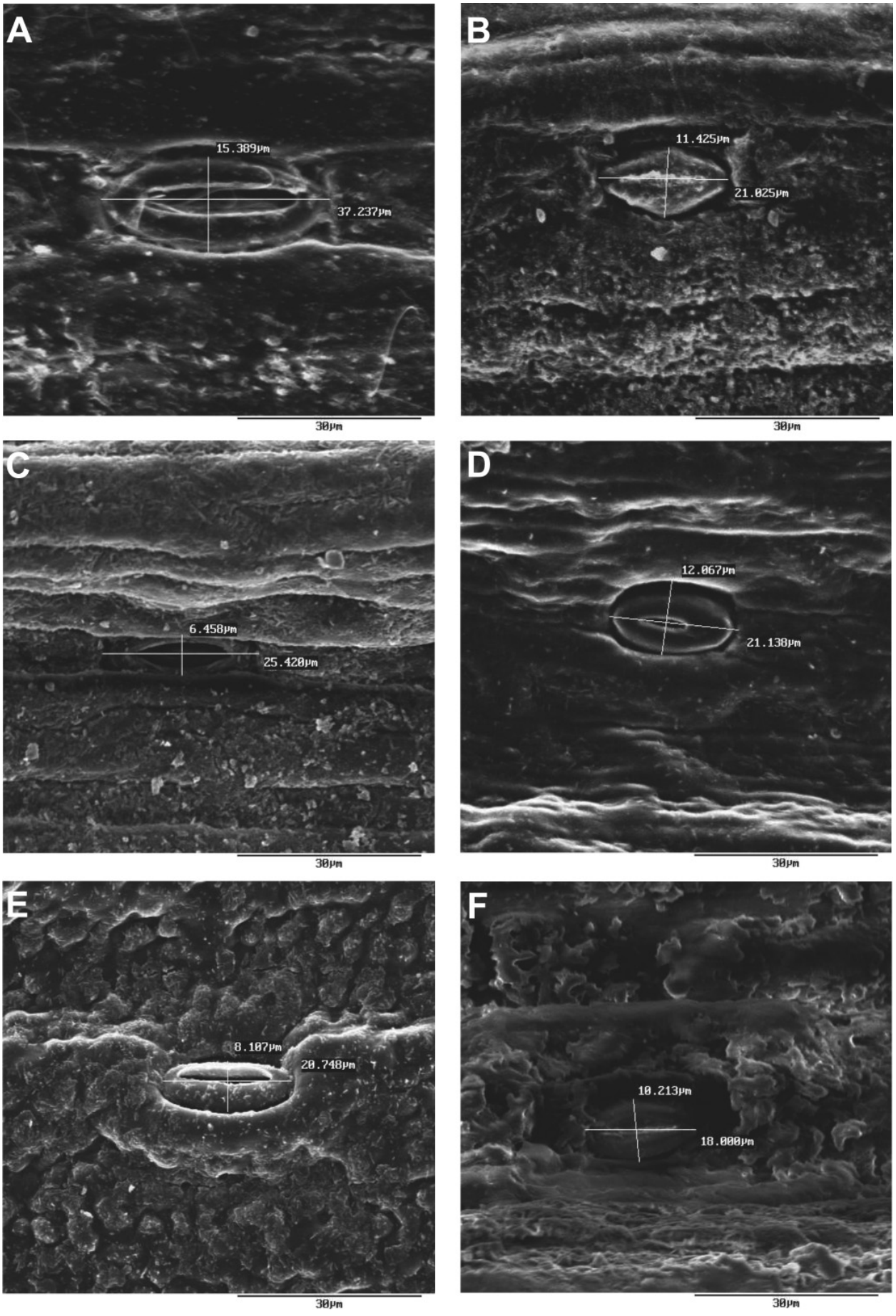

Fig. 1. SEM. Adaxial epidermis of *Dracaena* leaves with stomata, cuticle and wax: *D. arborea* (A), *D. aubryana* (B), *D. deremensis* (C), *D. fragrans* 'Lindenii' (D), *D. fragrans* 'Massangeana' (E), *D. draco* (F) (note young leaf)

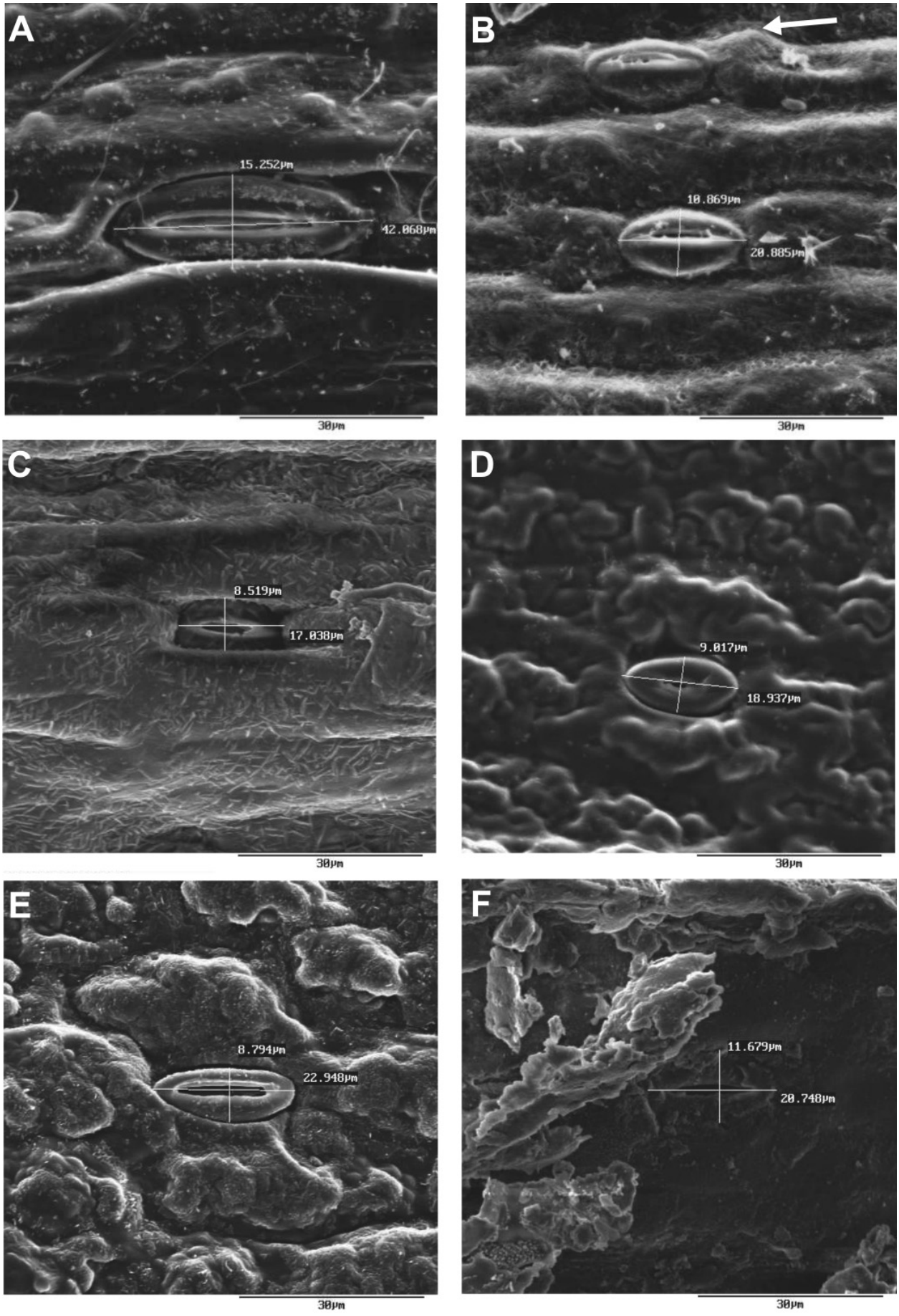

Fig. 2. SEM. Abaxial epidermis of *Dracaena* leaves with stomata, cuticle and wax: *D. arborea* (A), *D. aubryana* (B), note the concentration of cuticle, *D. deremensis* (C), *D. fragrans* 'Lindenii' (D), *D. fragrans* 'Massangeana' (E), *D. draco* (F) (note young leaf)

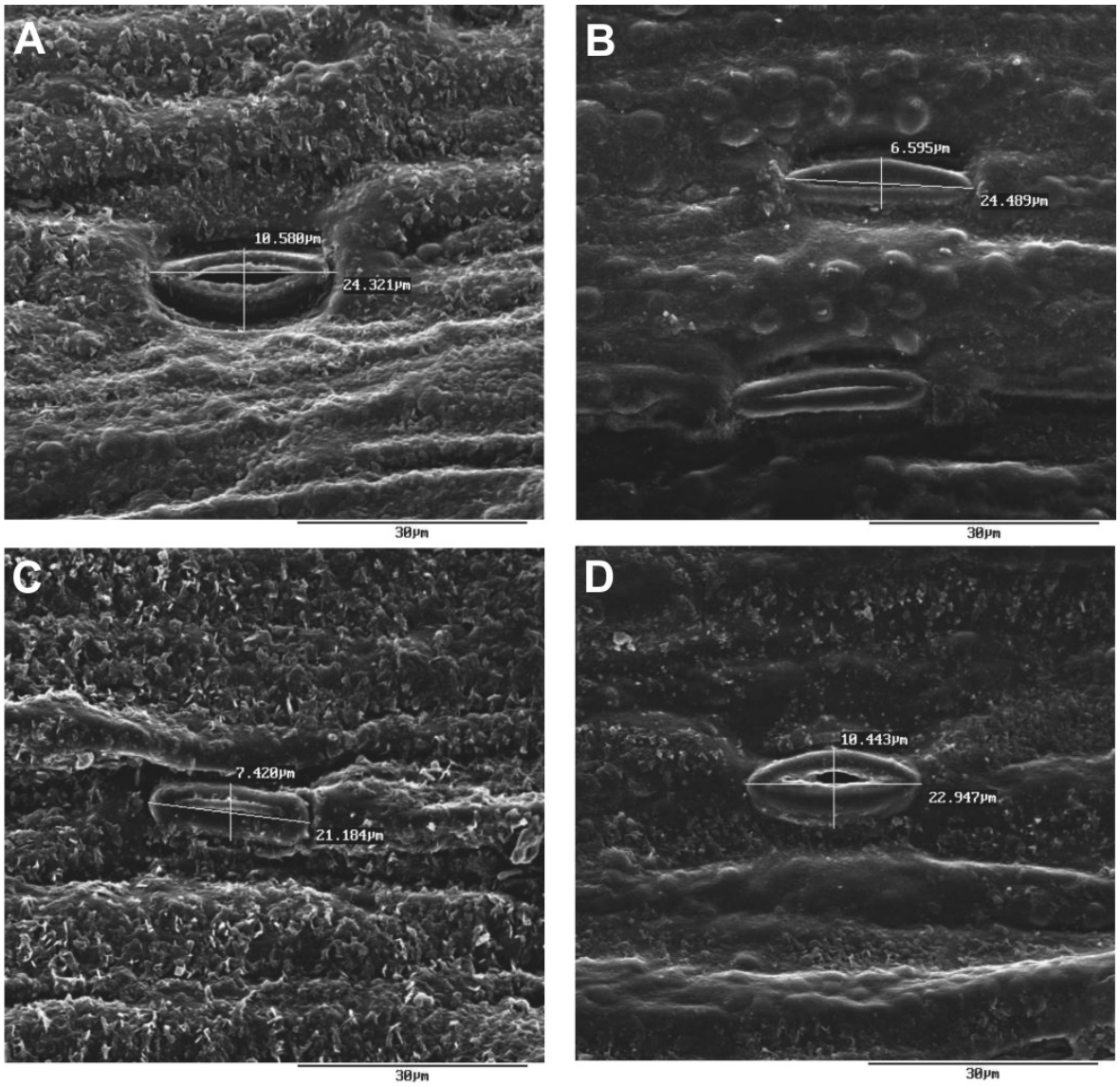

Fig. 3. SEM. Adaxial and abaxial epidermis of *Dracaena surculosa* leaves with stomata, cuticle and wax: var. *maculata* (A, B); var. *surculosa* (C, D). A, C the adaxial surface

without subsidiaries are practically confined to the Liliales and their more specialized derivatives. This type is independently derived from the primitive type, containing numerous parastomatal cells and is most advanced evolutionarily (Stebbins and Kush 1961, Esau 1967).

Most of the species have amphistomatic leaves with a nearly homogeneous distribution of stomata on either side. Hypostomatic leaves are found in *D. ellenbeckiana*, *D. reflexa* and *D. reflexa* 'Song of Jamaica', while 14 taxa have hypostomatic leaves with a strongly reduced density of stomata on the adaxial leaf surface. Their density on those leaves is as high as 1-3 stomata·mm^{-2}. Stomata are located in single rows, or in bands composed of two or several rows lying next to one another over the entire area (*D. cinnabari*, *D. ombet* and *D. schizantha*). The stomata of amphistomatic leaves are more abundant on the abaxial than adaxial surface. This is typical of most angiosperms (Fahn 1967).

Leaves of the studied taxa show remarkable variation in the distribution of stomata in the surface view under SEM. In 34 taxa, stomata are located ± at the level of the other epidermal cells on both surfaces, eg. in *D. arborea* (Figs 1A, 2A), *D. fragrans* 'Lindenii' (Figs 1D, 2D), *D. draco* (Figs 1F, 2F), *D. aurea* (Figs 3A, 4A), *D. marginata* (Figs 4B, 6F), and deeply sunken on both surfaces in *D. cinnabari* (Fig. 6), *D. schizantha* (Fig. 7), *D. ombet* (Fig. 8) and less deeply (Fig. 4D) in *D. ellenbeckiana* and *D. draco* (Fig. 5) (which was confirmed on the basis of transverse leaf sections).

Only stomata in *D. draco*, *D. cinnabari*, *D. ombet*, *D. schizantha* on both sides and in *D. ellenbeckiana* on the abaxial leaf surface are surrounded by a thick cuticular flange, square or rectangular in outline, which is characteristic of xerophytes (Figs 4D, 5, 6, 7, 8). Cuticular thickenings only along stomata were found on the adaxial side in *D. arborea* (Fig. 1A), *D. deremensis* (Fig. 1C), and on the abaxial side e.g. in *D. deremensis* 'Bausei' (Fig. 4A), *D. marginata* (Fig. 4B), *D. multiflora* (Fig. 4C, 6E), *D. mannii* Baker, *D. reflexa*, and *D. deremensis* 'Compacta'.

The presence of the cuticular flanges around stomata in only four species studied is of special importance. Most of the studied dracaenas have leaves that are rather thin and usually not fleshy. A number of xerophytic species have leaves that are rather rigid and coriaceous (leathery). Species of the dragon-tree group, e.g. *D. ta-*

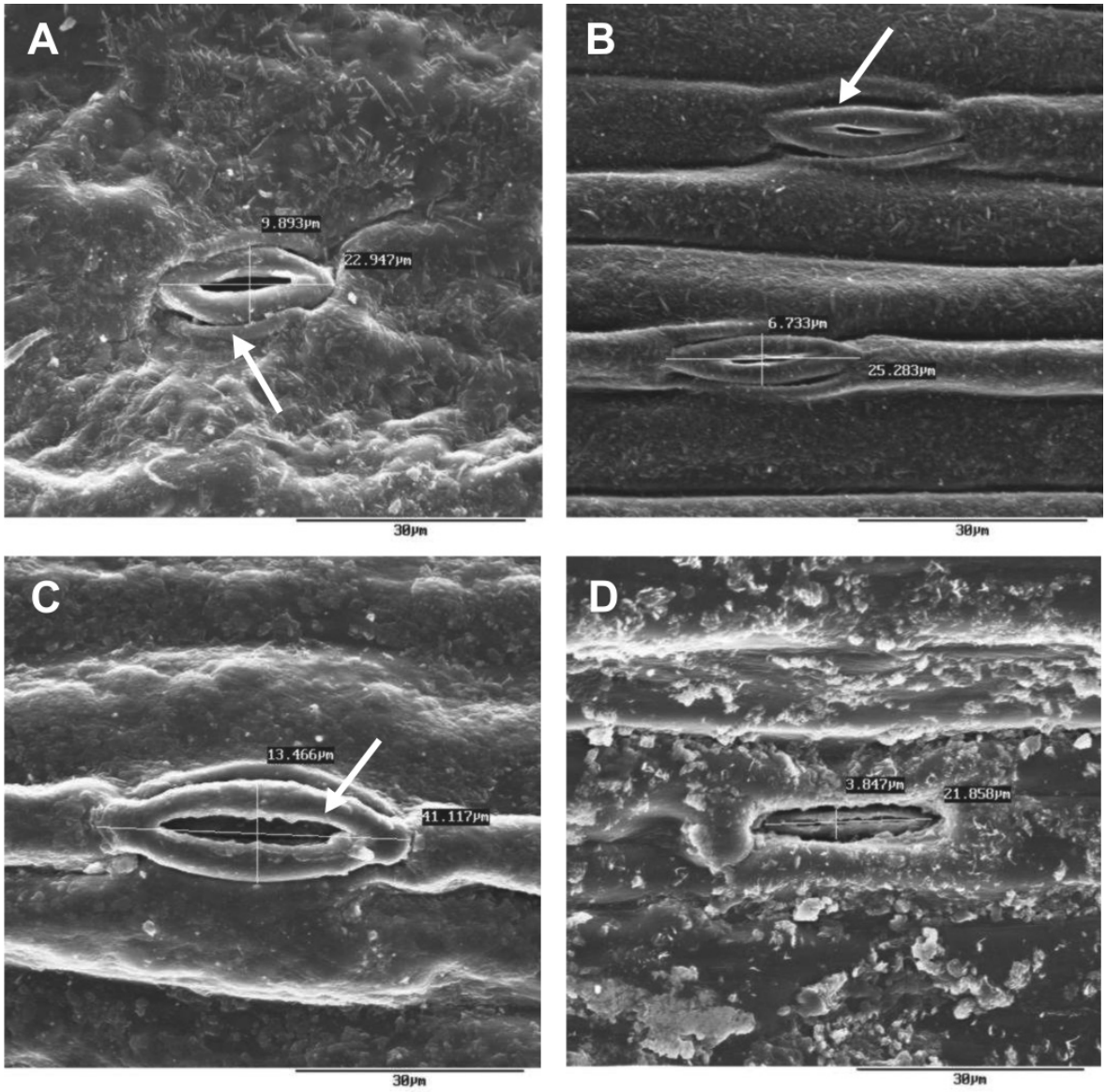

Fig. 4. SEM. Abaxial epidermis of *Dracaena* leaves with stomata, cuticle and wax: *D. deremensis* 'Bausei' (A), note cuticular thickening along stoma, *D. marginata* (B), note cuticular thickening along stoma, *D. multiflora* (C), note cuticular thickening along stoma, *D. ellenbeckiana* (D), note the concentration of cuticle

maranae, *D. ombet*, *D. schizantha* Baker, *D. serrulata* Baker, and *D. draco*, are regarded as very slightly or slightly succulent, while *D. cinnabari* as very succulent (Marrero et al. 1998).

Dracaena cinnabari and *D. schizantha* exhibit the largest number of xeromorphic features in foliar micromorphology, such as a thick layer of cuticle and wax; very strongly cutinised ledges of stomata, especially the outer ones, which cause leaf roughness; stomata very deeply sunken, surrounded by a thick cuticular ring; and high stomatal density (Figs 6, 7). Both species differ in the shape of the cuticular stomatal ring, the thickness of the epicuticular layer (thicker than in *D. schizantha*) and the pattern of cuticules.

Petroncini et al. (2003) reported that the leaves of *D. cinnabari* are most closely related to *D. draco*. Their study of the anatomy of the two species has revealed a considerable amounts of wax on the leaf lamina. The high concentration of wax found in *D. cinnabari* may possibly be connected with the unique climate (with mean annual precipitation of 400 mm) and environment of the Socotra Island where it grows (Petroncini et al. 2003). It results from conducted investigations that the variation in micromorphological leaf characteristics e.g. in *D. draco* is connected primarily with the age of plants. Young leaves have stomata located at the same level as the other epidermal cells without the cuticular ring, a thin layer of the cuticule and wax (Figs 1D, 2D). Significant interspecific differences are found in the distribution of stomata. In *D. cinnabari* stomata are arranged over the entire surface of leaf upper and underside, in *D. draco* in regular rows (Fig. 5) and in *D. ombet* irregular. In this study, we used plants growing under similar cultivation conditions, to minimize the modifying effect of environmental conditions on the variation in epidermal leaf traits.

Leaves of species of the dragon-tree group, i.e. *D. draco*, *D. cinnabarii*, *D. ombet* and *D. schizantha*, differ remarkably not only in their micromorphology (Figs 5-8), but also anatomy (Klimko and Wiland unpubl. data). Thus, species of the dragon-tree group require further detailed research, both concerning their micromorphology

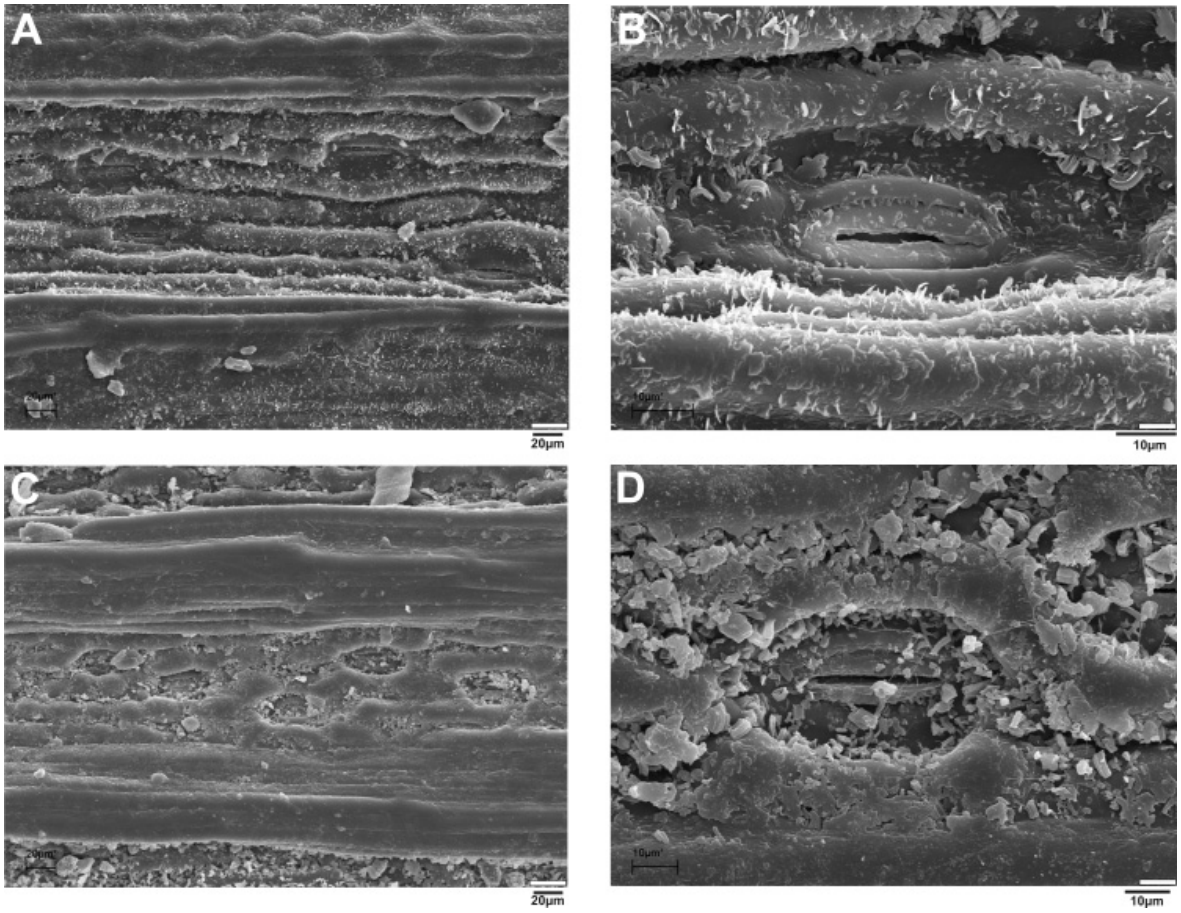

Fig. 5. SEM. Adaxial (A, B) and abaxial (C, D) epidermis of *Dracaena draco* leaves with stomata, cuticle and wax (note the concentration of cuticle)

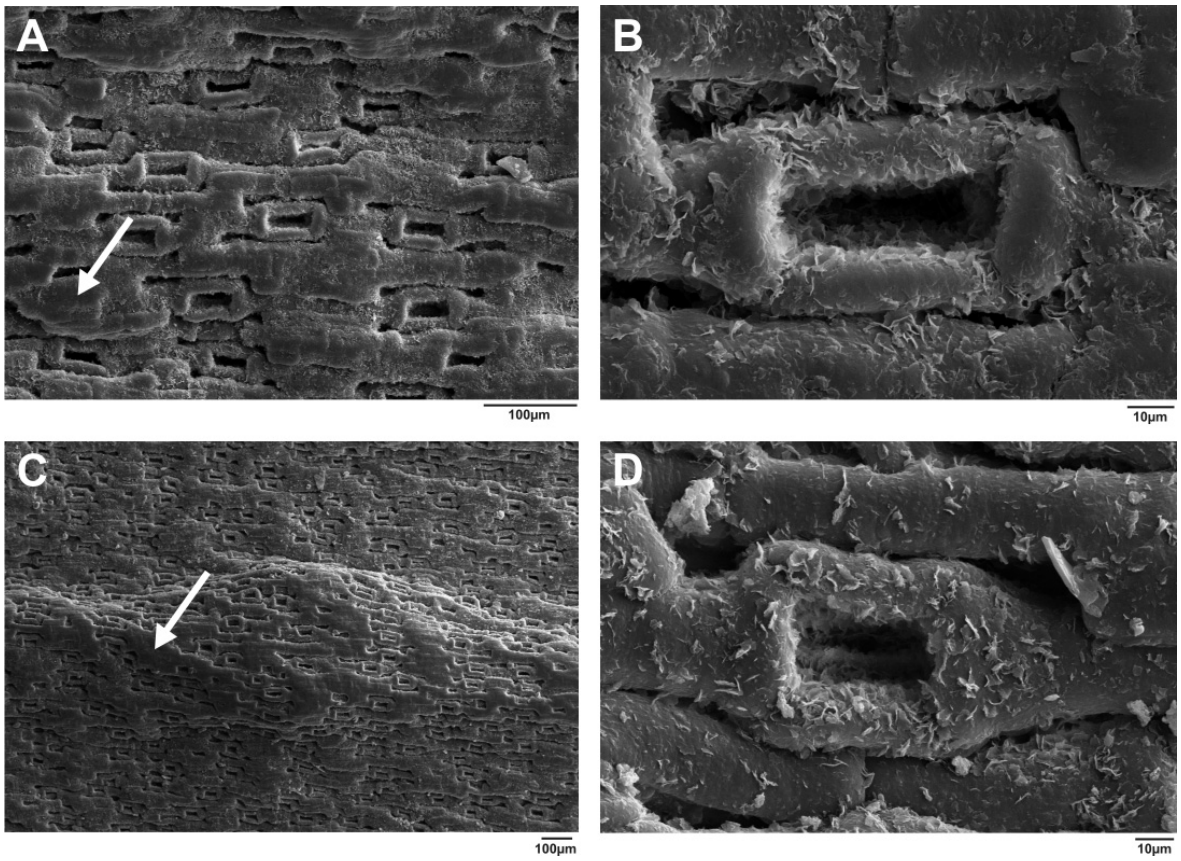

Fig. 6. SEM. Adaxial (A, B) and abaxial (C, D) epidermis of *Dracaena cinnabari* leaves with stomata, cuticle and wax (note the concentration of cuticle)

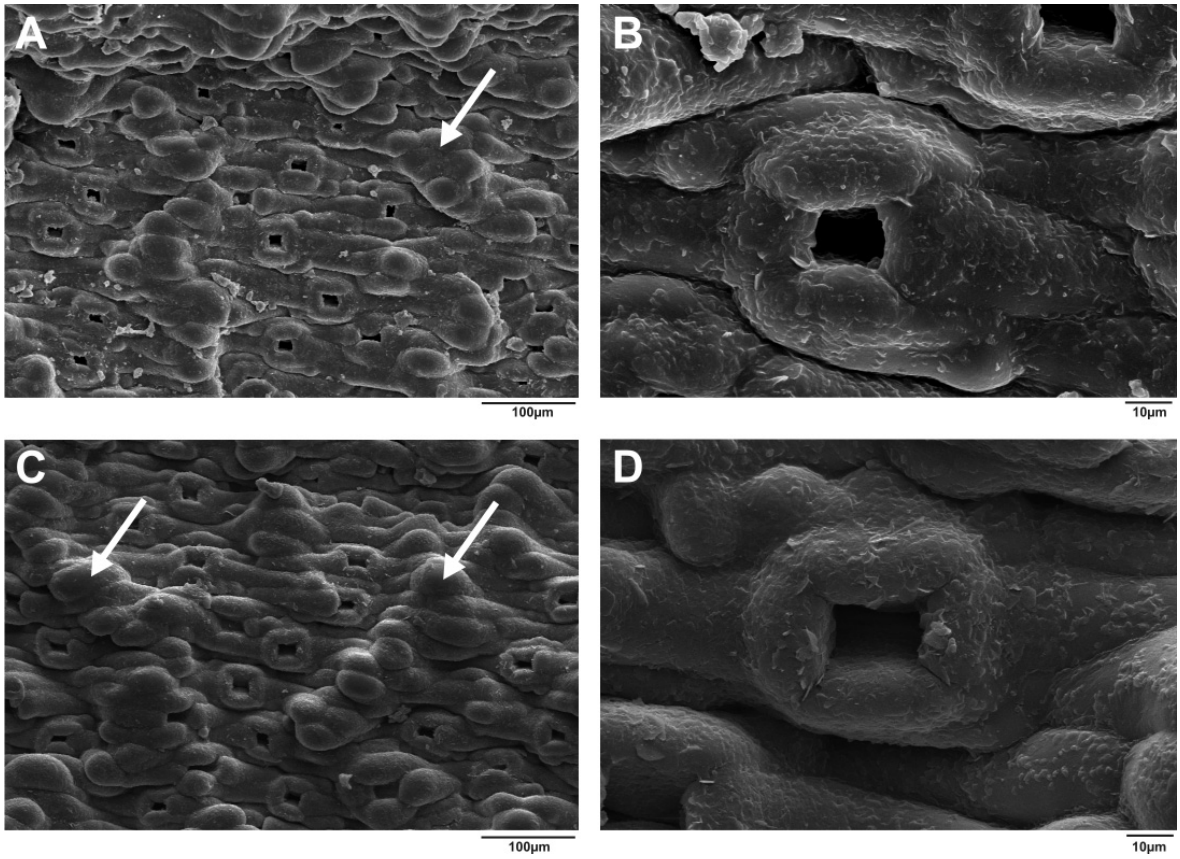

Fig. 7. SEM. Adaxial (A, B) and abaxial (C, D) epidermis of *Dracaena schizantha* leaves with stomata, cuticle and wax (note the concentration of cuticle)

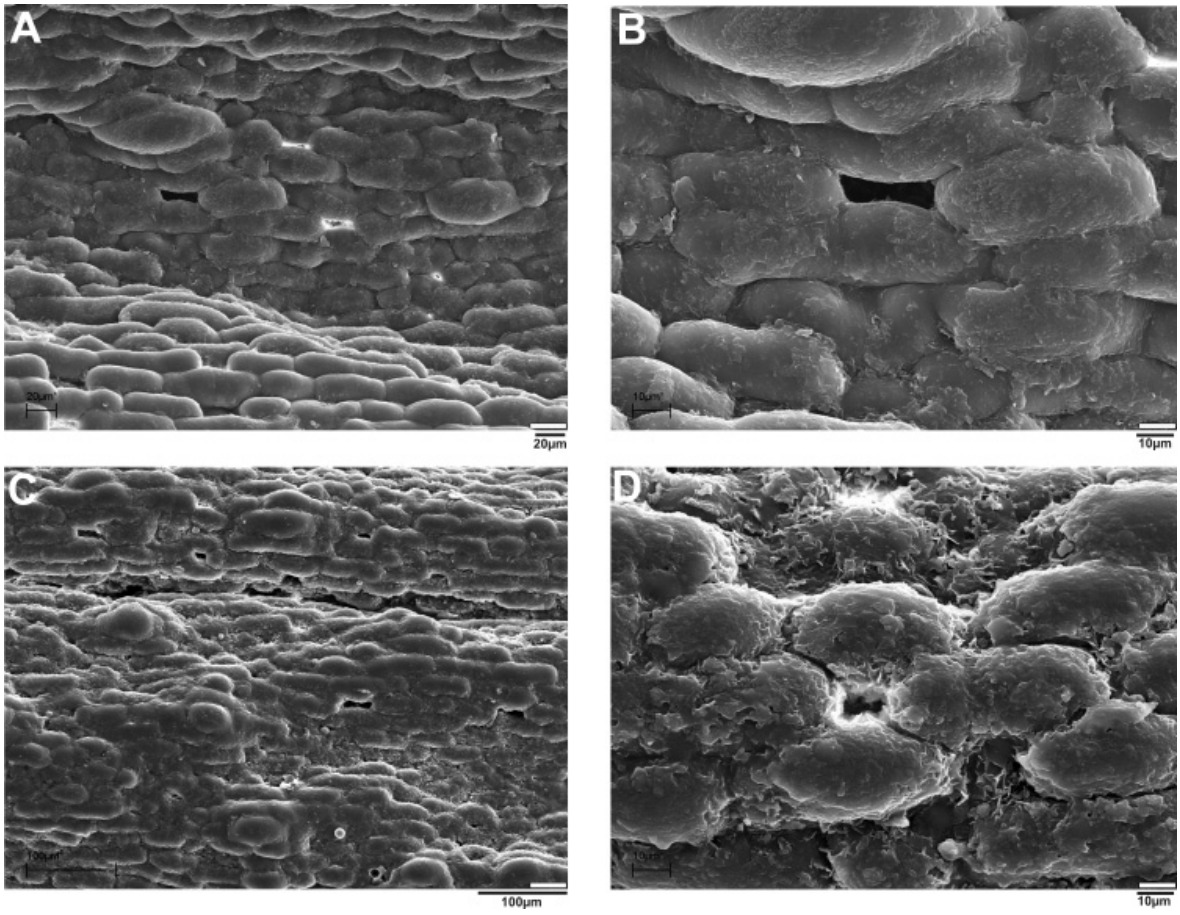

Fig. 8. SEM. Adaxial (A, B) and abaxial (C, D) epidermis of *Dracaena ombet* leaves with stomata, cuticle and wax (note the concentration of cuticle)

and anatomy, since Rudal et al. (2000) defined the Dracaenaceae as leaf succulents, while Jankalski (2003) regarded the genus *Dracaena* as not genuinely succulent.

This study of the foliar micromorphology of *Dracaena* has revealed for the first time a number of important micromorphological characters, some of which exhibit interesting interspecific variation, considered of significance for their identification. Micromorphological characters, especially those of the abaxial epidermis, show greater variation between taxa and thus are more useful in the taxonomy of this genus.

CONCLUSIONS

Epicuticular waxes and cuticle on both leaf surfaces exhibit great micromorphological diversity. In the genus *Dracaena* leaves are amphistomatic, hypostomatic and hypostomatic with a strongly reduced density of stomata on the adaxial surfaces. Stomata elliptic in outline are located in the level of the epidermis. Only stomata of *D. draco*, *D. cinnabari, D. ombet*, *D. schizantha* and *D. ellenbeckiana* are surrounded by a cuticular flange. The leaves are characterized by anomocytic stomata and have no trichomes.

Acknowledgements

The study was supported by a grant from the Agricultural University of Poznań and the Adam Mickiewicz University of Poznań (Poland). We are especially grateful to Dr. Beat Leuenberger from the Botanical Garden Berlin-Dahlem for his help and kindness.

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For citation: Klimko M., Wiland-Szymańska J. (2008): Scanning electron microscopic studies of leaf surface in taxa of genus *Dracaena* L. (Dracaenaceae). Rocz. AR Pozn. 387, Bot.-Stec. 12: 117-127.