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Morphology and Anatomy of the Peristome in *Dozya japonica* (Musci) and Reconsideration of Its Affinity to the Leucodontaceae

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Abstract. *The most distinctive features in sporophytes of* Dozya japonica *Lac. are the very thick capsule walls and the presence of parastomes around exostomes. Though* D. japonica *has no endostomes and its taxonomical position is not clear, the presence of parastomes and the very thick capsule walls indicate no close relationship to* Leucodon. Dozya japonica *should be included in a new subfamily, Dozyoideae (Leucodontaceae).*

The genus *Dozya* is monotypic, with a single species *D. japonica* Lac. Although the species is widely distributed in East Asia (Japan, Korea, China), it has been collected rarely, except in Japan. The species is restricted to the temperate zone, and is usually found growing on tree trunks and rocks in Japan.

The systematic position of *Dozya japonica* has been considered obscure (Noguchi 1947), and basic aspects of its morphology and biology are still poorly understood. The species has always been included in the Leucodontaceae but variously treated in its infrafamilial position (Table 1). Fleischer (1906), Brotherus (1926) and Noguchi (1947) placed *D. japonica* in the subfamily Antitrichioideae because of the smooth leaf cells, single costa, and absence of a properistome. This treatment has been employed by almost all students. Manuel (1974) recognized 4 subfamilies in Leucodontaceae on the basis of gametophytic characters, presence or absence of central strands in stems, paraphyllia and pseudoparaphyllia. He included the genus *Dozya* in the subfamily Leucodontoideae because of the presence of a central strand in the stem and the absence of paraphyllia and pseudoparaphyllia. He also proposed a new tribe Dozyeae to include this genus based on its smooth exostome and the absence of an endostome. His recognition of subfamilies, however, is based on a limited number of observations; for example, he stated that species of *Leucodon* lacked pseudoparaphyllia, but these structures have been found to be commonly present (Akiyama 1986). Buck (1980) paid special attention to peristome characters and transferred the subfamily Forsstroemioideae sensu Manuel (1974) to Leptodontaceae. Furthermore, the genera *Pterogonium, Antitrichia, Bestia,* and *Alsia* were transferred to the Pterogoniaceae. As a result, he recognized only two genera, *Leucodon* and *Dozya,* in the Leucodontaceae. He did not refer to peristomial features of *Dozya.* His placement of this genus as a member of Leucodontaceae was regarded as tentative. Thus, it is necessary to compare peristomes in *Dozya* and other genera of Leucodontaceae in order to clarify the taxonomic position of the genus.

Noguchi (1947) has pointed out the strange position of the peristome teeth in *Dozya japonica*; the mouth of the capsule is very wide and the teeth are situated at the innermost part of the mouth. He found that this curious position for the peristome teeth did not occur in other genera of Leucodontaceae, and suggested that *Dozya* was not closely related to *Antitrichia* (Antitrichioideae) nor to *Leucodon* (Leucodontoideae). Noguchi (1947), however, did not refer to the cell arrangement and structures around the peristome; they are treated in the present paper in detail.

Recently, familial affinities of some genera in the Musci were proposed on the basis of intensive observations of the morphology and anatomy of peristomes (Buck 1980; Shaw 1985; Shaw & Allen 1985). Such observations are needed in order to clarify the taxonomic status of the genus *Dozya.* In this paper I report observations on the peristome and adjacent structure of *Dozya* as compared with those of other genera of Leucodontaceae, especially those of *Leucodon.*

MATERIALS AND METHODS

The capsules used in this study were collected in the field or from dried herbarium specimens from Kyoto University (KYO), Hattori Botanical Laboratory (NICH) and Osaka Museum of Natural History (OSA). Young or nondehisced capsules were used to prepare transverse and longitudinal sections of peristomes for examination with the light microscope and the scanning electron microscope (SEM). Representative specimens for this study are: JAPAN: Kagoshima Pref. Osumi Peninsula, en route from Tashiro to Hetsuka, *Noguchi 8815* (NICH); Miyazaki Pref. Mt. Yanagi-take, *Noguchi 1353* (NICH); Ehime Pref. Mt. Shutsuganji, *Ochi 1064* (NICH); Tokushima Pref. Mt. Tsurugi, *Nakajima 6819* (OSA); Nara Pref. Mt. Odaigahara,

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TABLE 1. A summary of the systematic treatment of Leucodontaceae using generic names that are recognized today.

Fleischer (1906)	Brotherus (1926)	Manuel (1974)	Buck (1980)
Leucodonteae	Leucodontoideae	Leucodontoideae	*Leucodon*
Leucodon	*Leucodon*	*Leucodon*	*Dozya*
Antitrichieae	*Felipponea*	*Dozya*	
Leucodontopsis	Antitrichioideae	*Pterogonium*	
Dozya	*Leucodontopsis*	*Antitrichia*	
Pseudocryphaea	*Dozya*	*Bestia*	
Forsstroemia	*Antitrichia*	Felipponeoideae	
Antitrichia	*Pseudocryphaea*	*Felipponea*	
Pterogonieae	Pterogonioideae	Forsstroemioideae	
Pterogonium	*Pterogonium*	*Forsstroemia*	
		Leucodontopsis	
		Pseudocryphaea	
		Alsioideae	
		Alsia	
		Dendroalsia	

Akiyama 8208 (KYO), *Nakajima 8465* (OSA); Shizuoka Pref. Mt. Amagi, *Akiyama 7148* (KYO).

For examination with the SEM, fresh and dried capsules were soaked briefly in 70% alcohol, then in fresh water for one day, cut longitudinally into halves, and mounted on aluminum stubs with double-sided adhesive tapes, coated with gold at 1,200 V, 8–9 mA for 4 minutes, examined and photographed with a JEOL JSM T-20 SEM.

For anatomical studies, upper parts of capsules were cut longitudinally into quarters, and then cut with a razor under a binocular to get transverse and longitudinal sections. To make cutting easy, GAW (Glycerin-Alcohol-Water) was used (Deguchi 1983). Sections were mounted in water on glass slides and examined. An Appe's apparatus was used for drawing.

RESULTS

Properistomes are lacking in *Dozya japonica* (Fig. 1, 3, 15, 17–19). Peristomes consist of a single row of 16 teeth. On the dorsal surface, each tooth consists of two columns of cell wall plates which are marked by a conspicuous vertical ridge (usually zigzag) and horizontal lamellae (Fig. 3, 15). On the ventral surface, each tooth consists of one column of cell wall plates, marked only by horizontal lamellae. There is no other ornamentation on either surface (Fig. 4, 15).

Transverse sections just below the mouth show that two cell layers contribute to the peristomes and the proportion of cell numbers is 2:1 (Fig. 15). Thus the outer layer corresponds to the outer peristomial layer (OPL) and the inner one to the primary peristomial layer (PPL) (Edwards 1979). Peristomes of *Dozya japonica* are formed from wall material between cells in the PPL and OPL. It is clear from the cellular pattern observed by transverse sectioning and SEM that the sole row of teeth in *D. japonica* has the anatomical characteristics of an exostome of diplolepidous mosses.

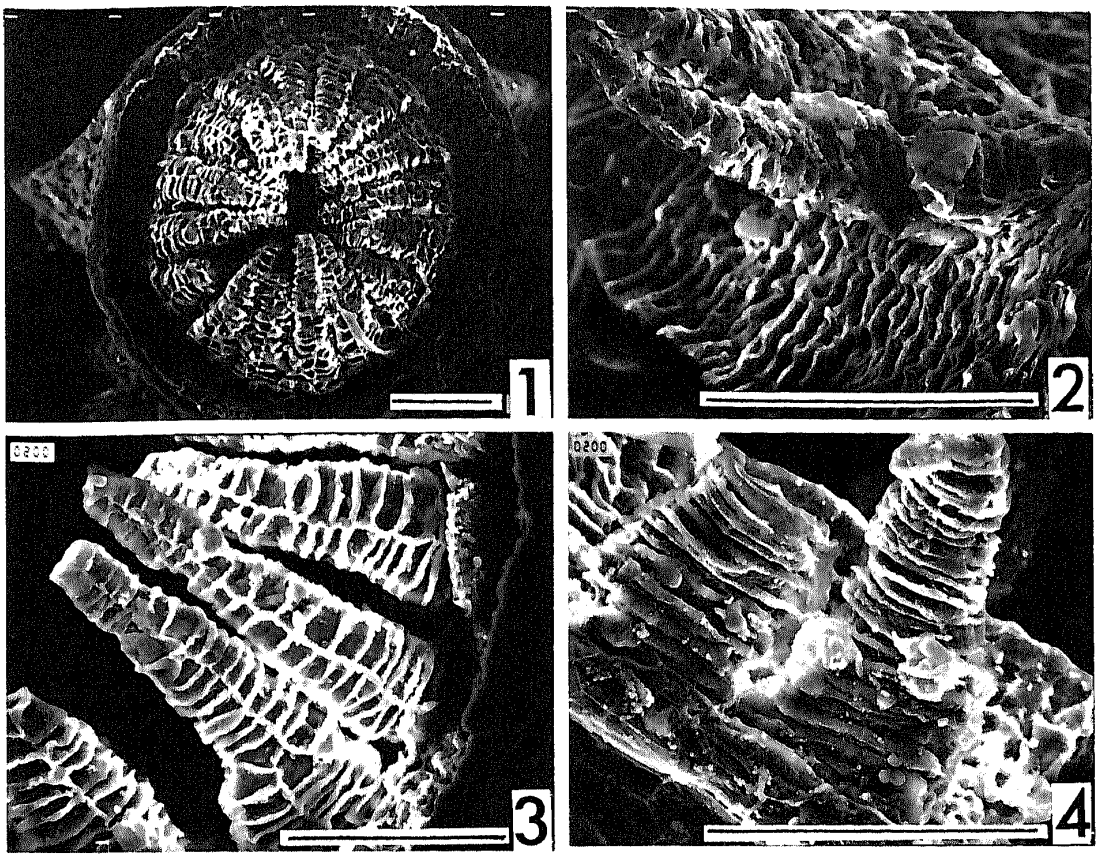
Endostomes are lacking (Fig. 4, 15, 17–19). The inner peristomial layer (IPL) is not observed when a capsule is mature (Fig. 15, 18). Thickenings in the inner cell walls of the PPL are poorly developed, and easily degenerate before shedding of the operculum. So it is clear that no endostome is present in *Dozya japonica*.

The thickness of cell depositions in exostomes is very different between the outer and inner columns (Fig. 19). The outer column is made from cell wall deposition of the OPL and exhibits a concave appearance. The inner one is made from the cell wall deposition of the PPL and the depositions occur evenly. This is also observable in the transverse sections of peristomes (Fig. 15).

Capsule walls of *Dozya japonica* are characteristically very thick. At the middle of the capsule, several outer layers are thick-walled with distinct cell lumens (Fig. 6). The 2–3 inner layers, which are bordered by an air space at the inner side, are very thin-walled. There are 4–5 layers of very thick-walled cells between these two layers.

At the peristomial level, there are 3–4 layers of exothecial cells and two layers of the peristomial ones (OPL and PPL). Three to four layers of thin-walled cells exist between the OPL and exothecium.

There are 3–4 columns of outer thick-walled cells (exothecial cells) and 2–3 columns of inner thin-walled cells (Fig. 15). The latter are of the peristomial layers which are connected with the OPL and PPL at the mouth level. Cells of the former are wider above. The number of columns does not increase but the exothecial cells become wider above, and then the capsule wall increases in width inwardly (Fig. 17–19). As a result, exostome teeth are situated at the innermost part of the mouth and a wide region lies between the outermost part of the mouth and the exostome teeth. The inner thin-walled cells, which represent the peristomial layer, are reduced



FIGURES 1–4. Peristomes of *Dozya japonica*. — 1. Upper part of capsule. — 2. Mouth of capsule and exostome teeth; note the wide ground outside the teeth. — 3. Dorsal surface of exostome teeth. — 4. Ventral surface of exostome teeth. 1. *Ochi 1064*. 2–4. *Noguchi 8815*. Scales = 100 μm.

in size. Their walls become thicker and comprise a group of very small cells at the bottom of the exostome teeth (Fig. 17–19).

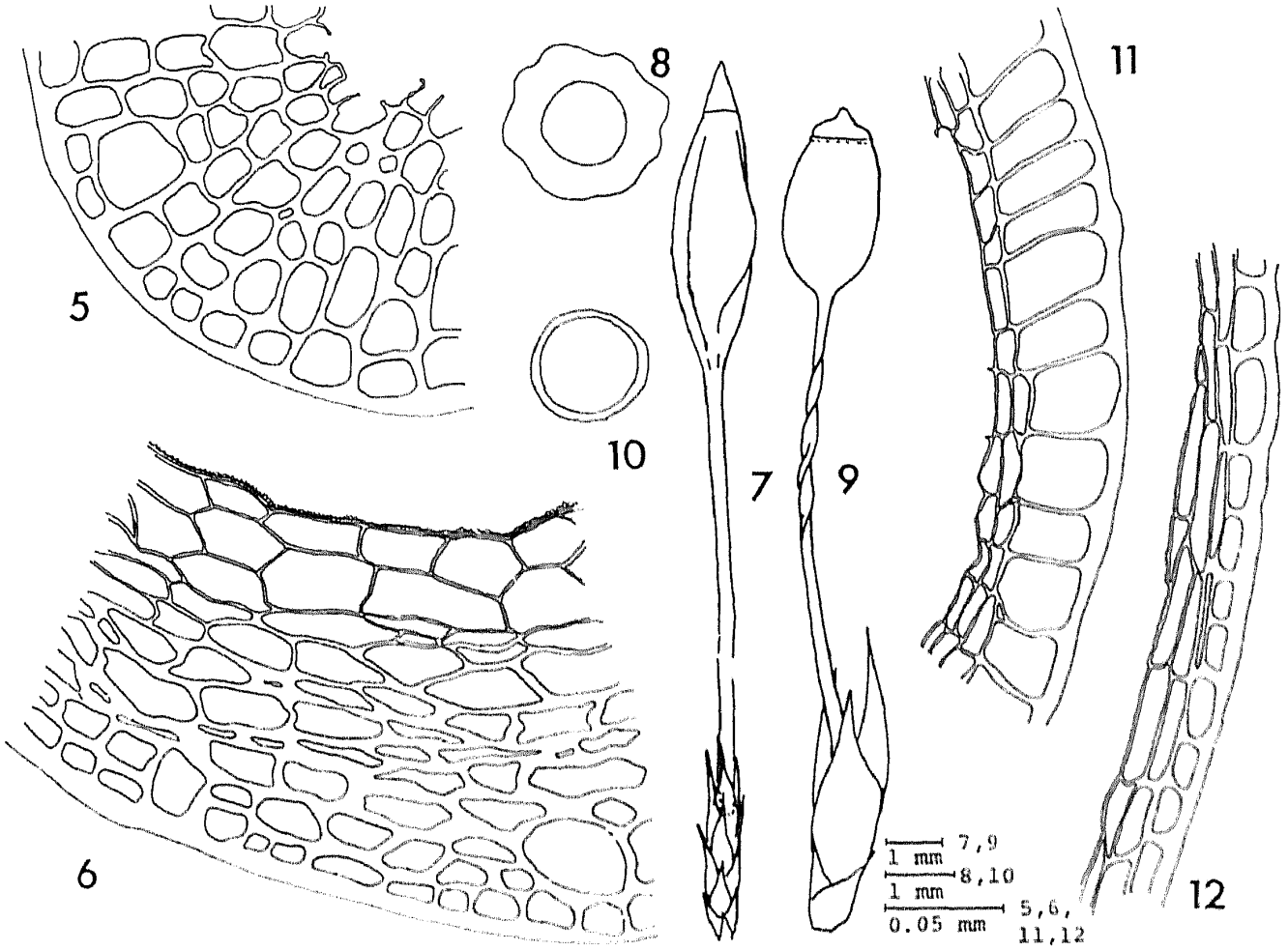
Cells of the operculum are weakly thickened in a young sporophyte. There are several layers of thin-walled cells between the exothecium of the operculum and the PPL (Fig. 17). As a sporophyte matures, most of these thin-walled cells become thick-walled and contribute to the inner part of the operculum (Fig. 18). On the other hand, the 1–2 layers of these thin-walled cells just outside of the exostome degenerate long before operculum dehiscence and this makes the exostome separate from the operculum. But the thin-walled cells below do not degenerate nor become thick-walled to make the inner part of the operculum. They persist as a group of thin-walled cells just outside of the exostome base (Fig. 19). As these cells do not show a regular arrangement, they are not considered to be peristomial layers. This also means that the OPL2 and OPL3, from which properistomes are made, are absent in *Dozya japonica*.

Dozya japonica does not have an annulus (Fig. 17, 18). The dehiscence line is recognized on the surface of the dark colored operculum by its pale color. Shedding of the operculum is caused by cell separation along the wider cells in the outer part, and by the separation between the thick-walled cells of the operculum and a group of thin-walled cells in the inner part. As a result, the group of thin-walled cells remains on the mouth just outside of the exostome base after operculum dehiscence.

DISCUSSION

There is a group of thin-walled cells on the mouth of the urn between the exostome and the operculum in *Dozya japonica*. They are clearly distinguishable from the transversely wide and thick-walled cells just below them. They remain as a distinct structure on the mouth of the urn even after the operculum is detached. Each cell of this structure is colorless and has no endopapillation nor cell wall deposition. Moreover, they do not show a regular arrangement as seen in the peristomial layers.

The term parastome was originally used for the structures situated just outside the exostome in the genus *Buxbaumia*. Edwards (1984) studied the parastome of *Buxbaumia* and Polytrichaceae and defined this structure. According to him, characteristics of parastomes are as follows: the units of construction are whole cells, rather than periclinal wall pairs between adjacent concentric layers of cells; they lack any kind of endopapillation; in their lower part, the cells are short and merge with the thick-walled isodiametric cells of the upper capsule wall; they are easily separable along the middle lamella



FIGURES 5–12. Sporophytes. — 5–8. *Dozya japonica* (*Akiyama 8208*). — 9–12. *Leucodon atrovirens* (*Akiyama 8387*). — 5, 11. Transverse sections of opercula. — 6, 12. Transverse sections of upper parts of urns. — 7, 9. Sporophytes. — 8, 10. Transverse sections of urn.

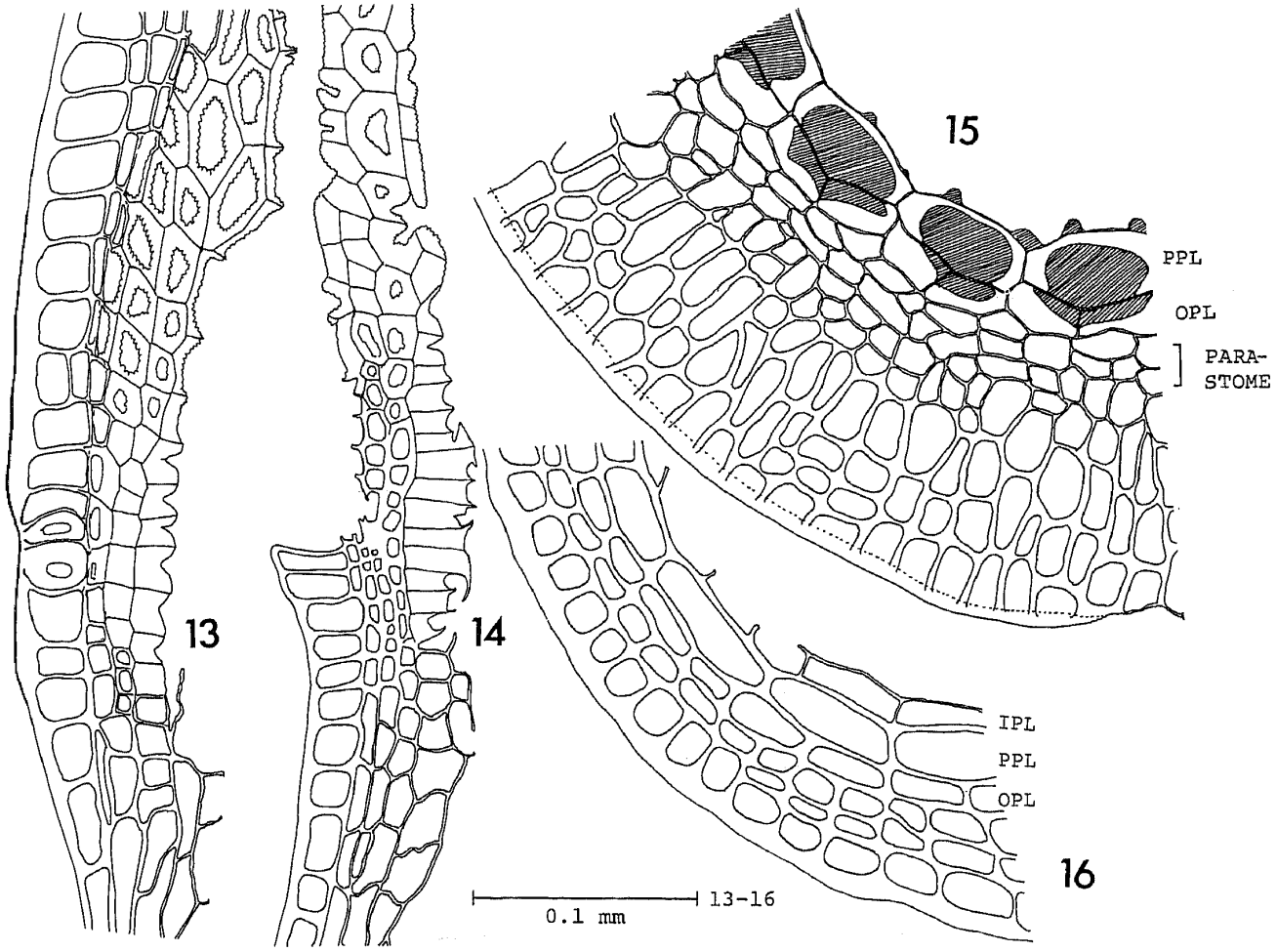
and assist in the shedding of the operculum. According to this definition, the group of thin-walled cells in *Dozya japonica* is a parastome and it agrees well with that of *Buxbaumia aphylla* (Edwards 1984) except for the smaller size of the cells which comprise the parastome.

The capsules of *Leucodon* have very different features from those of the genus *Dozya* (Fig. 9–14, 16). The distinctive features of *Leucodon* capsules are: (i) annuli are 2–3 layered; (ii) opercula are one layered below; (iii) properistomes are often developed. The thin-walled cells between the exothecium of opercula and the OPL are regularly arranged and differentiated into the properistomes (Fig. 16). Parastomes are not present at all and operculum shedding is caused by annuli (Fig. 13, 14). Capsule walls at the median level are not thick and are composed of about 3 cell layers (Fig. 12); the outer layer is thick-walled and comparable to the exothecium of the urn, and the inner two layers are very thin-walled. The latter proliferate their number of layers just below the mouth and are differentiated into peristomial layers (Fig. 14). The peristomial layers are situated just inside the one layered exothecium of the operculum, and are differentiated into IPL, PPL, OPL, OPL2, OPL3 and so on (Fig. 16). Put simply, OPL proliferates its layers to make OPL2 and OPL3, and these layers constitute the properistomes. Moreover there are no small thick-walled cells at the bottom of the peristome teeth as seen in *Dozya japonica*.

On the other hand, in *Dozya japonica* there is no properistome and the group of thin-walled cells, which are located between the exothecium of the operculum and OPL, are differentiated into the inner part of the operculum above and the parastome below.

Properistomes are derived from peristomial layers as described above. Parastomes have no relationship to peristomial layers. So we can consider that parastomes of *Dozya* and properistomes of *Leucodon* are different organs in their structure and origin. This suggests that there is no close interrelationship between *Dozya* and *Leucodon*. The differences in gametophytic characters, such as monopodial branching pattern, the absence of pseudoparaphyllia and the presence of a well-developed single costa in *Dozya*, reinforce this suggestion.

The genus *Dozya* has been treated as a member



FIGURES 13–16. —13, 16. *Leucodon atrovirens* (*Nakajima 30617*). — 14. *L. sapporensis* (*Une 5067*). — 15. *Dozya japonica* (*Akiyama 8208*). — 13, 14. Longitudinal sections of peristomes. — 15, 16. Transverse sections of capsules just below the mouths.

of the Leucodontaceae (Fleischer 1906; Brotherus 1926; Noguchi 1947; Manuel 1974, 1982; Zhang 1983; Vitt 1984). They emphasized the gametophytic features. There have been few studies on the morphology and anatomy of sporophytes. Noguchi (1947) observed the peristome structure by longitudinal sections. He noticed the curious position of the exostome teeth and pointed out that *Dozya* might not be closely related to *Antitrichia* or *Leucodon.*

Fleischer (1906), Brotherus (1926) and Noguchi (1947) treated the genus *Dozya* as a member of the subfamily Antitrichioideae because of the absence of properistomes, the presence of a single costa and smooth leaf cells. Though sporophytic characters of *Leucodontopsis* and *Pseudocryphaea* have been studied little, those of *Antitrichia* are well known; it has distinct endostome segments and smooth or papillose exostome teeth. *Pterogonium,* which belongs to the subfamily Pterogonioideae, has much different peristome characteristics than other members of the Leucodontaceae; exostome teeth are distinctly striated below, and they spread outward when dry.

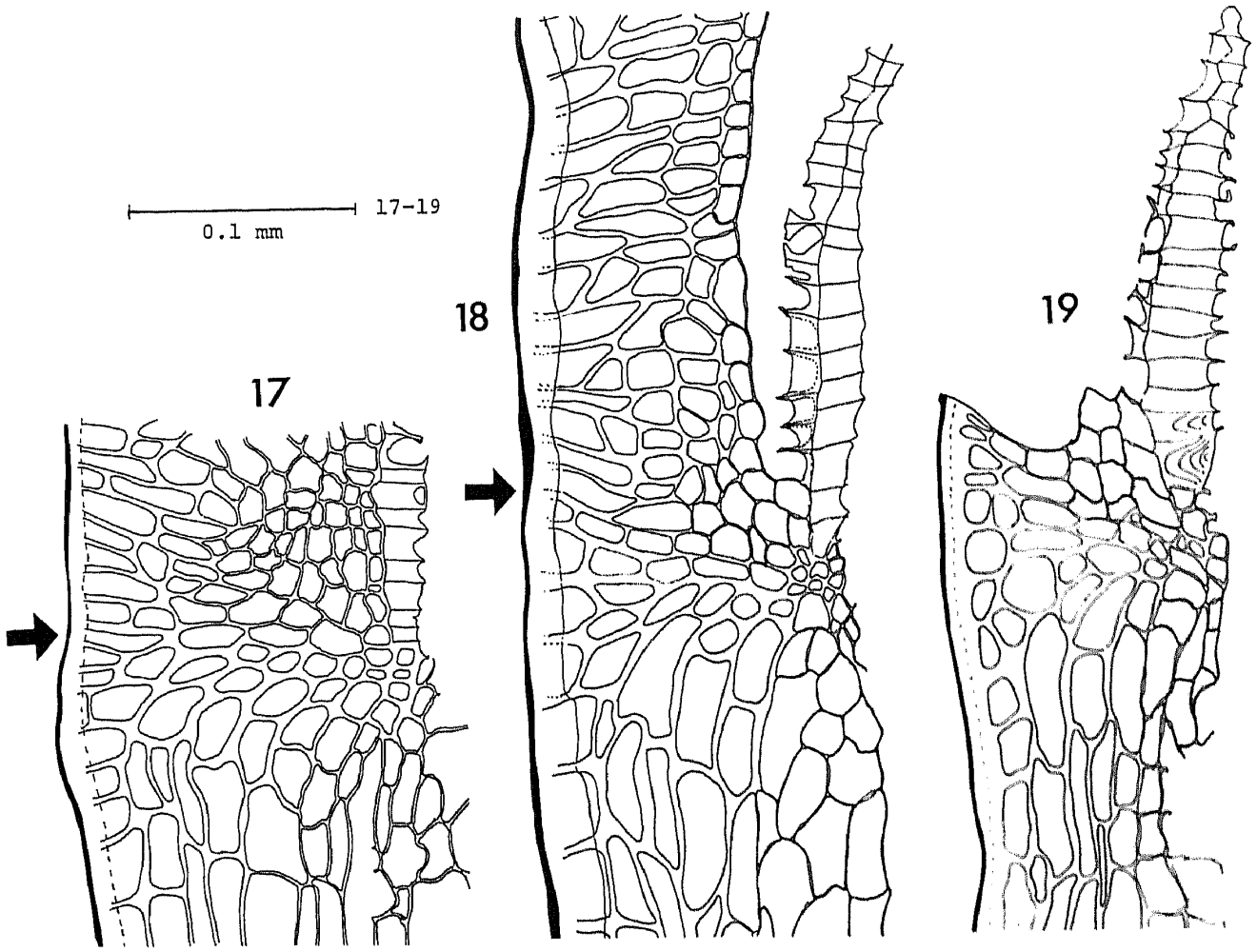
The peristomes of *Dozya* are also different from those of *Antitrichia, Pterogonium* and *Forsstroemia* in the surface ornamentation of exostome teeth, the absence of endostomes and the presence of parastomes. So the genus *Dozya* is not closely related to any subfamily of Leucodontaceae in the Fleischer-Brotherus system and should not be placed in any subfamilies of Antitrichioideae, Pterogonioideae, Forsstroemioideae and Leucodontoideae. The structures comparable to parastomes sporadically occur in several genera which are very remotely related; for example, in *Philonotis* and *Funaria* (Edwards 1984). Hence *Dozya* does not deserve a classificatory rank of family based on the presence of a parastome. Here I propose that the genus should be treated as representing a new subfamily Dozyoideae in Leucodontaceae.

TAXONOMICAL TREATMENT

Leucodontaceae subfamily **Dozyoideae** (Manuel) H. Akiyama, stat. nov.

Synonym: Leucodontaceae subfamily Leucodontoideae tribe Dozyeae Manuel, THE BRYOLOGIST 77: 536 (1974).

Laminal cells short or long rectangular, smooth. Alar cells differentiated, colored reddish brown. Costae single, to ⅘ of leaf length. Pseudoparaphyllia



FIGURES 17–19. Longitudinal sections of peristomes of *Dozya japonica*. Left one is in young stage and right one is just after deoperculation. Arrows indicate the positions where dehiscence occurs. — 17. *Noguchi 1353*. — 18. *Akiyama 7148*. — 19. *Akiyama 8208*.

and paraphyllia absent. Peristomes single. Exostome teeth lanceolate, smooth. Endostomes absent. Parastomes distinct. Properistomes absent.

Type genus: Dozya Lac.

This subfamily contains *Dozya*, a monotypic genus.

Dozya japonica Lac. *in* Miq. Ann. Mus. Bot. Lugdum. 1865.

Synonym: Dozya japonica var. *robusta* Sakurai, Bot. Mag. Tokyo 54: 8 (1940). (*Type:* Japan, Kiusiu, Prov. Higo, Yosio, *Sakurai 11839*, not seen.)

Branching mainly monopodial. Stoloniferous shoots black, densely foliated, indefinite, rather thick when creeping on substratum, long slender when pendent, apices pale green. Stems reddish brown below, pale green above, densely foliated, apices sometimes flagellate, to 8 cm, well branching when stems elongate; central strands present, sometimes colored reddish brown; many dormant buds present on stems. Flagellae present, often numerous, from stoloniferous shoots and stems, merging into stoloniferous shoots. Rhizoids distinct in stoloniferous shoots and flagellae, brown, thin-walled, smooth. Vegetative reproductive organs absent. Paraphyllia and pseudoparaphyllia absent. Axillary hairs 4–5 cells, yellowish brown; basal 2 cells short rectangular, smooth; upper 2–3 cells oblong, usually slightly mammillose, rarely smooth.

Stem leaves pale green, yellow to black when old, deeply plicate, appressed to stems, rarely strongly secund when dry, erect spreading when moist; long lanceolate, long attenuate at apices, 2.5–3.2 mm long, 0.6–0.9 mm wide at bases, margins entire or weakly crenulate at apices; costa single, extending to ¾ of the leaf length, smooth on back; upper laminal cells hexagonal or rhomboid to long rectangular, smooth, 27–43(–60) μm long, thick-walled; upper marginal cells short to long rectangular, smooth, 14–32 μm long, thick-walled; basal central cells long linear, strongly porose, smooth, 40–68 μm long, colored reddish brown. Alar regions extending to ca. ¼ of the leaf length, deeply colored reddish brown; cells quadrate, smooth, 8 × 8–15 μm.

Dioecious. Male plants slightly thinner than female plants. Perichaetial leaves increasing their sizes after fertilization and reaching to 4.5 mm long, lin-

FIGURE 20. Distribution map of *Dozya japonica*. Broken line indicates data taken from the literature cited.

ear lanceolate, acuminate, tightly involute, pale green but easily turned pale yellow; costae weakly developed, single; paraphyses sparse, filamentous, 4–11 cells long, smooth. Perigonial leaves ovate, acuminate, ca. 0.7 mm long, ecostate, yellow to brown; paraphyses numerous, 7–8 cells long, smooth; antheridia 14 in one perigonium on average. Calyptra cucullate, pale green to yellow, naked. Setae reddish brown, (3.5–)5–11 mm long, with distinct ridges, smooth, twisted from lower right to upper left. Capsules reddish brown, oblong, ca. 3.5 mm long and 1 mm wide, asymmetrical, with distinct ridges, narrowed at mouth; exothecial cells hexagonal, collenchymatous, verrucose; stomata present on apophysis. Columella present. Opercula rostrate, thick. Annuli absent.

Peristomes white, single. Properistomes absent. Exostome teeth 16, lanceolate, smooth, situated inwards; spread outward when moist, inward when dry; median line zig-zag or straight. Endostomes absent. Parastomes present just outside of exostome base.

Spores matured in late summer to autumn, papillose, tetrahedal; fertile spores green, 35–80 μm in diameter, sterile spores brown, ca. 30 μm or less in diameter.

Habitat: On tree trunks and rocks, in temperate zone.

Distribution: Japan (Kyushu, Shikoku, Honshu), Korea, China (Fig. 20).

Representative specimens examined: Kyushu: Kagoshima Pref., Isl. Yakushima, *Shin 6694* (NICH); Kumamoto Pref., Hitoyoshi, *Mayebara 1841* (NICH); Ohita Pref. Mt. Haidate, *Ohtsuka 7034* (NICH); Fukuoka Pref., Isl. Okinoshima, *Takeuti 18* (NICH). Shikoku: Tokushima Pref., Mt. Tsurugi, *Nakajima 6825* (OSA); Ehime Pref., Mt. Heigamori, *Oti 14216* (NICH). Honshu: Wakayama Pref., Mt. Koya, *Kurita s.n. 12 July 1932* (NICH); Saitama Pref., Mt. Mikuni, *Nagano 1587* (NICH); Miyagi Pref., Isl. Kinkazan, *Noguchi 66* (NICH).

Additional notes: i. Mammillae of axillary hairs are sometimes absent or indistinct.

ii. The degree of attenuation of apices of stem leaves are variable even on the same stem.

iii. Seta length is also variable even in the same colony.

iv. Sakurai (1940) described var. *robusta*. I could not find the type specimen of this variety in MAK where the original material should be deposited. According to Sakurai's original description, this variety is characterized by its robust size with stems 5–7 cm long, and leaves up to 5 mm long.

Variety *robusta* and var. *japonica* appear different; the former has long and thick stems and no pendent flagella-like shoots, while the latter has thin stems and long pendent flagella-like shoots. However, there are various intermediate forms between both varieties based on my observation. These differences seem to be caused by differences of habit; var. *robusta* almost always grows on rocks and var. *japonica* always occurs on tree trunks. Therefore, I regard these two as mere ecotypes of *Dozya japonica*.

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