Studies on *Leucodon* (Leucodontaceae, Musci) and related genera in East Asia III*. Notes on the systematic position of *Pterogonium* Sw.

Hiroyuki Akiyama**

秋山弘之：東アジア産イタチゴケ属（イタチゴケ科，藓類）およびその近縁属の研究III．*Pterogonium* 属，その分類学的

位置づけについての検討

Since Bruch et al. (1851) chose the lectotype of the genus, the generic composition of *Pterogonium* has been refined. *Pterogonium* is at present accepted as monotypic comprising only one species, *P. gracile* (Hedw.) Sm. (Wijk et al. 1967).

There are several opinions on the systematic position of *Pterogonium*. Bruch et al. (1851) and Schimper (1855) considered it as a member of the Pylaisiaceae because of its erect capsule and pleurocarpous habit. But, nowadays their family concept appears to be a mere assemblage based on a superficial resemblance and so, quite unnatural. Schimper (1860) established the Pterogoniaceae to accommodate *Pterogonium* and *Pterigynandrum*. He listed several characteristics for this family: (i) the presence of ascending shoots; (ii) the simple or forked costae; (iii) the smooth or dorsally papillose leaves; (iv) the presence of its symmetric and erect capsules, cucullate calyptrae and numerous paraphyllia; (v) the vestigial peristomes. But later he (1876) transferred *Pterogonium* in the Leucodontaceae because of rhomboidal to linear laminal cells. Limpricht (1895) included *Pterogonium* in the Leskeaceae s. lat. on the basis of the papillae on laminal cells and the forked costae; he did not distinguish papillae on cell lumens from prorations situated at the upper corner of cells. Brotherus (1905) followed Schimper (1876) and placed *Pterogonium* in the Leucodontaceae.

Until now, almost all bryologists have considered that *Pterogonium* should be included in the Leucodontaceae (Brotherus 1925, Fleischer 1906, Dixon 1924, Nyholm 1954, Lawton 1971, Vitt 1984, and many others). However, the position and relationships of *Pterogonium* within the family has been controversial.

Fleischer (1906) proposed a general system of moss classification accepted by most later bryologists. He pointed out that *Pterogonium* "lacked" costa and had a unique

** Department of Botany, Faculty of Science, Kyoto University, Kyoto 606, Japan
peristome similar to that of Leucodon, and assigned Pterogonium in the Leucodontaceae. But, because of its distinctiveness within the family, he placed Pterogonium in a new tribe of its own, Pterogoneae. Brotherus (1925) followed Fleischer but he raised the tribe to the rank of subfamily in the Leucodontaceae.

Manuel (1974) divided the Leucodontaceae into four subfamilies on the basis of three gametophytic characters: presence or absence of paraphyllia, pseudoparaphyllia, and a central strand in the stem. He was the first to point out the close relationship between Pterogonium, Antitrichia, and Bestia. He placed these genera in the Pterogoneae in the Leucodontoideae. According to him, these three genera share the following features: (i) the exostome teeth horizontally striated below and smooth or papillose above; (ii) the well developed endostome.

Buck (1980a) adopted Manuel's infrafamilial classification. He, however, proposed to transfer the above three genera together with another genus, Alisia, from the Leucodontaceae to a distinct family Pterogoniaceae. He pointed out that these four genera were closely related each other in sharing (i) the short, thick-walled laminal cells, (ii) the costae frequently forked at base into 2–3 main branches, (iii) the shelf-like habit, (iv) the short exerted capsules, and (v) the peristome papillose or with a hint of striation on the base of the exostome teeth.

Any treatments mentioned above, however, do not seem to be based on adequate morphological observations of both gametophytes and sporophytes. In order to clarify the systematic position of Pterogonium, re-examination of them are needed not only for Pterogonium itself but also for the genera hitherto considered to be closely related to it.

Observations

Gametophytes of Pterogonium

1. Habit

Plants consist of three parts, i.e., stoloniform shoots, ascending shoots and flagella. Stoloniform shoots prostrate on substratum (tree trunk or rock) and branch irregularly. Ascending shoots consist of lower parts forming stipes and of upper parts with many branches densely and pinnately arranged. Each branch is at a right angle to the main axis of the ascending shoot. Tips of branches and main axis are often flagelliform. They never break away as in the case of brood branchlets often observed in the Leucodontaceae. Ascending shoots show julaceous habit. Branches curve on one side, and so plants show characteristic appearance in dry conditions.

2. Leaves

Distinct differentiations occur in shape and size among stipe, stem, and branch leaves. Stipe leaves have cordate bases which are abruptly narrowed into slender upper parts. They are appressed to the stipe even in wet conditions. Laminal cells of stipe leaves are slightly longer than those of stem and branch leaves. Serration of upper
Fig. 1. 1–16. *Pterogonium gracile*. 17. *Antitrichia curtipendula*. 18. *Antitrichia californica*. 1, stem leaf (×25); 2, branch leaf (×25); 3, stipe leaf (×25); 4, tip of stem leaf (×270); 5, upper laminal cells with distinct proration (×270); 6, median laminal cells (×270); 7, upper margin of stem leaf (×270); 8, lower margin of stem leaf (×270); 9, scale-like leaf of branch primordium (×270); 10 and 11, axillary hairs (×270); 12, plant in wet condition (×3); 13, capsule (×7); 14, spores (×270); 15, perichaetal leaf (×25); 16, transverse section of stem (×270); 17 and 18, stem leaves (×25). 1–10 and 12–16, Schofield 29014 (NICH). 11, Revik s.n. (NIC). 17, Schofield et al. 43836 (HIRO). 18, Schofield 28453 (HIRO).
margins is low. Stem leaves are ovate-lanceolate with distinct serration (Fig. I 4, 7); each tooth is composed of 1–3 cells. Branch leaves are similar to stem leaves but usually much smaller.

In spite of these differences of stipe, stem, and branch leaves, the following features are shared among them; (i) the proration at the upper corner of several cells, (ii) the presence of serration, (iii) the distinct alar region composed of quadrate cells, (iv) the forked costa with several short protrusions in the basal part. The degree of proration varies among specimens and in a few case no proration is observed.

3. Stems

Stems of ascending shoots are more or less rounded in transverse sections and the constituent cells are differentiated into three layers; epidermis, cortical layer and a central strand (Fig. I 16). Paraphyllia and pseudoparaphyllia are absent; branch primordia are covered by small, scale-like leaves which are derived from the branch primordium itself (Fig. I 9). Axillary hairs consist of brownish, quadrate basal cells (1–2 cells high) and colorless, oblong upper cells (1–3 cells high); the height varies among specimens.

4. Perichaetial leaves

Perichaetial leaves lengthen after fertilization and are much longer than stem leaves. There are low serrations only at the upper part. Costae are forked at base and lack protrusions in the basal part. Laminal cells are much elongated-rectangular without proration. Hairs arising from vaginula are few to numerous and usually uniseriate (partly biseriate).

5. Others

Calyptrae are cucullate and provided with few hairs. Sexuality is dioecious. Female and male plants are nearly of the same size. Gametangia are restricted to the main axis of ascending shoot.

Sporophytes of Pterogonium

The peristome consists of exostome and endostome. The properistome (=prostome) is absent. Each tooth of exostome is lanceolate. The outer surfaces of exostome teeth have horizontal or oblique striae at base and dense papillae above (Fig. II 3–4). These striae are, however, difficult to observe with a light microscope. The endostome consists of a high basal membrane and short segments (Fig. II 2), which are smooth on both surfaces, lacking any ornamentation. The segments are arranged alternately against exostome teeth. Gillia are lacking.

In moist conditions, exostome teeth curve inward. In dry conditions, they spread outward at first and then only their upper parts become incurved (Fig. IV upper). The endostome is immobile in any conditions.

Capsules are long exserted from perichaetal leaves, cylindric and slightly narrowed at mouth, smooth (slightly plicate when dry). Stomata are present at apophyses.
Exothecial cells are short rectangular and thick-walled. Spores are spherical, thin-walled, minutely papillose, 13–16 μm in diameter, isosporic.

Discussion

Comparison with *Leucodon*

It seems evident from the present study that the observations by Fleischer (1906) on *Pteragonium* and *Leucodon* are incorrect. Indeed, concerning the suggested resemblances in costa and peristome morphology, *Pteragonium* has distinct forked costae, while *Leucodon*

---

**Fig. II.** Peristomes of *Pteragonium gracile* (1–4) and *Anomodon giralldii* (5–6). 1, whole view (×80). 2, endostome and inner surface of exostome (×400). 3, basal part of outer surface of exostome (×540). 4, ditto (×1040). 5, whole view (×60). 6, basal part of outer surface of exostome (×1040). 1–4, Schofield 28831 (HIRO). 5–6, Tagawa 1924 (KYO).
Fig. III. Peristomes. 1-2, Antirichia curtipendula. 3-4, A. californica. 5-6, Alsia californica. 7-8, Bestia longipes. 1, outer surface of exostome (×200). 2, endostome and inner surface of exostome; only segments are seen (×200). 3, outer surface of exostome (×260). 4, ditto (×420). 5, outer surface of exostome (×540). 6, endostome and inner surface of exostome (×140). 7, whole view; note the shoulder of exostome (×80). 8, basal part of outer surface of exostome (×800). 1-2, De Sloover 13112 (NICH). 3-4, Schofield 28453 (HIRO). 5-6, Schofield 29254 (NICH). 7-8, Tracy 7371 (NICH).
does not have any costae; the peristome of Pterogonium is not similar to that of Leucodon at all (Fig. II and Akiyama 1986). Unlike those of Pterogonium, the peristome of Leucodon lacks any kind of striation on the outer surface of exostome, and its endostome consists only of a low basal membrane and lacks distinct segments (Akiyama 1988). Leucodon further differs from Pterogonium in having no stipes and the similar sized and shaped stem and branch leaves. Therefore, based on these differences, I cannot support any close relationship between Pterogonium and Leucodon as Fleischer (1906) suggested.

Comparison with Alsia, Antitrichia and Bestia

Manuel (1974) and Buck (1980a) pointed out that Pterogonium, Alsia, Antitrichia, and Bestia resembled each other in exostome teeth morphology. Critical comparison, however, do not necessarily agree with them. Pterogonium and Bestia share distinct horizontal or oblique striae on the base of exostome teeth (Fig. II 2–3, III 8). A similar ornamentation is found in several unrelated taxa, i.e., Entodon, Pterigynandrum and others (Buck 1980b). On the other hand, in Antitrichia and Alsia the exostome teeth have only papillae on their base (Fig. III 3–5), or they are quite smooth (Fig. III 2); this represents a common type of ornamentation in the Leucodontaceae and related families. These papillae, however, are arranged in a line and appear as striae under a light microscope. Regrettably no detailed studies have appeared on the developmental morphology of the exostome ornamentation, and it is uncertain whether a stria is homologous with a line of papillae or not. Though much more detailed studies on this difference in ornamentation is needed, I have an intention to regard this difference significant.

As regards the endostome, that of Pterogonium consists of a high basal membrane and short segments alternate to exostome teeth and lacks cilia, and its basal membrane is...
shorter than exostome teeth. *Antitrichia* and *Alsia* have a structure similar to that of *Pterogonium*. On the other hand, the endostome of *Bestia* is very different from those of three other genera: the basal membrane is higher (to 2/3 length of exostome teeth); segments are taller than exostome teeth, and keeled and perforate along a median vertical line (Fig. III 7); there are 1–2 distinct cilia between segments. Moreover capsules of *Bestia*, unlike those of other genera, are sometimes inclined and asymmetric. Because of the striated ornamentation and complete endostome, the peristome of *Bestia* is of the *Hypnum* type; that of other three genera is of the *Nackera* type in possessing the smooth or papillose endostome teeth and a reduced endostome. For *Bestia Crum* (1987) placed *B. longipes* (type species of *Bestia*) in the Brachytheciaceae: one of the basis which he presented was its hypnoid peristome.

Beside the peristome morphology, the movement pattern of exostome teeth may also distinguish a genus from another. In *Pterogonium* exostome teeth tightly close the mouth of urn in moist conditions, and spread outward in dry conditions (Fig. IV, upper). On the other hand, in *Antitrichia* and *Alsia* they move reversely (Fig. IV, lower). In *Bestia* the exostome teeth move as seen in the usual *Hypnum* type (Fig. IV, upper). In the Leucodontaceae, Cryphaeaceae and related families, peristome is hydrocastique, that is, exostome teeth spread outward in moist conditions and inward in dry conditions. This is one of the characteristic features of this group (Stark 1987). Therefore the reverse movement pattern of exostome teeth offers evidence for distant relationship of *Bestia* and *Pterogonium* from the Leucodontaceae and Cryphaeaceae and related families.

As a result, sporophytic characters do not suggest close relationship among these four genera. Some authors (e.g., Lawton 1971) described in detail the peristome characters of *Pterogonium*. However, they did not estimate its taxonomical value, and included this genus in the Leucodontaceae.

Among the three genera, *Antitrichia* has been considered to be the closest relative of *Pterogonium* (Manuel 1974). In fact, they share: (i) the erect and cylindric capsules with narrow mouth; (ii) the forked costa; (iii) the absence of paraphyllia, pseudoparaphyllia, and a central strand in the stem (Manuel 1974, Buck 1980a). The characters (i) and (iii), however, are usually not considered important for classification of families or genera in mosses (Buck 1980b). As shown in Figure I-17 and 18, *Antitrichia californica* has a single, strong costa, and *A. curtipendula* a single costa even though with several short protrusions at base. Therefore the genus *Antitrichia* has a single costa, rather than a forked one as seen in *Pterogonium* (Figure I, 1–3).

From the above discussion, I conclude as follows: (i) *Pterogonium* is not so closely related to *Antitrichia, Bestia* and *Alsia* to be grouped together in any infrafamilial rank; (ii) on the basis of the peristome character comparison (i.e., ornamentation and movement pattern of exostome teeth), *Pterogonium* should be excluded from the Leucodontaceae; (iii) *Pterogonium* should be assigned not to the Hypnobryales but to the Isobryales, on the basis of the gametophytic and sporophytic features of the genus (i.e., the rhomboidal and
thick-walled laminal cells, the differentiation of stoloneform shoots and ascending ones, the presence of stipes in ascending shoots, the erect and symmetric capsules, and the reduced peristome).

Relationships of *Pterogonium*

Given that *Pterogonium* is safely placed in the Isobryales, the *Anomodon* affinity for the genus may be suggested. Limpricht (1895) early placed *Pterogonium* next to *Anomodon* in the Leskeaceae s. lat. Recently *Anomodon* and related genera are excluded from the Thuidiaceae and classified in the Isobryales as a distinct family, Anomodontaceae (Buck & Witt 1986). In the Anomodontaceae (especially in *Anomodon*), ascending shoots are differentiated from stoloneform ones; laminal cells are rhomboidal; alar regions are well differentiated; the peristome has horizontal or oblique striae on the base of exostome teeth in several species (e.g., *Anomodon giraldii* C. Müll.; Figure II 5–6); the exostome teeth spread outward in dry conditions; and the endostome is reduced. These coincidences suggest a close relationship between *Anomodon* and *Pterogonium*. However, further observations on the Anomodontaceae are needed to clarify the relationship of *Pterogonium* within that family.

**Acknowledgments**

I express my sincere thanks to Prof. Dr. N. Kitagawa for his valuable suggestions and criticism. My cordial thanks are due to Drs. H. Deguchi, N. Nishimura, and Mr. H. Nagamasu for their comments on manuscript. I am deeply obliged to the directors and curators of the herbaria HIRO, KYO, NIC, and TNS. My appreciations is extend to Prof. Dr. Kawano and the other members of our laboratory for their kind advice through the course of this study.

**Literature cited**


摘 要  Pterogonium 属(藓類)の分類学上の位置づけについての検討をおこなった。
本属は Bruch et al. (1831) によって設立された古い属でこれまでに多数の種が報告されているが、そのほとんどは他属へ移されため現在では唯一種 Pterogonium gracile (Hedw.) Sm. のみとなる単型属と考えられている。この種はヨーロッパ及び北米に分布している。中国からの報告があるが記載から判断するとイタチゴケ属の種と混同したものである。

Pterogonium 属の分類学上の位置については Bruch et al. (1851) が Pylaisaeaceae に所属させて以来、Pterogoniaceae として独立させる (Schimper 1860, Buck 1980a), シノブゴケ科を含む広義のウスグロゴケ科に所属させる (Limprecht 1895), イタチゴケ科に含める (Fleischer 1906, Brotherus 1925 等) など様々な解釈がなされてきた。

著者はイタチゴケ科の各属について特に朔歯の形態に注目して検討を進めてきた。Pterogonium 属についても配偶体・胞子体の形態を近縁とされてきた諸属と比較し、上記の解釈の妥当性を調べた。

本属の特徴は以下のとおりである。配偶体：顕著な柄をもち、枝・茎・柄各部に薄い葉が異なり、中肋は叉分し、葉長の1/3-1/2；葉上半部には顕著な鋸歯をもつ；葉細胞は短い刃円形でそのいくつかに大きな突起をもつ。胞子体：朔歯は二層からなり前朔歯を持たない；外朔歯の歯は外面に顕著な横線をもち、湿ると閉じる；内朔歯は高い基底膜と短く細いセグメントからなり、このセグメントは外朔歯の歯とは互い違いの位置にある；朔は長い円筒形で直立する；胞子は短柄性高く、直径 13-16 \mu m である。

イタチゴケ属とは外朔歯の歯の構造、中肋の形など多くの点で異なり、近縁とは考えられない。同様に Alsia, Antitrichia, Bestia 各属との近縁性も見いだすことはできなかった。Limprecht はキナイトゴケ属との類縁を示唆している。キナイトゴケ属は葉細胞が短い刃円形であること、顕著な柄をもつこと、外朔歯表面に横線をもつ種が存在することなど、Pterogonium 属と連続性を示す特徴が多い。このことは Limprecht の見解を支持するものと考える。