Notes on little known species of the genus *Leucodon* with immersed or laterally exserted capsules

Hiroyuki Akiyama*

The Japanese Society for Plant Systematics

* Department of Botany, Faculty of Science, Kyoto University, Kyoto 606, Japan

The genus *Leucodon* shows a considerable amount of diversity in such morphological features as the seta length, the leaf shape, the peristome structure, etc. Among them the seta length is especially variable not only among species but also within a species (for example, it is from 3 mm to 17 mm in *L. sapporensis* Besch.) and often hardly reliable as a criterion for the discrimination of species. Some species are, however, stably possessed of very short setae and their capsules are immersed or laterally exserted from perichaeta! leaves. As far as known to me, this type of sporophytes is seen only in four species, *L. brachypus* Brid., *L. cryptotheca* Hampe, *L. immersus* Lindb. and *L. sinensis* Thér. These four species are different from each other in the range of distribution as well as in the pattern of peristome structures; thus, they are not closely interrelated and the immersed or laterally exserted capsules seem to have been achieved by a parallelism in the genus *Leucodon*.

Some arguments have been referred to the taxonomical relationships between Leucodontaceae and Cryphaeaceae (Fleischer 1908, Brotherus 1926, Manuel 1974, Buck 1980). These two families are generally regarded to be closely interrelated and difficult to distinguish from each other. Manuel (1974) argued most intensively about the interrelationships of these two families and proposed three-character combination to separate them from each other; plants are dioecious, capsules are exserted and calyptrae are cuneate in Leucodontaceae, while plants are autoicous, capsules are immersed to short exserted and calyptrae are mitrate in Cryphaeaceae. This Manuel’s classification seems to be untenable and should be reexamined, because some species of *Leucodon* have obviously immersed or laterally exserted capsules as shown below.

Here are given brief descriptions and notes on little known species of *Leucodon* with immersed or laterally exserted capsules as well as some discussions on the systematic position of the genus *Forsstroemia* which is usually placed in the family Cryphaeaceae. As *Leucodon brachypus* known from North America has repeatedly been described...
(Sullivant 1864, Grout 1934, Crum and Anderson 1981, Ireland 1982), the species is mentioned here only in the key.

Key to the species with immersed or laterally exserted capsules

1. Central strands of stems present. Branches numerous, short. (Peristomes yellowish brown to pale white. Properistomes present, one-layered. Endostomes fragile. Spores 35–41 µ in diameter. Leaves widely ovate and narrowed into long slender acumen; alar regions extending to 1/4–2/5 of leaf length. Setae 0.5–1.0 mm long.) Middle and Near East. .................................................. Leucodon immersus BRID.

1. Central strands of stems absent. Branches sparse. ................................................. 2

2. Peristomes pale white. Properistomes present, one-layered. Setae more than 4 mm long. (Spores 55–64 µ in diameter. Leaves 2.5–3.2 mm long, narrowly ovate and narrowed into long slender acumen; alar regions ca. 1/3 of leaf length. Setae 4–6 mm long. Stomata absent.) China.................. Leucodon sinensis Thér.

2. Peristomes yellow. Properistomes absent. Setae less than 4 mm long. ............... 3

3. Stems thick. Leaves 3.0–3.8 mm long, oblong and narrowed into short acumen; alar regions less than 1/5 of leaf length. Endostomes indistinct. Stomata present at capsule necks. Spores 50–80 µ in diameter. Setae 1.0–2.0 mm long. Capsules 1.8–3.0 mm long. Central America. ...................... Leucodon cryptotheca Hampe

3. Stems thin and terete. Leaves 1.7–2.2 mm long, ovate and narrowed into slender acumen; alar regions more than 2/5 of leaf length. Endostomes papilllose on both surfaces, with distinct basal membrane. Spores 30–50 µ in diameter. Setae 2–4 mm long. Capsules 1.2–2.0 mm long. North America. ........ Leucodon brachypus BRID.

(Figs. 1–3, Plates I: 1–4)

Plants pale brown to green in herbarium materials. Stoloniferous shoots present. Stems ca. 4 cm long, 1.0–1.2 mm wide; central strands absent; sparsely branched in upper part. Fragella few. Pendent stems absent. Paraphyllia absent. Pseudoparaphyllia linear lanceolate. Brood bodies absent.

Stem leaves appressed to stems when dry, erect-spreading when moist, slightly plicate; ecostate, 2.5–3.2 mm long, ovate below and narrowed into long slender acumen; alar regions ca. 1/3 of leaf length; margins plane, entire or weakly denticulate at tips; upper laminal cells 32–41 × 4 µ, smooth, not thick-walled; upper marginal cells 19–23 × 4 µ, thin-walled; transitional cells 22–27 × 5 µ, smooth, thin-walled; basal central cells 68–92 × 5–6 µ, slightly porose; alar cells quadrate, 8 × 8 µ, smooth, colored reddish brown.

 Dioecious. Perichaetae leaves 7–7.5 mm long, convolute. Setae 4–6 mm long, helically coiled from lower right to upper left, smooth. Capsules brown, laterally exserted (rarely erect-emergent), ovoid, 1.5 × 1.0 mm, smooth; stomata absent; exothecial cells hexagonal, verrucose. Opercula shortly rostrate. Calyptrae unknown.
Annuli present.

Peristomes pale white, double; properistomes present, one-layered, densely papillose; exostome teeth short-lanceolate (ca. 120 µ high, 20 µ wide), densely papillose; endostomes membrane, vestigial (2–3 cells high), densely papillose.

Spores, minutely papillose, 55–64 µ in diameter.

Distribution.  China.

Specimens examined.  China: Prov. Hunan, in monte Yun-shan prope, ca. 1250 m alt. Handel-Mazzetti 12175 (H); ditto., 750 m alt. Handel-Mazzetti 10979 (H). Prov. Hubei, Schennongjia Forest District, 1300 m alt. B. Bartholomew et al. 296-b (NY); ditto. 1300 m alt. B. Bartholomew et al. 297-a (H, NY); ditto. 1900 m alt. B. Bartholomew et al., 1145 (H, NY).

Distinctive characters of this species are: (i) central strands of stems are present; (ii) properistomes are present; (iii) alar regions are ca. 1/3 of leaf length; (iv) leaves are narrowly ovate with long, slender acumens; (v) peristomes are pale white and densely papillose on both surfaces.

Leucodon coreensis CARD., distributed in China, Korea and Japan, is often confused with this species, because it sometimes has very short setae and its capsules are emergent from perichaetial leaves (usually its setae are 6–15 mm long). L. coreensis is different from L. sinensis in the ovate leaves with short acumens, and wider alar regions (more than 1/2 of leaf length).

As Leucodon sinensis has very short setae and long perichaetial leaves, capsules are seen laterally exserted from the perichaetial leaves. But they are not so deeply immersed as those of Cryphaeaceae. This type of laterally exserted capsules of L. sinensis made some students confuse Shoenobryum and Cryphaea species in the Himalaya region with L. sinensis. For example, the figures by GANGLEE (1976) are nothing but those of a Cryphaea species.
Plate I. 1–4: *Leucodon sinensis* (Handel-Mazzetti 12175); 1, dorsal view of exostome teeth; 2, ditto; 3, ventral view of exostome teeth and endostomes; 4, ditto. 5–8: *L. immersus* (Szyrnob 1178); 5, dorsal view of exostome teeth; 6, ditto; 7, ventral view of exostome teeth and endostomes; 8, endostomes. Arrows indicate endostomes. Scale for 1 and 3, 100 μ; 2 and 4, 50 μ; 5 and 7, 64 μ; 6 and 8, 33 μ.

(Fig. 7–9, Plate I: 5–8.)


Stem leaves appressed to stems or sometimes secund, rarely falcate secund, weakly plicate, ecostate, 2.6–3.4 mm long, widely ovate at bases and narrowed into long slender acumens; alar regions extending to 1/4–2/5 of leaf length; slightly concave; margins plane, entire below, often denticulate at tips; upper laminal cells 27–49 × 5 μ, smooth, not thick-walled; upper marginal cells 16–32 × 5 μ, smooth; transitional cells 22–41 × 5 μ, smooth; basal central cells 54–95 × 5 μ, smooth, not porose; alar cells 8 × 8–14 μ, colored reddish brown.

Dioecious. Male plants slightly slenderer than female plants. Perichaetial leaves

Plate II. 1–4: *Leucodon cryptotheca* (Sharp 1732); 1, dorsal view of exostome teeth; 2, ventral view of exostome teeth; 3, ditto (note the bifid tips); 4, side view of exostome teeth (note the absence of properiostomes). Scale for 1–3, 100 μ; 4, 33 μ.
up to 6 mm long, convolute. Perigonal leaves ovoid, ca. 1 mm long, reddish brown. Setae very short, 0.5–1.0 mm long, straight, smooth, reddish brown. Capsules deeply immersed among perichaetal leaves, oblong, 2.0–2.3 mm long, yellow to pale brown, plicate when dry, not narrowed at mouths; exothecial cells hexagonal, thin-walled, verrucose; stomata absent. Opercula rostrate. Calyptrae cucullate. Annuli present.

Peristomes brownish yellow to pale white, double; properistomes present, up to the middle of exostome teeth, one-layered, smooth or slightly papillose; exostome teeth 16, lanceolate up to 270 μ high, perforate along the middle line, papillose; endostomes sparsely papillose, fragile, adhering to the inner surfaces of exostomes.

Spores, minutely papillose, (27–)35–41(–46) μ in diameter.

Distribution. Middle and Near East (USSR, Turkey, Iran)

Specimens examined. USSR: Transcaucasia, Dylevskaja s.n. 22 VII 1956 (NICH); Caucassus, E. Szynoba s.n. (NICH). Iran: Mazanderan Province, 30 km south of Amol, P. Goldblatt 1221 f (NICH). Turkey: 45 km south of Trabzon, 870 m alt., P. Votila 14780 (NICH).

Distinctive characters of *Leucodon immersus* are: (i) setae are very short and capsules are deeply immersed among the perichaetal leaves; (ii) central strands of stems are present; (iii) leaves are widely ovate and narrowed into long, slender acumens; (iv) capsules are yellow or pale brown even when mature and well plicate when dry.

Lindberg (1870) describes that this species has 32 exostome teeth and lacks annuli. According to my observation, exostome teeth are 16 and distinct annuli are present.

*Leucodon immersus* has wide ovate leaves with slender, long acumens. The shape of leaves, the presence of central strands of stems and the small size of spores suggest that *L. immersus* is related most closely to *L. secundus* (Harv.) Mitt., distributed in East Asia. The latter is distinguished from the former by the long exerted capsules (setae are 9–15 mm long) and the well-developed, 2–3 layered properistomes.

**Leucodon cryptotheca** Hampe *Linnaea* 12: 350. 1838.

(Figs. 4–6, Plate II: 1–4)

Plants green to blackish brown in herbarium materials. Stoloniferous shoot present. Stems long and thick, up to 10 cm long and 2 mm wide including leaves, densely foliated; central strands absent. Branches few. Flagella few. Rhizoids mostly on stoloniferous shoots. Brood bodies absent. Paraphyllia absent. Pseudoparaphyllia triangular to linear lanceolate.

Stem leaves secund when dry, erect-spaying when moist, oblong at bases, rather abruptly narrowed into short, obtuse acumens; alar regions extending up to 1/5 of leaf length; exostate, 3.0–3.8 mm long, deeply concave, usually keeled at backs; margins recurved at bases, denticulate at tips; upper laminal cells 27–41×5 μ, smooth, not thick-walled; upper marginal cells 10–24×5–7 μ, smooth; transitional cells 27–43×5–7 μ, smooth; basal central cells 68–95×5–7 μ, smooth, not porose; alar cells 8×8 μ, smooth, slightly colored.
Dioecious? Perichaetal leaves convolute, up to 7 mm long. Setae 1.0–2.0 mm long, straight, reddish brown, smooth. Capsules yellow to pale brown, immersed or laterally exerted, ovoid, 1.8–3.0 mm long; smooth, rarely plicate when dry; exothelial cells hexagonal, thick-walled, verrucose; stomata present at necks, few. Opercula rostrate. Calyptrae cucullate. Annuli absent.

Peristomes single? pale yellow, transparent. Properistomes absent. Exostome teeth 16, up to 270 μ high, smooth below on both surfaces, sparsely and minutely papillose above, often bifid or deeply perforate. Endostomes indistinct.

Spores, minutely papillose, 50–80 μ in diameter.

Distribution. Central America (Mexico, Costa Rica).

Specimens examined. Mexico: Desierto de los Leones, 10300 ft alt. A.J. Sharp 78 (NICH); ditto, A.J. Sharp, 1723 (NICH); ditto, 10000 ft alt. Alexander and Hernandez s.n. 9 Sept. 1945 (NICH); District Federal, ca. 3300 m alt. on trees in forest, Frye and Frye 2829 (NICH). Costa Rica: Cerro de la Muerte, ca. 11500 ft., on sandy soil, Schultes 12036 (NICH).

Distinctive characters of Leucodon cryptotheca are: (i) leaves are oblong, deeply concave and keeled; (ii) alar regions are narrow, up to 1/5 of the leaf length; (iii) annuli are absent; (iv) endostomes are indistinct; (v) capsules are yellow to pale brown even when mature; (vi) spores are large; (vii) central strands of stems are absent; (viii) stomata are present at capsule necks; (ix) exostome teeth are smooth and often bifid.

This species occupies an isolated position in the genus Leucodon because of its unique highly reductive character of sporophytes: the total absence of annuli, and papillation on the surfaces of exostomes; endostomes are indistinct—only very minute and smooth fragments are present at bases of inner surfaces of exostomes. No other species has such sporophytic characters and seems to be confused with L. cryptotheca. Only L. brachypus, distributed in North America, resembles this species in the bifid exostome teeth and the immersed or laterally exerted capsules. But L. brachypus is a very thin plant with slender leaf acumens, and easily distinguished from L. cryptotheca as shown in the key.

The Leucodon species can be classified into three groups by the characters of peristome structures. The first group has pale white peristomes with well developed properistomes (2–3-layered or sometimes one-layered) and endostomes composed only of basal membrane and adhering to the inner surfaces of exostomes. The second one has pale yellow peristomes without properistomes and rather well developed endostomes with papillose short segments. The third one has no properistomes and indistinct endostomes. The first group includes L. secundus (Harv.) Mitt., L. sapporensis Besch., L. coreensis Card., L. immersus Lindb., L. sciuroides (Hedw.) Schwaegr., L. sinensis Thér., and many others. The second one does L. pendulus Lindb., L. julaceus (Hedw.) Sull., L. brachypus Brid., and some others. The third one is represented only by L. cryptotheca Hampe, which shares with the genus Forstroemia some sporophytic characters—the yellow and smooth peristomes, the vestigial endostomes, and the total absence of properistomes.
There are many different opinions on the systematic position of the genus *Forsstroemia*, which is traditionally distinguished from *Leucodon* by a series of criteria; the autoecious and/or dioecious sexuality, the pinnate pattern of branching, the presence of costaes in stem leaves, the immersed or short exserted capsules, and the presence of pseudoparaphyllia. Fleischer (1908) and Manuel (1974) treated *Forsstroemia* as a member of Leucodontaceae, while Brotherus (1926) regarded it as a member of Cryphaeaceae and almost all students followed him. Recently, Buck (1980) reestablished Leptodontaeeae and advocated that *Forsstroemia* should be placed in this family because of the resemblance between *Leptodon* and *Forsstroemia*—the two genera are similar in aerolation, the single costa, the short exserted capsule, the white peristome with a very reduced endostome, and the cucullate, sparsely hairy calyptra.

Table 1 shows a comparison of the gametophytic and sporophytic features between *Leucodon* and *Forsstroemia*. We can see there that some of the criteria mentioned above are ineffective to distinguish these two genera; the capsule position, the absence/presenee of pseudoparaphyllia, and the peristome structures are all not sharply discriminated between both genera. Now it is evident that the two genera are separated from each other only by the characters of sexuality, the presence of paraphysis of perichaetia, and the presence of costaes of stem leaves. I think these differences are not enough to regard them as belonging to separate families. And the characters which Buck (1980) thought to define Leptodontaeeae also apply to Leucodontaceae except the single costa and the hairy calyptra. Therefore I agree with the opinion that *Forsstroemia* should be assigned to the family Leucodontaceae.

Table 1. Gametophytic and sporophytic characters of *Leucodon* and *Forsstroemia*.

<table>
<thead>
<tr>
<th></th>
<th>Leucodon</th>
<th>Forsstroemia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laminal cells</td>
<td>short rhomboid to linear</td>
<td>short rhomboid</td>
</tr>
<tr>
<td>Central strands of stems</td>
<td>present/absent</td>
<td>absent</td>
</tr>
<tr>
<td>Costaes</td>
<td>absent</td>
<td>well to weakly developed, single or double</td>
</tr>
<tr>
<td>Pseudoparaphyllia</td>
<td>triangular to linear lanceolate</td>
<td>triangular to linear lanceolate</td>
</tr>
<tr>
<td>Paraphysis of perichaetia</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Paraphysis of perigonia</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Sexuality</td>
<td>dioecious</td>
<td>autoecious/dioecious</td>
</tr>
<tr>
<td>Calyptrae</td>
<td>cucullate, smooth</td>
<td>cucullate, more or less hairy</td>
</tr>
<tr>
<td>Opercula</td>
<td>short to long beaked</td>
<td>short to long beaked</td>
</tr>
<tr>
<td>Capsule position</td>
<td>immersed to long exserted</td>
<td>immersed to short exserted</td>
</tr>
<tr>
<td>Setae</td>
<td>0.5–17 mm, smooth rarely papilllose</td>
<td>0.5–4 mm, smooth</td>
</tr>
<tr>
<td>Stomata</td>
<td>present/absent</td>
<td>absent</td>
</tr>
<tr>
<td>Properistomes</td>
<td>well developed to absent</td>
<td>absent</td>
</tr>
<tr>
<td>Exostomes</td>
<td>papilllose, very rarely smooth, usually perforate</td>
<td>smooth, usually perforate</td>
</tr>
<tr>
<td>Endostomes</td>
<td>rudimentary, usually only with basal membrane</td>
<td>rudimentary, usually fragile</td>
</tr>
</tbody>
</table>

* Mainly based on Japanese species.
I wish to express my cordial thanks to Prof. N. Kitagawa, Nara University of Education for his valuable suggestions and criticism. I am deeply obliged to the curators of the herbaria, H, NIC and NY for their kind loan of specimens. I also wish to express my appreciation to Prof. S. Kawano and the member of our laboratory for their kind advice through the course of this study.

References


———. 1929. Symbolae Sinicae 4. i-v+147 pp. 5 plates.


概要　藓類のイタチゴケ属（イタチゴケ科）植物において卵が雌包葉内に沈生ないしは側方
に外出する種について述べた。

一般にイタチゴケ属植物においては卵柄の長さは同種間においても変異が大きく、種を認識
する上での安定した形質とはみなせない場合がおおい。しかし本論文で述べた四種はその変異
巾が小さく、かつ卵はつねに雌包葉内に沈生するか側方に外出する状態である。このような卵
の状態の存在は本属においてはいずれ広く認識されることがなかった。

スズゴケ属 Forstroemia は、従来その所属についてイタチゴケ科あるいはツルゴケ科に属
するかが議論されてきた。スズゴケ属とイタチゴケ属を区別する際重視されてきたいくつかの
形質のうち、少なくとも卵の状態（および偽毛葉の有無）においては両属を明確に識別するこ
とはできないことがわかった。