

***FISSIDENS GRANDIFRONS*: A POSSIBLE EXPLANATION FOR THE RARITY OF SPOROPHYTES**

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Abstract. Perigonia are described for the first time in *Fissidens grandifrons* Brid. A possible explanation for the rarity of sporophytes in this species, the result of perigonial and perichaetial plants separated in different mats, is presented. Sexual reproduction in *F. grandifrons* is compared with that of *F. perdecurrens* Besch. and *F. ventricosus* Lesq. The peristome of *F. perdecurrens* is described for the first time.

Key words: aquatic mosses, Asia, California, Europe, *Fissidens grandifrons*, *F. perdecurrens*, *F. ventricosus*, North America, perichaetia, perigonia, peristome, rarity of sporophytes, rheophytes

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INTRODUCTION

Fissidens grandifrons Brid. [subg. *Pachyfissidens* (Müll. Hal.) Kindb. sect. *Pachyfissidens* (Pursell & Bruggeman-Nannenga 2004)] is a large and conspicuous aquatic species found principally in streams and springs of limestone geology or aquatic systems with concentrations of calcium ions. The species has a circumpolar distribution in North America, Europe, and Asia. In eastern North America the species ranges from Ontario in Canada into the adjacent states Michigan and Wisconsin of the United States, and, south into the states of Alabama, Kentucky, Tennessee, Missouri, and Arkansas. In western North America the species extends from British Columbia in Canada south into the states of Washington, Oregon, California, Nevada, Idaho, Montana, Utah, Wyoming, and Arizona and also Mexico. In Europe *F. grandifrons* is found in the Pyrenees mountains of southwestern France and northeastern Spain, southeastern Germany, north central Switzerland, and the Caucasus of southern Russia. In Asia, the species occurs in Japan, China, northern Vietnam,

Taiwan, Pakistan, the western Himalayas, southern India, and Siberia. Throughout the range of the species, however, sporophytes are rare, and have been described and illustrated only from collections from Asia, the probable center of distribution for the species. It is remarkable that a species with such limited sporophyte production and no known gemmae has attained such a broad distribution. Hill (1902), however, maintained that the species spreads by radiculose branches that are easily detached in rapidly running streams. When encountered, populations can be extensive, forming large, robust colonies. Recent collections by the second author in which perigonia were found in a California collection, and perichaetia and sporophytes were found in a China collection prompted a survey of the holdings of this species in MO to determine if these structures were present in other collections of the species. The purposes of this paper are to report the finding of sporophytes in a collection from China; the finding of perigonial and perichaetial plants; to describe and illustrate the perigonia and to describe the perichaetia; to propose a possible explanation for the rarity of

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sporophytes; to compare the sexual reproduction of *F. grandifrons* with that of other dioicous aquatic to rheophytic species of *Fissidens*, and to describe the peristome of *F. perdecurrens* Besch.

SPOROPHYTES OF *FISSIDENS GRANDIFRONS* IN CHINA

Only three collections of *Fissidens grandifrons* with sporophytes have been reported previously in the literature: TAIWAN, *Lin 8699* (Li 1985; Pursell 2007), *Lin 12831* (Iwatsuki & Suzuki, 1982; Pursell 2007); PAKISTAN, *Higuchi 20161* (Pursell, 2007). These collections are in NICH.

The second author found immature sporophytes from the following site in China: SICHUAN PROVINCE. MULI CO: Hengduan Mts., ca 10 km N of the city of Muli, 28°00'32.3"N, 101°12'38.0"E, elev. 2550 m [ca 8366 ft], on vertical wall of a road bank with dripping water, *Shevock 36240* (MO).

Sporophytes of *Fissidens grandifrons* are indeed rare. The MO holdings of the species (including the one listed above) total 362 collections. Iwatsuki and Suzuki (1982) examined 91 specimens from Japan, giving a grand total of 453 collections of which approximately 0.009% had sporophytes.

PERIGONIA AND PERICHAETIA IN *FISSIDENS GRANDIFRONS*

Fissidens grandifrons is a species that once recognized is probably not further examined in detail. However, a close examination of the holdings of the specimens in MO has resulted in finding 11 collections (0.03%) with either perigonial or perichaetial plants. Unfortunately, Iwatsuki and Suzuki (1982) did not record Japanese collections seen with perigonia or perichaetia.

SPECIMENS EXAMINED WITH PERIGONIA: NORTH AMERICA. U.S.A. CALIFORNIA. Siskyou Co.: *Shevock 40560*. CANADA. British Columbia: Queen Charlotte Islands, *Schofield 45292*. – EUROPE. FRANCE. Pyrénées-Orientales: *Husnot, Musci Galliae 163*. GERMANY. Rheinland: *Frahm 11361*. SPAIN. Huesca: *Granzow de la Ceta 2245*.

SPECIMENS EXAMINED WITH PERICHAETIA: NORTH

AMERICA. U.S.A. CALIFORNIA. Plumas Co.: *Koch 1893*. MICHIGAN. Mecosta Co.: *Smith B734*. MISSOURI. Carter Co.: *Haggerty 2*; Shannon Co.: *Redfearn et al. 703*. CANADA. ONTARIO. Bruce Co.: *Ireland 20598*; Grey Co.: *Mixley s.n.*, 7 July 1971. – ASIA. CHINA. Sichuan Province: *Shevock 36240*.

Both perigonial and perichaetial plants are produced in *Fissidens grandifrons*, although never in great numbers and not in the same mat. Both types of plants are present in North America. However, perigonial plants were not found among those collections from Asia with sporophytes. Interestingly, only perigonial plants were seen in European collections. The latter, however, may be due to the small sample (three collections). In North American specimens, gametangia are present from the later part of June through mid-August. This is also the case for the collection from France, but in the collections from Germany and Spain, perigonia are present on the plants in February.

DESCRIPTION OF THE PERIGONIUM

Perigonial branches develop primarily on the outermost stems of a mat. They are acropetalous in development and occur in rows in the axils of leaves on both sides of the upper one-third of a stem, but they can also occur further down on the stem and in the axils of leaves of branches of the primary stem. Mature perigonial branches protrude from the leaves and are easily seen. At maturity, a perigonial branch is ca 2 mm long and consists of a short stem with lateral or basal rhizoids, and the perigonium (Fig. 1). Two perigonial branches are usually present in each axil; the second branch originating from a small lower leaf on the stem of the primary perigonial branch (Fig. 1). The mature perigonial branches can easily detach from the parent stem or branch or be tightly attached. Usually four pairs of leaves make up a perigonium, the lowest pair is very small, ecostate or nearly so, and either rounded or obtuse. Each of the remaining leaves consists of two very broad vaginant laminae, at least one of which is notched at the place where it joins the proboscis i.e., costa and very narrow dorsal and ventral laminae. The largest leaf is ca 1 mm long. All laminae are unistratose. Juxtacostally in the vaginant laminae there



Fig. 1. *Fissidens grandifrons* Brid. Two perigonal branches from a leaf axil on the parent stem. Lowermost leaf is small and ecostate (from Husnot, *Musci Galliae* 163).

is a broad area of large, oblong, nearly hyaline cells (few chloroplasts) bordered by a broad area of small, mostly quadrate, chlorophyllose cells (Fig. 2). Together, the two uppermost and largest perigonal leaves form a cup that envelopes the very short stalked antheridia that number around

six, the largest of which is *ca* 60 μm long. Paraphyses are absent.

The presence of two perigonal branches present in the axil of a leaf is probably a rare condition among aquatic *Fissidens*. Loosely attached perigonal branches were found in *Shevock*

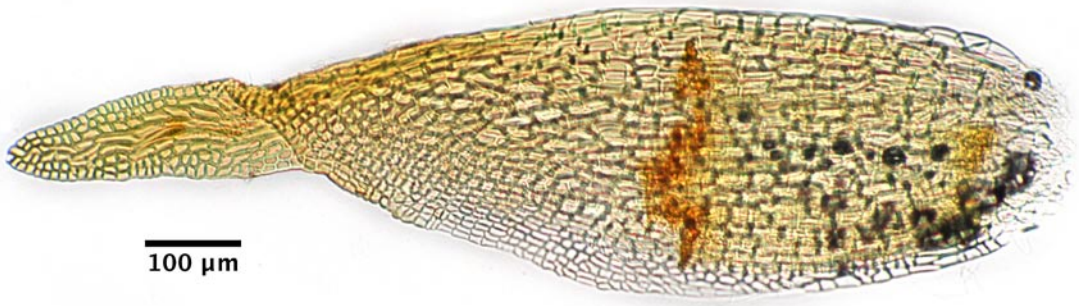


Fig. 2. *Fissidens grandifrons* Brid. Single perigonal leaf showing the enlarged area of translucent cells (from Frahm 11361).

40560 from California, while in all three of the collections from Europe they tightly adhered to the stem. This perhaps indicates that at maturity the entire perigonal branch is detached or only the mature sperms are released.

DESCRIPTION OF THE PERICHAETIUM

Perichaetial branches, like perigonal branches, are found on the outermost stems of a mat, but are less numerous. Like perigonal branches, the perichaetial branches occur in the axils of leaves in the upper one-third or lower of the parent stem where they protrude at maturity. A mature perichaetial branch is *ca* 7 mm long and consists of a short stem with basal rhizoids that firmly attach the branch to the parent stem and 2–3 pairs of leaves. Each of these leaves consists of a pair of broad, more or less equal vaginant laminae that are occasionally notched at the juncture with the long proboscis. The uppermost pair comprises the perichaetial leaves, the larger of which is *ca* 6 mm long, and forms a cup that envelopes the archegonia. The vaginant laminae of these leaves are unistratose and consist juxtacostally of a broad area of more or less hyaline (few chloroplasts) cells bordered by a broad band of much smaller, quadrate chlorophyllose cells. The ventral and dorsal laminae of the proboscides are bistratose. Paraphyses are absent.

SEXUAL REPRODUCTION

Sporophytes for many aquatic and rheophytic dioicous mosses throughout the world remain unknown or are rarely encountered. Based on the few specimens studied, there follows a discussion of the difficulty of sexual reproduction in *Fissidens grandifrons* and why there are so few sporophytes produced. The probability of sexual reproduction occurring in *F. grandifrons* apparently is extremely low and among aquatic and rheophytic mosses is perhaps the most difficult to accomplish. From the hundreds of collections of this species examined only four had sporophytes, including the one recorded here. Since the species is dioicous, plants of both sexes must be in proximity to one another. And, since the species is in aquatic systems with flowing water, perigonal plants must be positioned

upstream to perichaetial plants, and the water flow strong enough to dislodge the loosely attached perigonal branches and transport them to the exerted perichaetial branches firmly attached to the parent stems. Or, in the case when the perigonal branches are not detached, the sperm must be carried to the perichaetial plants. This probably does not occur in plants in rapidly running streams but rather in those found along banks, in dripping water sites, or in splash zones where those collections with sporophytes or either perichaetial or perigonal branches have been documented. Perigonal branches, or the naked sperm, having survived this journey, are probably directed downward into the perichaetium by the long rigid proboscides of the perichaetial leaves where they become lodged by the perigonal leaves close to the archegonia. Only then can fertilization occur.

Fissidens grandifrons is streamlined for existence in its usual habitat of fairly rapidly running streams. The leaves are tightly imbricate, multistratose (except the margins), and narrowly lanceolate with costae ending below the rounded apices; entire margins; and, smooth cells, (Iwatsuki & Suzuki 1982; Pursell & Allen 1994). The plants are rigid and firm to the touch, and therefore, portions of plants eroded by abrasion during peak flows are uncommon. Unlike other aquatic to rheophytic species, however, *F. grandifrons* has a terrestrial sporophyte – one with a long exerted capsule, but which is estomatose. On several occasions the first author and Bruce Allen visited an area in eastern Missouri that seemed to be the perfect habitat for sporophyte development. The stream has a modest flow and mats of the moss cover the bed of the stream for some distance and extend onto the low banks. Neither perigonia nor sporophytes were ever found. Conditions for sexual reproduction of aquatic mosses, especially dioicous species, must be rare indeed. Currently, nothing is known about the ecological factors – light, temperature of the water, and nutrients – affecting the development of gametangia. Is a photoperiod involved, and, if so, do the hyaline cells of the vaginant laminae of the perichaetial and perigonal leaves that admit diffuse light to the interior of the perigonia and perichaetia play a role in the maturation of the

gametangia? Aquatic species form linear distributional patterns within the water column. The founder effect may also come into play depending on which sexual plant arrives first at a suitable riparian area for colonization. The amount of unsuitable habitat between riparian systems can also be formidable for a plant where gemmae are unknown and spore dispersal through the production of sporophytes is so infrequent. *Fissidens grandifrons* is an aquatic species that requires sufficient time in a hydrated state and the velocity of water flow over the plants probably also contributes to a narrow window when successful fertilization could occur. Gametangia of both sexes would need to develop about the same time. The cost of producing gametangia when reproductive success seems extremely low may be another factor why these structures are so rarely observed in nature.

COMPARISON WITH THE SEXUAL SYSTEMS OF OTHER DIOICOUS AQUATIC AND RHEOPHYTIC *FISSIDENS* SPECIES

Two species were selected for comparison of their sexual systems with that of *Fissidens grandifrons*, a species belonging to the same subgenus and section and a second species belonging to a different subgenus and section.

Fissidens perdecurrens Besch.

Subg. *Pachyfidens* (Müll. Hal.) Kindb. sect. *Pachyfidens* (Pursell & Bruggeman-Nannenga 2004).

This species is restricted to Japan, China, and Taiwan, where it occurs on dripping wet rocks or seasonally submerged in small streams. The species is close to *Fissidens grandifrons*, differing essentially in a slightly smaller size, acute leaves that usually end in a small, hyaline cell, and prominent guide cells in the upper part of the costa as seen in surface view. Iwatsuki and Suzuki (1982) examined 43 specimens from Japan, all lacked sporophytes but one [Iwatsuki & Suzuki 11801 from Honshu, Aichi-ken (NICH)] had perichaetial branches. A total of 17 specimens in MO from China, Japan, and Taiwan were examined. Of these, only 6 from Taiwan had perichaetial branches. Per-

igonial branches were not observed. Mature sporophytes were found in two collections or 0.05% of the total of 40 collections, one from Japan and one from Taiwan. Perichaetial branches of *F. perdecurrens* are very similar to those of *F. grandifrons*. It can probably be safely assumed from their similar habitats, close similarity in vegetative features, and perichaetial branch structure that the reproductive system in this species is similar to that of *F. grandifrons*. In addition, *F. boninensis* Z. Iwats. in Inoue & Z. Iwats., known only from the Bonin Islands, and *F. pachyphyllus* Dixon and *F. nigroviridis* E. S. Salmon, known from Sawawak and Borneo, respectively, may eventually be seen to have a similar sexual reproductive system.

The peristome of *Fissidens perdecurrens*, not seen by either Iwatsuki and Suzuki (1982) or Li (1985), is herein described for the first time.

Sporophytes one per perichaetium. Setae smooth, to ca 12 mm. long; thecae \pm inclined, \pm bilaterally symmetric, ca 1 mm long; exothecial cells \pm quadrate, thin-walled, stomatose in base of thecae; peristome taxifolius type, i.e., trabeculae prominent throughout a tooth, the lower undivided part finely papillose dorsally, gradually changing to erect ornamentations at the bifurcation, and filaments with spiral ornamentation operculum long-rostrate, \pm oblique, to ca 0.9 mm long. Calyptra cucullate, smooth, naked, ca 1.1 mm long.

The sporophytes of *Fissidens perdecurrens* differ essentially from those of *F. grandifrons* in the presence of stomata. The taxifolius type of peristome is fully described and illustrated in Allen (1980), and Bruggeman-Nannenga and Berendsen (1990).

SPECIMENS EXAMINED WITH SPOROPHYTES: JAPAN. [HONSHU] Ôyama-saki, Tosa, S. Okamura 3750. – TAIWAN. HSINCHU Co.: Shevock 41446.

Fissidens ventricosus Lesq.

Subg. *Fissidens* Hedw. sect. *Fissidens* (Pursell & Bruggeman-Nannenga 2004).

This species is restricted to the Pacific Coastal Region of North America (British Columbia in

Canada, and the states of Washington, Oregon and California in the United States) with a disjunct population in the adjacent state of Idaho (Ireland & Schofield 1967), and is found on wet rocks beside streams and is often submerged in streams, or exposed during low water levels. The species is characterized by smooth, unistratose to irregularly bistratose laminal cells, multistratose limbidia on all laminae, and emergent capsules on thick, often geniculate setae. The perigonia and perichaetia are terminal and at maturity neither is shed, unlike the loosely attached perigonia of *F. grandifrons*. The uppermost leaves of a perichaetial stem form the perichaetial leaves and differ from lower leaves only in being larger. A perigonium is nested between the uppermost stem leaves and consists of one or two smaller perigonial leaves enclosing the antheridia. Both perigonial and perichaetial plants are usually intermingled, in contrast to their counterparts in *F. grandifrons* so that fertilization is frequent. Sporophytes were present on 16 of the 46 (34.8%) specimens examined.

The genus *Fissidens* has a remarkable number of species that are either aquatic or rheophytic and occur on all continents except Antarctica. Several of these rheophytic *Fissidens* are localized or regional endemics. Generally, populations of aquatic and rheophytic *Fissidens* can be locally common. In some cases, however, such as the exceedingly rare *F. aphelotaxifolius* Pursell, only a few collections have been obtained and sporophytes remain unknown. In other *Fissidens* species only perigonia or perichaetia have been reported. There is a need to examine aquatic and rheophytic *Fissidens* populations carefully in the field before making collections to determine if perigonia, perichaetia or sporophytes are present at that locality. *Fissidens* within aquatic systems, especially in the splash

zone or even those species seasonally submerged, may indeed have a few plants with sporophytes but their coloration can be similar or nearly identical to the gametophytes and grow parallel to the plants so they can be easily overlooked.

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