

Fissidens in the Neotropics

Ronald A. Pursell

208 Mueller Laboratory, The Pennsylvania State University, University Park, PA 16802

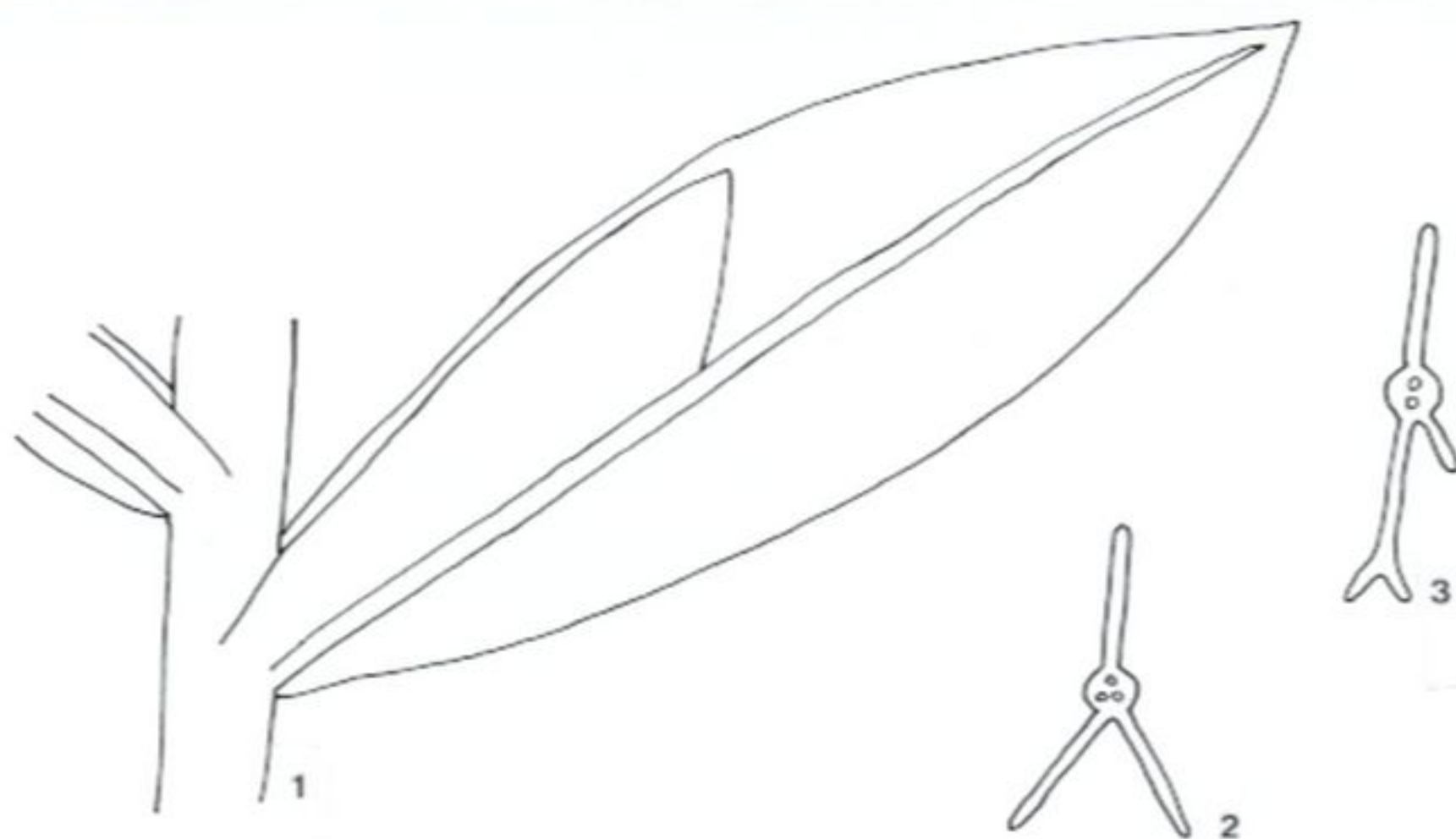
Abstract. The land areas of the Western Hemisphere south of the United States support over 276 species of *Fissidens* (Wijk et al. 1962, 1969). This number is approximately 30% of the total number of species known. Progress made on a monograph of the family in the neotropics and the adjacent areas is summarized; approximately 50% of the species have been studied. Commonality among the neotropical, African and Asian species of *Fissidens* is discussed. Changes to be made in the classification of the family are indicated. New characters used in distinguishing species and the classification of the family are enumerated.

Resumen. En la region del hemisferio Occidental al sur de los Estados Unidos de Norte América, estan representadas mas de 276 especies de *Fissidens* (Wijk et al. 1962, 1969). Esta cifra corresponde aproximadamente al 30% del total de especies conocidas en este genero. En este trabajo, en el cual se han estudiado aproximadamente el 50% de las especies, se resumen los avances de una monografia de la familia Fissidentaceae. También se discuten las semejanzas entre las especies de *Fissidens* del neotrópico con las especies de Africa y Asia. Se indican cambios que deben de hacerse en la clasificación de la familia. Además, se enumeran nuevos caracteres usados para la clasificación de la familia y para distinguir entre especies de la familia.

This report consists of a review of the overall classification of the Fissidentaceae and a synopsis of the progress made toward producing a monograph of this family for the neotropics. As defined by the Organization for Flora Neotropica, the neotropics consist of "the Western Hemisphere continental land mass lying between the Tropics of Cancer and Capricorn, together with adjacent islands and including the West Indies and Galápagos." The part of Mexico north of the Tropic of Cancer and the portion of South America south of the Tropic of Capricorn, inclusive of the Falkland (Malvinas) Islands in the South Atlantic Ocean and the Juan Fernandez Islands in the South Pacific Ocean, are also included. The monograph, thus, will embrace all of

the Western Hemisphere south of the United States.

The Fissidentaceae are a monogeneric family represented by *Fissidens* and constitute one of the larger families of mosses. When established by Hedwig (1801), the genus *Fissidens* consisted of 14 species. On the basis of current interpretation of the genus, 10 of these 14 species are retained in *Fissidens*. I have no accurate count of the number of species currently recognized on a worldwide basis. However, a total of 927 accepted species (inclusive of the species in segregate genera) are listed in Index Muscorum (Wijk et al. 1962, 1969). Remarkably, these hundreds of species are distinguished, for the most part, on



Figures 1-3. Leaf of *Fissidens*. 1. Generalized outline of a leaf showing the two vaginant laminae, ventral lamina, dorsal lamina and costa. 2. Outline of a cross-section through the proximal half of a leaf showing the two vaginant laminae, costa and dorsal lamina. 3. Outline of a leaf cross-section near the distal ends of the vaginant laminae showing the presence of an additional lamina.

sists of two vaginant laminae (the *lamina vera*), a dorsal lamina (*lamina dorsalis*), a ventral lamina (*lamina ventralis*, *lamina apicalis* or apical lamina), and a single costa (absent in a few species). The basic features of the leaf are illustrated in Figure 1.

When cut in cross-section through the region of the vaginant laminae, the leaf of *Fissidens* has a more or less Y-like appearance (Figure 2). The leaves are distichous and equitant in arrangement, the vaginant laminae straddling the stems. Leaves of genera such as *Bryoxiphium*, *Distichium*, *Eustichium*, and *Sorapilla* are similar to the leaves of *Fissidens* in arrangement and also somewhat in appearance. Of these, however, only *Bryoxiphium* and *Sorapilla* have been considered to be closely allied to *Fissidens*. According to the latest considerations on the classification of mosses by Vitt (1984), *Fissidens* occupies its own suborder, Fissidentineae, and *Bryoxiphium* and *Sorapilla* are placed in separate families of suborder Dicrani-

neae. Both suborders are maintained in the order Bryales. Peristomes of both suborders are haplolepideous, i.e., a single ring of 16 teeth derived from two layers of the amphithecium. Allen (1981) considered *Sorapilla* to have a reduced double peristome, and on this basis, and other characters, followed Fleischer (1907) and concluded that the genus belongs in the Isobryales. Iwatsuki (1985) concurred with this decision.

In the past 175 years a number of interpretations of the *Fissidens* leaf have been proposed. These have been reviewed by Robinson (1970). Perhaps the best known and most widely accepted interpretation is the one originated by Brown (1819) but championed by Salmon (1899) and most recently by Mishler (1988). In brief, according to this interpretation, the vaginant laminae (the *lamina vera*) represent the true leaf and the dorsal and ventral laminae are an outgrowth from this. Robinson, however, elaborating on an interpretation originated by

Robinson (1970). Perhaps the best known and most widely accepted interpretation is the one originated by Brown (1819) but championed by Salmon (1899) and most recently by Mishler (1988). In brief, according to this interpretation, the vaginant laminae (the *lamina vera*) represent the true leaf and the dorsal and ventral laminae are an outgrowth from this. Robinson, however, elaborating on an interpretation originated by Spruce (1881), considers the whole leaf of *Fissidens* as the true leaf whose form has been achieved by the "reorientation of the mitotic spindle of the apical cell of the leaf . . ." It is not the intent of this report to choose between these interpretations. The poorly developed additional laminae that are infrequently found on leaves [viz. an unrecorded specimen of *F. taxifolius* Hedw. *Sharp 2405b* (PAC), and *F. bourgaeanus* Besch., see Figure 3] indeed can support either of these two explanations.

The need to approach the study of mosses from a worldwide perspective has been demonstrated a number of times, e.g., by the work of Frahm (1982) on the widely distributed and taxonomically difficult genus *Campylopus*, by the work of Ochi (1972, 1980) on the family Bryaceae, and recent work on *Fissidens* subgenera *Octodiceras* and *Sarawakia* (Pursell 1987, Pursell et al., 1988). Knowledge of the relationship between the moss floras of Africa and the neotropics and between the neotropics and Asia is increasing (for a review of the relationship between Africa and the neotropics see Reese 1985). One example of a species of *Fissidens* described originally from the neotropics that is pantropical is *F. asplenioides* Hedw. The neotropical species of *F. kegelianus* C. Müll. is conspecific with the Asiatic *F. zollingeri* Mont. (Pursell 1979). Moreover, this species is also known from Africa (Bizot & Pócs 1979, Kis 1985, Sappa & Piovano 1947) and, as species from other areas are studied and names synonymized,

probably will be found to be pantropical. A third example is *F. garberi* Lesq. & James, a species of broad distribution in the neotropics which extends northward into the United States. Iwatsuki and Suzuki (1982) reduced this species to the synonymy of *F. microcladus* Thwait. & Mitt. which occurs throughout much of Asia (see also Iwatsuki 1982 and Li 1985). Although *F. microcladus* has not been recognized from Africa, Dury's (1974) review of the African species in section *Semilimbidium* certainly will facilitate the problem of determining synonymy among the many species described.

During July 1989, Drs. M. A. Bruggeman-Nannenga and Zenoske Iwatsuki, two eminent specialists on the systematics of the Fissidentaceae in Africa and Asia, respectively, were able to come to the United States and, with me, address problems about the commonality of species in the neotropics, Asia and Africa. The overall classification of the family Fissidentaceae was also discussed. As mentioned below, results of this highly successful period will be published soon in a series of papers.

The classification of the Fissidentaceae most widely used today was published by Brotherus (1901, 1924, see Table I for an outline of the scheme), based essentially on an earlier one by Müller (1901). In this classification four genera are recognized, *Fissidens*, *Fissidentella*, *Moenkemeyera* and *Simplicidens*. A more recent classification, based in part on chromosome number correlated with sexuality, was published by Iwatsuki (1985, see Table 2 for an outline of this system). According to Iwatsuki, subgenera *Aneuron* (= *Polypodiopsis* sensu Brotherus) and *Fissidens* are characterized by $n = 10$ or $n = 12$ in monoicous species while subgenera *Pachyfissidens* and *Serridium* (= section *Serridium* sensu Brotherus) have $n = 12$ in dioicous species.

Genus 1. Fissidens Hedw.Subgenus 1. Polypodopsis C. Müll. (8)Subgenus 2. Eufissidens Mitt. [= Fissidens]

- Section 1. Weberiopsis C. Müll. (9)
- Section 2. Reticularia Broth. (24)
- Section 3. Bryoidium C. Müll. (151) [= Fissidens]
- Section 4. Pachylomidium C. Müll. (21)
- Section 5. Pycnothallia C. Müll. (17)
- Section 6. Heterocaulon C. Müll. (30)
- Section 7. Semilimbium C. Müll. (157)
- Section 8. Aloma C. Müll. (55)
- Section 9. Crenularia C. Müll. (72)
- Section 10. Crispidium C. Müll. (28)
- Section 11. Amblyothallia C. Müll. (74)
- Section 12. Serridium C. Müll. (52-55)

Subgenus 3. Pachyfissidens C. Müll. (8)Subgenus 4. Octodiceras (Brid.) Mitt. (17-27)Genus 2. Simplicidens Herz. (2)Genus 3. Moenkemeyera C. Müll. (10)Genus 4. Fissidentella Card. (1)

The number in parenthesis = no. of species total = 736-749

Table 1. Classification of the Fissidentaceae according to Brotherus (Engler & Prantl, 1924)

Genus 1. *Fissidens* Hedw.

- Subgenus 1. *Aneuron* Kindb. (n = 10)
 Subgenus 2. *Fissidens* (n = 10 or 12)
 Sections: not defined
 Subgenus 3. *Serridium* (C. Müll.) Z. Iwats. (n = 12)
 Subgenus 4. *Pachyfissidens* (C. Müll.) Kindb. (n = 12)
 Subgenus 5. *Octodiceras* (Brid.) Broth. (n = ?)
 Subgenus 6. *Sarawakia* (C. Müll.) Z. Iwats. (n = ?)

Genus 2. *Nanobryum* Dixon (n = ?)

Table 2. Classification of the Fissidentaceae according to Iwatsuki (1985)

rank of subgenus, *Serridium* (C. Müll.) Iwatsuki and *Sarawakia* (C. Müll.) Iwatsuki.

Octodiceras in the sense of Broth. consists of a number of disparate aquatic species. This disparity is immediately evident once one begins to examine the species. One species among these, *Fissidens beccarii* (Hampe) Broth., represents one of the most unusual species of the genus known. Iwatsuki (1985), accordingly, proposed that the species be recognized in its own subgenus, *Sarawakia*, now known also from South America (Pursell et al., 1988). Other species of *Octodiceras* (sensu Broth.) belong correctly in subgenus *Fissidens* (Li 1985, Pursell 1987, Pursell et al., 1988). In the restricted sense, *Octodiceras* consists of only those aquatic species characterized by rather lax cells in long linear leaves that are extremely fragile when dry.

Subgenus *Fissidens* is the largest and most diversified of the subgenera of genus *Fissidens*. The 12 sections recognized by Broth. are now considered to be distinguished along unnatural lines. The status of these sections, not discussed by Iwatsuki (1985), was recently reviewed (Pursell 1988). Problems relative to some of the sections of *Fissidens* were resolved in the discussions in July. At this time, it can be noted that the resolution of these problems involved the use of characters heretofore not used or seldom used. For example, Allen (1980) published a short paper describing peristomal variations observed in an SEM study of 19 species of *Fissidens*. Bruggeman-Nannenga & Berendsen (1988) refined and expanded this work to include 200 species representing all subgenera and sections of the family.

The structure of the costa, heretofore not emphasized to any great extent, appears to be

In the restricted sense, *Octodiceras* consists of only those aquatic species characterized by rather lax cells in long linear leaves that are extremely fragile when dry.

Subgenus *Fissidens* is the largest and most diversified of the subgenera of genus *Fissidens*. The 12 sections recognized by Brotherus are now considered to be distinguished along unnatural lines. The status of these sections, not discussed by Iwatsuki (1985), was recently reviewed (Pursell 1988). Problems relative to some of the sections of *Fissidens* were resolved in the discussions in July. At this time, it can be noted that the resolution of these problems involved the use of characters heretofore not used or seldom used. For example, Allen (1980) published a short paper describing peristomal variations observed in an SEM study of 19 species of *Fissidens*. Bruggeman-Nannenga & Berendsen (1988) refined and expanded this work to include 200 species representing all subgenera and sections of the family.

The structure of the costa, heretofore not emphasized to any great extent, appears to be of considerable diagnostic value. Bruggeman-Nannenga has been studying the costa extensively and will soon be prepared to publish on her observations. Moreover, section *Amblyothallia*, heretofore rather difficult to define, can be recognized readily by the structure of the costa. A paper dealing with the circumscription, synonymy, relationship, distribution and illustrations of this section will be published soon.

The number of exothecial cells in the circumference of the theca (Bruggeman-Nannenga & Berendsen 1988) and the axillary hyaline nodules (Iwatsuki & Pursell 1980), although less important, nevertheless are also useful.

Two additional papers will be published

also by Iwatsuki, Bruggeman-Nannenga and myself. One will be a world-wide revision of the 'ecostate' species of *Fissidens*, i.e., subgenus *Aneuron*. The second, based somewhat on Iwatsuki's (1985) scheme will address the overall classification of the Fissidentaceae above the species level.

There are 276 species of *Fissidens* recorded in Index Muscorum in the area of the western hemisphere to be included in the monograph. This is approximately 30% of the total number of 927 species stated previously. According to a study by Touw (1974), modern monographic studies have reduced the number of species by 20-45%. If this is the case in *Fissidens* the final number of species recognized in the western hemisphere south of the United States should be between 221 and 152.

It has become increasingly evident during the course of my studies that subtle differences, often thought to be highly variable, are remarkably consistent and are useful in distinguishing species. For example, *Fissidens fontanus* was thought to be a highly variable and widespread species. In this complex (Pursell 1987), not only are there good differences in the peristome but gametophytically such characters as vaginant laminae length/leaf length, the nature of the distal end of the minor lamina (a term introduced by Robinson 1970) and even costa length, are important in distinguishing species. The pluripapillose species in section *Semilimbidium* (including species from section *Pycnothallia*) are another example. In the neotropics these species are centered nomenclaturally around *F. elegans* Brid. Florschütz (1964) recognized only two species, but as a recent study (Pursell 1984) indicates, differences important in distinguishing species include: 1) the thickness of limbidia; 2) the length of limbidia; 3) the kinds of stems (sterile, perichaetial and perigonal) on which limbate leaves are found; and 4) the

particular leaves of a stem on which limbidia are found.

As stated earlier, it is becoming increasingly apparent that large and extensive genera of bryophytes must be studied from a worldwide perspective. From discussions with Iwatsuki and Bruggeman-Nannenga it is apparent that several species of *Fissidens* of frequent occurrence in the neotropics, in addition to those already mentioned, do not differ from rather common species found in Asia and Africa. Species already so identified will be enumerated in a paper soon. As work progresses this number of species reflecting degrees of commonality will surely increase.

I estimate that 50% of the work on the monograph is near completion. Most major groups have been studied to some extent. Work on sections *Aloma* and *Crenularia* is nearing completion. Much remains to be done with section *Fissidens* (including section *Heterocaulon*) and the unipapillose species of section *Semilimbidium*. Within 3 years, or at most 4 years, the monograph should be completed.

Acknowledgement.

The National Science Foundation is gratefully acknowledged for Grant BSR-8905431 to The Pennsylvania State University, which not only made this report possible, but also afforded the means to bring Drs. M. A. Bruggeman-Nannenga and Z. Iwatsuki to the United States for consultation and cooperative study.

LITERATURE CITED

Allen, B. H. 1980. Peristome variations in the genus *Fissidens*: an SEM study. *Bryologist* 83:314-327.
 _____. **1981.** A reevaluation of the Sorapillaceae. *Bryologist* 84:335-338.
Bizot, M. 1963. *Nanobryum gladiolum* (Mitt.) Biz. comb. nov. *Revue Bryologique et Lichnologique* 32:82-83.
 _____. & **T. Pócs.** 1979. East African Bryophytes, III. *Acta*

Botanica Academiae Scientiarum Hungaricae 25:223-261.
Brotherus, V. F. 1901. Fissidentaceae. In: A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien* 1(3):351-363. Leipzig.
 _____. **1924.** Fissidentaceae. In: A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien*, ed. 2, 10:143-155. Leipzig.
Brown, R. 1819. Characters and description of *Lyellia*, a new genus of mosses, with observations on the section of the order to which it belongs; and some remarks on *Leptostomum* and *Buxbaumia*. *Transactions of the Linnean Society of London* 12:560-583.
Bruggeman-Nannenga, M. A. & W. Berendsen. 1988. On the peristome types found in the Fissidentaceae and their importance for the classification. In: M. A. Bruggeman-Nannenga, *Systematic studies on Fissidens (Musci)*. Ph.D. dissertation, Univ. of Utrecht.
Dixon, H. N. 1941. *Sainsburia*, a new genus of Fissidentaceae. *Bryologist* 44:40-41.
Dury, M.-N. 1974. Etude taxonomique des espèces africains de la section *Semilimbidium* C. Müll. du genre *Fissidens* Hedw. Thèse. Université de Dijon.
Fleischer, M. 1907. *Die Musci der Flora von Buitenzorg*. Vol. 3. Leiden.
Florschütz, P. 1964. The mosses of Suriname. Part I. Leiden.
Frahm, J.-P. 1982. Grossdisjunktionen von Arealen südamerikanischer und afrikanischer *Campylopus*-Arten. *Lindbergia* 8:45-52.
Hedwig, J. 1801. *Species Muscorum Frondosorum*. Lipsiae.
Iwatsuki, Z. 1982. Speciation of the moss genus *Fissidens* in New Caledonia (preliminary report). *Journal of the Hattori Botanical Laboratory* 52:113-126.
 _____. **1985.** A new approach to the classification of the Fissidentaceae (Musci). In: H. Hara (ed.), *Origin and Evolution of Diversity in Plants and Plant Communities*, pp. 132-141. Tokyo.
 _____. & **R. A. Pursell. 1980.** Axillary hyaline nodules in *Fissidens* (Fissidentaceae). *Journal of the Hattori Botanical Laboratory* 48:329-335.
 _____. & **T. Suzuki. 1982.** A taxonomic revision of the Japanese species of *Fissidens* (Musci). *Journal of the Hattori Botanical Laboratory* 51:329-508.
Kis, G. 1985. Mosses of south-east tropical Africa. An annotated list with distributional data. 170p. Institute of Ecology and Botany of the Hungarian Academy of Sciences Vácrátót.
Li, A.-H. 1985. A revision of the Chinese species of *Fissidens*. *Acta Botanica Fennica* 129:1-65.
Mishler, B. D. 1988. Relationships between ontogeny and phylogeny, with reference to bryophytes. In: C. J. Humphries (ed.), *Ontogeny and Systematics*, pp. 117-136. New York.
Müller, C. 1901. *Genera Muscorum Frondosorum*. Leipzig.
Ochi, H. 1972. A revision of African Bryoideae. *Musci* (first

part). Journal of the Faculty of Education Tottori University, Natural Science 23:1-126.

_____. **1980.** A revision of the neotropical Bryoideae. Musci (first part). Journal of the Faculty of Education Tottori University, Natural Science 29:49-154.

Pursell, R. A. 1979. On Fissidens. Nomenclatural and distributional notes on some American species. Bryologist 82:58-64.

_____. **1984.** A preliminary study of the Fissidens elegans complex in the neotropics. Journal of the Hattori Botanical Laboratory 55:235-252.

_____. **1987.** A taxonomic revision of Fissidens subgenus Octodiceras (Fissidentaceae). Memoirs of the New York Botanical Garden 45:639-660.

_____. **1988.** Fissidens amazonicus sp. nov. from Brazilian Amazonia, with comments on the relationship and taxonomy of subgenus Fissidens sections Areofissidens, Weberiopsis and Reticularia and subgenus Aneuron (Bryopsida: Fissidentaceae). Beiheft zur Nova Hedwigia 90:345-355.

_____, **M. A. Bruggeman-Nannenga & B. H. Allen. 1988.** A taxonomic revision of Fissidens subgenus Sarawakia (Bryopsida: Fissidentaceae). Bryologist 91:202-213.

_____ & **W. D. Reese. 1980.** The taxonomic status of the Nanobryaceae (Bryopsida). Bryologist 83:559-562.

Reese, W. D. 1985. Tropical lowland mosses disjunct between Africa and the Americas, including Calypothecium planifrons (Ren. & Par.) Argent, new to the Western Hemisphere. Acta Amazonia, Suplemento 15:115-121.

Robinson, H. 1970. Observations on the origin of the specialized leaves of Fissidens and Schistostega. Revue Bryologique et Lichénologique 37:941-947.

Salmon, E. D. 1899. On the genus Fissidens. Annals of Botany, London 13:103-130.

Sappa, F. & G. Piovano. 1947. La raccolta briologica dei Missionari della Consolata nel Kenya Tanganyka. (1 contributo, Sphagnaceae-Pottiaceae). Lavori dell' Istituto Botanico dell' Università di Torino 8:223-233.

Schultze-Motel, W. 1969. Nanobryaceae - ein neuer Name für eine Familie der Laubmoose. Willdenowia 3:385-387.

Spruce, R. 1881. The morphology of the leaf of Fissidens. Journal of Botany 19:98-99.

Stone, J. G. 1982. Nanobryum thornesbornei, a remarkable new moss from Australia. Journal of Bryology 12:199-208.

Touw, A. 1974. Some notes on taxonomic and floristic research on exotic mosses. Journal of the Hattori Botanical Laboratory 38:123-128.

Vitt, D. H. 1984. Classification of the Bryopsida. In: R. M. Schuster (ed.), New Manual of Bryology, volume 2, pp. 696-759. Nichinan.

Wijk, R. van der, et al. (eds.) 1962, 1969. Index Muscorum II and V. Utrecht.