

TAXONOMIC STUDIES IN THE AQUATIC MOSS GENUS
PLATYHYPNIDIUM (BRACHYTHECIACEAE)

A Thesis

by

JUSTIN WYNNS

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TAXONOMIC STUDIES IN THE AQUATIC MOSS GENUS
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JUSTIN WYNNS

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APPROVED BY:

Zack E. Murrell
Chairperson, Thesis Committee

Mary U. Connell
Member, Thesis Committee

William R. Buck
Member, Thesis Committee

Kenneth D. McFarland
Member, Thesis Committee

Steven W. Seagle
Chairperson, Department of Biology

Edelma Huntley
Dean, Graduate Studies and Research

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ABSTRACT

TAXONOMIC STUDIES IN THE AQUATIC MOSS GENUS *PLATYHYPNIDIUM* (BRACHYTHECIACEAE). (May 2006)

Justin Wynns, B. A., University of California – Santa Cruz.

M. S., Appalachian State University

Thesis Chairperson: Zack Murrell

The generic affinities of the aquatic moss genus *Platyhypnidium* were investigated by several analytic techniques: traditional light microscopy, phenetic analyses of dimensional measurements (Analysis of Variance and Principal Components Analysis), and phylogenetic analyses of morphological and molecular data. Ten rostrate-operculate Brachytheciaceae were closely studied. The internal transcribed spacer (ITS) region of the nuclear ribosomal DNA was used as a molecular marker in three of the phylogenetic analyses. *Platyhypnidium*, represented by *P. riparioides*, *P. aquaticum*, *P. muelleri*, *P. fuegianum*, and *P. pringlei*, was compared with five terrestrial species belonging to *Rhynchostegium* and *Eurhynchium*.

The taxa studied did not form a monophyletic lineage within the family. *Platyhypnidium* itself was resolved as polyphyletic. *Platyhypnidium aquaticum* and *P. riparioides* are closely related to terrestrial species of *Rhynchostegium*. *Platyhypnidium fuegianum* shares characteristics with both *Rhynchostegium* and *Eurhynchium*. *Platyhypnidium pringlei* is a congener of *Oxyrrhynchium hians*.

A genetic basis for recognition of *Platyhypnidium* was not identified. Molecular data indicated that some closely-related species of *Platyhypnidium* do not form a monophyletic lineage within the Brachytheciaceae, but are all related to species of *Rhynchostegium*. *Eurhynchium striatum*, the type species of *Eurhynchium*, was resolved sister to this monophyletic *Rhynchostegium* + *Platyhypnidium* lineage.

A genetic basis for recognition of *Oxyrrhynchium*, a segregate of *Eurhynchium*, was clearly identified. The new combinations *O. pringlei* and *O. selaginellifolium* are made. The relationship of *Oxyrrhynchium* to *E. striatum* and other species of *Eurhynchium* was not resolved. Problems of generic delimitation in the rostrate-operculate Brachytheciaceae are discussed.

Keywords: *Platyhypnidium*, Brachytheciaceae, ITS, phylogeny, moss

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INTRODUCTION

I. Systematic position of *Platyhypnidium*

Pleurocarpous mosses are characterized by reproductive structures which are borne laterally on stems rather than terminating stem apices. Apical growth of the plants is therefore indeterminate, and as a consequence, many pleurocarps have a prostrate or pendent habit, forming conspicuous mats. Since pleurocarpy is a broad term used to describe growth habit, not all mosses which might be termed “pleurocarpous” belong to a single lineage (La Farge-England 1996). However, a core group of pleurocarpous mosses, comprised of the two orders Hypnales and Hookeriales, is now widely accepted as a monophyletic taxon (superorder Hypnanae cf. Buck et al. 2005).

Pleurocarps are characteristic of angiospermous forests and may have speciated rapidly with the rise of flowering plants in the Cretaceous (Buck & Goffinet 2000). The Hypnanae are a very speciose, very closely related group of diminutive plants which only offer a limited number of morphological characters; consequently, morphological convergence among unrelated pleurocarpous lineages (homoplasy) is extremely common (Hedenäs 1998).

The Brachytheciaceae (Hypnales) are a well-circumscribed family of pleurocarps. The gametophytes are characterized by ovate to lanceolate or triangular, often plicate

leaves with single strong costae and fairly long cells. The sporophytes are characterized by rather short, somewhat inclined, usually asymmetric capsules, and they often have roughened setae. The plants generally occupy mesic, shaded habitats. A recent treatment of the family by Ignatov & Huttunen (2002) recognized 41 genera, and estimated that 250–350 species of Brachytheciaceae occur worldwide.

The position of the family within the Hypnales is not entirely clear. Fleischer (1923) claimed that the Brachytheciaceae were derived from the Cryphaeaceae through the Alsiaceae. He rejected his earlier view, shared by Loeske, that the family was derived from the Leskeaceae. Robinson, in his revision of the family for North America (1962), stated that the closest relatives of the Brachytheciaceae are the Thuidiaceae and the Amblystegiaceae. Vitt, in his “Classification of the Bryopsida” (1984), also placed them sister to the Amblystegiaceae. A close relationship with the Plagiotheciaceae (costa short and double) has also been postulated (Vitt 1984; Tsubota et al. 1999; Buck et al. 2000b), and this relationship is also supported by molecular data (Arikawa & Higuchi 1999; Buck et al. 2000a). Recent morphological (Buck 1994) and molecular studies (Huttunen & Ignatov 2004) place the Meteoriaceae, a family of epiphytic mosses, sister to the Brachytheciaceae.

The main genera of Brachytheciaceae were first described in the “Bryologia europaea” (Bruch et al. 1836–1855). Many species placed in the new genera *Brachythecium* Schimp. and *Rhynchostegium* Bruch & Schimp. had been previously described under the name *Hypnum* Hedw. (long used as a catchall name for any pleurocarpous moss). Some authors (e.g., Hampe 1863; Sullivant 1864) did not immediately accept the new generic names and continued to describe brachytheciaceous

mosses as species of *Hypnum*. The family Brachytheciaceae was given formal status by Schimper in 1876 (*vide* Ignatov & Huttunen 2002).

Rhynchostegium is a very homogenous genus of medium-sized to robust plants. The leaves are glossy, and sometimes bronzed or reddish. They are large and smooth, \pm concave, slenderly costate, and twisted medially when dry. Some species are distinctly complanate (e.g., *R. serrulatum* (Hedw.) A. Jaeger), but others are terete or even julaceous (e.g., *R. murale* (Hedw.) Schimp.). The leaf cells are long throughout. Gametophytically *Rhynchostegium* is very similar to *Brachythecium*, but the two genera can be separated by operculum shape: conic in *Brachythecium*, rostrate in *Rhynchostegium*. Additional differentiae from *Rhynchostegium* are the occurrence of biventrose plicae and/or distinctive alar cells in many species of *Brachythecium*. All species of *Rhynchostegium* are autoicous and have smooth setae. *Rhynchostegium confertum* (Hedw.) Schimp. was selected as the type species of the genus by Robinson in 1967.

Eurhynchium Bruch & Schimp. was first described in the “Bryologia europaea” in 1854, to include twelve species in two sections (*Eurhynchium* and *Oxyrrhynchium*). As suggested by the sectional split, species traditionally placed in *Eurhynchium* form a rather heterogenous assemblage. The genus may be broadly characterized by leaves with strong costae, rather short cells, and a few apical cells conspicuously truncated and dilated (this trait being more noticeable in the branch leaves). The costa frequently projects as a stout dorsal spine, and in many species the leaves are plicate or striate. Leaf size is totally variable. In contrast to *Rhynchostegium*, most species of *Eurhynchium* are dioicous, somewhat to distinctly heterophyllous, and/or have roughened setae. The genus was

lectotypified with *E. striatum* (Hedw.) Schimp. [= *E. longirostre* Schimp.] by Robinson in 1967.

Platyhypnidium M. Fleisch. was erected by Fleischer in 1923 to accommodate broad-leaved aquatic mosses with rostrate opercula. He included seventeen species in his original diagnosis, and placed the genus in the Amblystegiaceae, a family with many aquatic representatives. His concept was primarily based on the work of Loeske (1911), who saw strong generic ties between *R. rusciforme* (Brid.) Schimp. [syn. *P. riparioides* (Hedw.) Dixon] and *Hygrohypnum dilatatum* (Schimp.) Loeske, and he united them in the new genus *Platyhypnum* (*nom. illeg.*). Brotherus (1925) followed Fleischer's concept of the genus, omitting two of his names and adding six more. Many of these have since fallen into synonymy, mainly with *Platyhypnidium riparioides*, the most cosmopolitan and morphologically variable species of the genus.

Platyhypnidium riparioides is a very common moss on rocks in creeks in the eastern United States. It has a circumboreal distribution, and is also found in southern California, Mexico and Central America (McFarland 1994), the Kilimanjaro Mountains of Africa (Ochyra & Sharp 1988), Turkey, northern Iraq (Agnew & Vondracek 1975), and the Himalayas (Gangulee 1978). *Platyhypnidium muelleri* (A. Jaeger) M. Fleisch. is another widespread aquatic species found on wet rocks in and along watercourses in Java, Sumatra, Hawaii, and Papua New Guinea. Both species are recorded from Japan, China, and India.

Until recently most authors did not recognize *Platyhypnidium* at the genus level. Robinson (1962) was apparently the first to formally include *Platyhypnidium* in the Brachytheciaceae, as a subgenus of *Eurhynchium*. Crum (1969) called *Platyhypnidium* a

“weak segregate” of *Eurhynchium*. Many authors (e.g., Gangulee 1978, Crum & Anderson 1981, Noguchi 1991, Hedenäs 1992) recognized *Eurhynchium* and *Rhynchostegium*, but not *Platyhypnidium*. McFarland (1994) treated all three genera as *Rhynchostegium*. Buck (1998) used the name *Platyhypnidium* for *P. aquaticum* (A. Jaeger) M. Fleisch; and he designated *P. muelleri* lectotype of the genus. He suggested that *Platyhypnidium* is more closely related to *Rhynchostegium* than to *Eurhynchium*, on the basis of its tapering costa and autoicous sexuality.

Ignatov et al. (1998) studied scanning electron micrographs of the exostome of 63 species of Brachytheciaceae, including several rostrate-operculate taxa. While it does not appear that they found characters to consistently separate *Rhynchostegium* and *Eurhynchium*, they did find *Platyhypnidium* to be more or less distinct from both in having more massive teeth lacking delicate upper parts. Thicker, blunter teeth would be less susceptible to mechanical damage from running water, so in *Platyhypnidium* the peristome may have differentiated in response to the selective pressures of the aquatic environment.

Stech & Frahm's (1999a) systematic study of eight species of rostrate-operculate Brachytheciaceae based on *trnL*-F chloroplast and internal transcribed spacer (ITS) sequence data also argued for the recognition of the genus *Platyhypnidium*. However, the data set was quite small. In that study, two distinct clades were resolved: one containing *R. murale*, *R. rotundifolium* (Brid.) Schimp., *P. riparioides*, and *E. striatum*; and one containing *E. praelongum* (Hedw.) Schimp., *E. hians* (Hedw.) Sande Lac., and *E. pumilum* (Wils.) Schimp. The position of *Rhynchostegiella jacquinii* (Garov.) Limpr.

was not fully resolved, but it also appeared to belong to the latter clade. The *Rhynchostegium* + *E. striatum* clade was well supported by ITS data.

Ignatov & Huttunen, in their recent classification of the Brachytheciaceae based largely on molecular data (2002), recognized *Platyhypnidium* as a genus, to include *P. riparioides*, *P. muelleri*, *P. aquaticum*, and *P. pringlei* (Cardot) Broth., and also perhaps *E. fuegianum* Cardot. Buck (1998) questioned the specific distinctiveness of *P. aquaticum*, but also perceived enough difference between it and *P. riparioides* to reject Robinson's (1967) synonymy of these two taxa. Ignatov et al. (1999) noted the similarity between *P. aquaticum* and *P. muelleri*; more recently, Ignatov et al. (2005) claimed that *P. muelleri* and *P. riparioides* are not totally distinct.

Platyhypnidium pringlei is a Mexican species with ovate leaves and very strong costae that is disjunct to a small area of the Blue Ridge Mountains in eastern North America. The regular occurrence of Mexican and Guatemalan species as disjunct populations in the Southern Appalachians was discussed by Crum (1951). Such populations may be relicts of a Miocene flora which escaped glaciation in the sheltered coves of the mountains.

Eurhynchium fuegianum, an endemic of southern South America, was studied by Matteri & Ochyra (1989), who described the sporophytes for the first time. The correct generic placement of this species is somewhat puzzling, as it shares morphological characters with both *Eurhynchium* (a stout costa) and *Rhynchostegium* (autoicy), and like *Platyhypnidium*, it is aquatic. The new combination *Platyhypnidium fuegianum* (Cardot) Vanderpoorten, Ignatov, Huttunen & Goffinet was recently made based on a study combined morphological and molecular characters (Vanderpoorten et al. 2005).

In their molecular phylogeny of the Brachytheciaceae, Huttunen & Ignatov (2004) used both morphological characters and nucleotide sequence data (two chloroplast loci, *psbT*-H and *trnL*-F; and one nuclear locus, ITS2) to divide the family into four subfamilies: Brachythecioideae, Homalothecioideae, Rhynchostegioideae, and Rhynchostegielloideae. All six species of *Rhynchostegium* sampled were placed in Rhynchostegioideae. The genus *Eurhynchium* turned out to be severely polyphyletic, with traditional species of the genus scattered throughout the different subfamilies. *Eurhynchium pulchellum* (Hedw.) Jenn. was placed in the Homalothecioideae (as *Eurhynchiastrum pulchellum* (Hedw.) Ignatov & Huttunen); *Eurhynchium hians* in Rhynchostegielloideae (as *Oxyrrhynchium hians* (Hedw.) Loeske); *E. praelongum* in Brachythecioideae (as *Kindbergia praelonga* (Hedw.) Ochyra); and *E. striatum* in Rhynchostegioideae.

Platyhypnidium also appeared to be polyphyletic, as represented in their study by *P. riparioides*, *P. austrinum* (Hook. & Wilson) M. Fleisch. and *P. patulifolium* (Cardot & Thériot) Broth. *Platyhypnidium riparioides* was resolved in a nested position within *Rhynchostegium*; *P. austrinum* was resolved in the Rhynchostegielloideae, sister to a clade containing *Rhynchostegiella* (Schimp.) Limpr. and *Cirriphyllum* Grout; and *P. patulifolium* (a Chinese endemic) was also resolved in the Rhynchostegielloideae, close to *E. hians*, and sister to *Donrichardsia macroneuron* (Grout) H. A. Crum & L. E. Anderson. *Donrichardsia macroneuron* is an aquatic species with an unusually stout costa that had formerly been placed in the Amblystegiaceae (Crum & Anderson 1981). In fact, the close relationship of *P. patulifolium* and *D. macroneuron* led Ignatov

& Huttunen (2002) to suggest a transfer of the former species to *Donrichardsia*
H. A. Crum & L. E. Anderson.

Since it is now well established that certain morphologies are favored in aquatic environments (Vitt & Glime 1984), polyphyly in aquatic taxa should not come as such a surprise. As in other plants, mosses can change their phenotype in response to changing environmental conditions. For example, some amphibious species have different phenotypes depending on whether they are submerged or emergent (Zastrow 1934). Turbulent habitats like running water are expected to strongly favor certain phenotypes, leading to morphological similarity between unrelated taxa (convergent evolution). The problem of morphological convergence has led to much debate over the taxonomy of aquatic mosses. Herzog (1916) found the morphological similarity between some aquatic species of *Hygrohypnum* Lindb. (Amblystegiaceae) and *Oxyrrhynchium* (Schimp.) Warnst. (Brachytheciaceae) so striking as to make their placement in separate families problematic. Fleischer (1923) followed Loeske (1911) and included at least one species of *Hygrohypnum* in his original diagnosis of *Platyhypnidium*. The tendency of aquatic mosses to adopt convergent morphologies makes them ideal candidates for molecular analysis and other modern taxonomic methods (e.g., chemotaxonomy).

The species and varieties of *Platyhypnidium* which seem to be currently accepted are listed in Table 1. Not all of these are distinct; and some do not belong to *Platyhypnidium* in the typical sense. For instance, Fleischer described the seta in *Platyhypnidium* as smooth, but still included the rough-setaed *P. austrinum* [and *P. moorei* (Broth. & Geh.) M. Fleisch., a synonym] in the genus. Brotherus (1925) noted

this fact but did not exclude the species from the genus. *Platyhypnidium austrinum* is autoicous.

Brotherus' (1925) circumscription of the genus included twenty-one species. Nine of these names are still used. Three new species of *Platyhypnidium* were recently described by Ochyra; and he transferred four other taxa to the genus (Ochyra 1999; Ochyra & Bednarek-Ochyra 1999; Ochyra et al. 1998; Ochyra & Sharp 1988; Ochyra & Vanderpoorten 1999). A couple of these taxa are morphological oddities; none are widely distributed. A great number of forms and varieties of the morphologically plastic *P. riparioides* have been described (mostly under *Rhynchostegium rusciforme* or *Eurhynchium rusciforme* Milde). Podpera (1954) invalidated most of these by listing them as “formae et oecomorphae” of *P. riparioides*.

Table 1. Currently accepted species and varieties of *Platyhypnidium*.

<i>P. aquaticum</i> (A. Jaeger) M. Fleisch.
<i>P. austrinum</i> (Hook. & Wilson) M. Fleisch.
<i>P. brotheri</i> (Paris) Wijk & Margad.
<i>P. fuegianum</i> (Cardot) Vanderpoorten, Ignatov, Huttunen & Goffinet
<i>P. grolleanum</i> Ochyra & Bednarek-Ochyra
<i>P. hedbergii</i> (P. de la Varde) Ochyra & Sharp
<i>P. intermedium</i> Herzog
<i>P. lusitanicum</i> (Brid.) Ochyra & Bednarek-Ochyra
<i>P. mac-owanianum</i> (Müll. Hal.) M. Fleisch.
<i>P. muelleri</i> (A. Jaeger) M. Fleisch.
<i>P. muelleri</i> var. <i>minus</i> (Dixon)
<i>P. mutatum</i> Ochyra & Vanderpoorten
<i>P. obscurum</i> (Besch.) M. Fleisch.
<i>P. patulifolium</i> (Cardot & Thér.) Broth.
<i>P. peruviansense</i> (R. S. Williams) Ochyra
<i>P. pringlei</i> (Cardot) Broth.
<i>P. riparioides</i> (Hedw.) Dixon
<i>P. riparioides</i> var. <i>atlanticum</i> (Brid.)
<i>P. riparioides</i> var. <i>coreanum</i> (Cardot) Wijk & Margad.
<i>P. riparioides</i> var. <i>minus</i> (Wint.) Wijk & Margad.
<i>P. riparioides</i> var. <i>vulgare</i> Podp.
<i>P. subrusciforme</i> (Müll. Hal.) M. Fleisch.
<i>P. torrenticola</i> (Ochyra, C. Schmidt & Bültmann) Ochyra & Bednarek-Ochyra
<i>P. validum</i> (Herzog) Ochyra

II. Systematic techniques

The advent of DNA sequencing techniques represents a real breakthrough for pleurocarp systematics, because a new suite of characters has become available for evaluating the relationships among organisms. Molecular characters can provide insight into natural relationships among pleurocarpous mosses which may not be well resolved by morphological analysis.

Coding gene sequences from both nuclear (18S) and chloroplast (*rps4*) loci have been used to resolve the highest-level relationships among mosses, including *Sphagnum* L. and *Andreaea* Hedw. (Capesius & Stech 1997; Goffinet et al. 2001). At the ordinal level and above, many phylogenetic studies of mosses have obtained better resolution by adding *trnL*-F chloroplast DNA sequences, which include a non-coding intergenic spacer region (Cox & Hedderson 1999; Buck et al. 2000a; De Luna et al. 2000; La Farge et al. 2000). The *rbcL* chloroplast gene has also been broadly sampled (e.g., Maeda et al. 2000; Tsubota et al. 2002). Hyvönen et al. (1998) and Buck et al. (2005) combined morphological data with chloroplast and nuclear DNA sequences to resolve phylogenetic relationships within orders (Polytrichales and Hookeriales, respectively). However, the DNA sequences of these loci appear to be too highly conserved to be useful in phylogenetic reconstruction at lower taxonomic levels.

Baldwin (1992) was the first person to sequence the internal transcribed spacer (ITS) region of the ribosomal DNA in plants. Before this, 18S–26S rDNA sequences had been obtained for phylogenetic studies of primates (Gonzalez et al. 1990) and oomycetes (Lee & Taylor 1991), and it was noted that the highly-variable ITS region provided a lot of the resolution. Chiang & Schaal (1999) obtained the first ITS sequences for mosses,

testing the monophyly of a single species (*Hylocomium splendens* (Hedw.) Schimp.). Shaw (2000b) performed a population-level phylogenetic study of *Mielichhoferia elongata* (Hoppe & Hornsch.) Nees & Hornsch. and *M. mielichhoferiana* (Funck) Loeske using ITS sequences. Vanderpoorten et al. (2001) used ITS sequence data to test the monophyly of *Drepanocladus* (Müll. Hal.) G. Roth, *Campylium* (Sull.) Mitt. and *Amblystegium* Schimp. (Amblystegiaceae). Internal transcribed spacer data have been used in concert with chloroplast DNA sequences in higher-level phylogenetic studies of mosses (Shaw 2000a; Vanderpoorten et al. 2002a; Huttunen & Ignatov 2004). Internal transcribed spacer sequences have also been used in attempts to resolve the affinities of taxonomically troublesome species. For instance, Stech & Frahm (1999b, 2000, 2001) used ITS data to help place several odd aquatic species with bizarre morphologies into their correct genera and families. Vanderpoorten et al. (2003) used ITS in addition to three chloroplast loci to investigate the generic and familial relationships of some polystratose aquatic taxa.

DNA sequence data can be incorrectly aligned due to the bias of the researcher, but otherwise are non-subjective (therefore such data are very appropriate for phylogenetic studies). In contrast, the process of coding morphological data for cladistic analysis is very subjective, both in terms of character choice and character-state delimitation. Hedenäs (1998) pointed out two problems inherent to the cladistic study of pleurocarps using morphological data: 1) the difficulty of distinguishing between homology and convergence in pleurocarps; and 2) the rather artificial nature of character-state delimitation in such a morphologically plastic group. However, morphology is the fundamental basis for a classification of the mosses, and the utility of morphological data

in phylogeny reconstruction should not be underrated – merely approached with caution. Rohrer (1985) performed dual phenetic and phylogenetic analyses of the Hylocomiaceae and Rhytidiaceae using morphometric data. Because his study group included species belonging to several families, and he wanted to elucidate the affinities of some of the families as well, he used a very broad sampling of pleurocarpous mosses. While he was able to distinguish a large, monophyletic Hylocomiaceae (including Rhytidiaceae), he noted that a majority of the morphometric characters showed homoplasy, and that inferences drawn about evolutionary relationships based on such characters are open to question. Hedenäs (1994, 1995, 1997) also performed several cladistic analyses of pleurocarpous mosses based on morphological data. His data also showed very high levels of homoplasy; with consistency indices ranging from 0.17 to 0.66.

III. Goals of research

This study was designed to investigate the systematic position of certain aquatic mosses currently placed in the genus *Platyhypnidium*. First, I wanted to test the monophyly of the genus as represented by five species (those suggested by Ignatov & Huttunen, 2002): *P. riparioides*, *P. aquaticum*, *P. muelleri*, *P. pringlei* and *P. fuegianum*. Second, I wanted to verify that all five of these species are distinct. Third, I wanted to test the biological basis for recognition of the genus itself. Last, I wanted to identify the closest generic relative(s) of the *Platyhypnidium* lineage, presumed to be either *Rhynchostegium* or *Eurhynchium*. All of these objectives represent traditional problems in the taxonomy of the Brachytheciaceae that have not been resolved by microscopic study alone. Therefore, in addition to a general study of the plants using the light

microscope, I thought it appropriate to obtain other kinds of characters for this group (i.e., DNA sequence data). I was able to then perform cladistic analyses of morphological and molecular data, as well as phenetic analyses of dimensional differences among the taxa.

MATERIALS AND METHODS

One object of this research was to evaluate the natural relationships among the species under study using traditional methods: field collection and light microscopy. Over 400 herbarium specimens of Brachytheciaceae were studied, plus some closely related specimens for comparative purposes. Almost all of the specimens are listed under the taxonomic descriptions in the “Discussion” section. A portion of the specimens were collected in the field; most were borrowed from the herbaria of the New York Botanical Garden (NY), Duke University (DUKE), and the University of Tennessee at Knoxville (TENN). Two duplicate specimens of *Platyhypnidium pringlei* were kindly donated by Dr. Claudio Delgadillo of the Universidad Nacional Autonoma de Mexico (MEXU). Two collecting trips to the Southern Escarpment of the Blue Ridge Mountains of North and South Carolina (Southern Appalachians) in the summer of 2004 and the spring of 2005 yielded many of the specimens included in this study, particularly of *P. pringlei* and *P. riparioides*. Voucher specimens are in the herbarium of Appalachian State University (BOON) or in the author’s private herbarium. Duplicates of some specimens are deposited in the herbarium of the Highlands District Ranger Station, Nantahala National Forest, in Highlands, NC.

Dried plants were studied using a Leica ZOOM 2000 dissecting microscope and a Leica ATC 2000 compound microscope (Leica Microsystems, Wetzlar, Germany) fitted with an ocular micrometer. The micrometer was calibrated at the beginning of the study. Dry herbarium material was mounted in water, and small portions were dissected with forceps and a needle. Semi-permanent slides were made of many of the specimens (especially those included in the morphometric analysis; see below) by applying nail-polish to the corners of coverslips.

I. Morphometric techniques

Morphometric methods were applied to a subset (88) of the specimens, for several reasons: first, to obtain character-state data to use in a cladistic analysis of *Platyhypnidium* and other rostrate-operculate Brachytheciaceae; second, to identify taxonomic clusters based on phenetic similarity; third, to find statistically significant dimensional differences among taxa; and fourth, to generate descriptive statistics for these taxa. To satisfy all these criteria, it was necessary to collect two kinds of variables: character-state data (coded data), and measurements.

At least five collections each of *Eurhynchium hians*, *E. pulchellum*, *E. striatum*, *Platyhypnidium aquaticum*, *P. fuegianum*, *P. muelleri*, *P. pringlei*, *P. riparioides*, *Rhynchostegium murale* and *R. serrulatum* were included in the morphometric study (Appendix 1). Two collections each of *E. praelongum* and *R. confertum* were also included, as well as several collections of doubtful identity. One specimen of *E. angustirete* (Broth.) T. Kop. (*Klaus s. n.*, Austria) was mistakenly lumped with its sister species *E. striatum* in the Analysis of Variance (ANOVA). For most taxa, at least

two fertile specimens were included. An emphasis was placed on gametophytic characters because of their greater abundance, and because they were available for all specimens. Each specimen was treated as a separate Operational Taxonomic Unit (OTU) to ensure that infraspecific variation was not lost, to investigate the affinities of specimens of doubtful identity, and to maintain compatibility with the molecular component of this study. Three specimens of non-rostrate-operculate Brachytheciaceae were included as close outgroups, as well as one specimen of *Hygrohypnum eugyrium* (Schimp.) Loeske (Amblystegiaceae) as a distant outgroup. This seemed like a reasonable choice based on the possible sister relationship between the two families (Vitt 1984), and the fact that *H. eugyrium* is also obligately aquatic.

A. Measurement data

Leaf length, width, and costal length were measured for five 'typical' leaves of each specimen listed in Appendix 1. The lengths and widths of five basal cells, five median cells, and five apical cells were also taken. One of each cell type was measured on a single leaf (in nearly all cases). Basal cells close to the costa were chosen from the lowermost row which did not appear to be transitional to the stem epidermis (cells of the stem epidermis tend to be longer and more inflated than leaf cells). The uppermost non-marginal leaf cell was always used to represent the apical cell. Median cells were chosen at random, but from a flat and well-developed part of the lamina. An incomplete set of gametophytic measurements was taken for five specimens (indicated with an asterisk in Appendix 1), which were as a consequence excluded from the phenetic analyses.

When available, the lengths and widths of five capsules were also measured under low power on the compound microscope. Width was measured at the broadest point of the capsule. Length was measured along a median longitudinal line, from the usual bend that distinguishes the neck of the capsule, to the rim of the capsule mouth. If a distinct apophysis (basal swelling) was present, the swelling was included in the measurement, and the seta proper was deemed to begin below the swelling.

Length-to-width ratios were then calculated for each leaf, capsule and cell measured; costa length-to-leaf length ratios were also calculated for each leaf. Each set of five measurements or ratios (occasionally fewer if the set was incomplete) was then averaged, creating a final data set of fourteen gametophytic and three sporophytic characters based on leaf, cell and capsule measurements.

Principal Components Analysis

Statistical analyses of measurement data were performed using SAS v. 9.1.3 (SAS Institute Inc., Cary, NC). The data were determined to be normally distributed using the PROC MEANS and PROC UNIVARIATE procedures. Because different morphological features came in a wide variety of sizes (for example, leaf length was recorded in mm, but cell length in μm), it was necessary to standardize the data (i. e., convert it to a new data set with a mean = 0 and a standard deviation = 1) using the PROC STANDARD procedure. Principal Components Analysis (PCA) was then performed in two separate analyses on the measurement data to identify clusters of OTUs based on phenetic similarity. A few variables (e.g., costa length) were deemed to be insignificant or redundant, and were excluded from the analyses. One analysis (“PCA11”) included

eleven characters for 83 OTUs; whereas the other analysis (“PCA13”) included thirteen characters for 31 fertile OTUs. The characters are listed in Table 2. Principal Component Eigenvectors were generated using the PROC PRINCOMP procedure in SAS. For each analysis, the first Principal Component was plotted against the both the second and third Principal Components using the PROC GPLOT procedure and running the program in Enterprise Guide v. 3.0.1.396 (SAS Institute). To distinguish taxa in the PCA plots, each taxon was identified by a unique shape + color.

Principal Components Analysis was used to test several hypotheses in a general way:

1. *Platyhypnidium muelleri* and *P. aquaticum* are conspecific.
2. *Platyhypnidium aquaticum* and *P. riparioides* are distinct.
3. *Platyhypnidium muelleri*, *P. aquaticum* and *P. riparioides* form a tight-knit group which is close to, but distinct from, *Rhynchostegium*.
4. *Rhynchostegium murale*, *R. serrulatum*, and *R. confertum* are congeneric.
5. *Platyhypnidium fuegianum* is closely related to *E. striatum* and *E. pulchellum*.
6. *Eurhynchium angustirete* is not distinct from *E. striatum*.
7. Mexican and Southern Appalachian collections of *P. pringlei* are conspecific.
8. *Platyhypnidium pringlei* is more closely related to *E. hians* than it is to *P. riparioides*.
9. One specimen (*Buck 23824*, China; NY) identified as *R. murale* does not belong to that species, but rather to *P. pringlei*.
10. One dioicous specimen (*Bryant 1682*, Grand Canyon; NY) identified as *E. pringlei* (Cardot) H. A. Crum & L. E. Anderson does not belong to that species.

11. One specimen (*Schofield et al. 108026*, Alaska; TENN) identified as *E. pulchellum* does not belong to that species. I have identified this plant as *Bryhnia hultenii* Bartram *ex* Grout based on the description and illustrations in Takaki (Figure 32, 1956), Robinson (as *B. novae-angliae* (Sull.) Grout, Figure 189, 1962), and Noguchi (Figure 432.A,B; 1991). This julaceous Alaskan material falls outside my concept of *B. novae-angliae*.

Table 2. Continuous variables averaged for each specimen for use in Principal Components Analysis.

Gametophytic characters	Sporophytic characters
leaf length	capsule length
leaf width	capsule length : capsule width
leaf length : leaf width	
costa length : leaf length	
basal cell length	
basal cell width	
basal cell length : basal cell width	
median cell length	
median cell width	
apical cell length	
apical cell width	

Analysis of Variance

To identify dimensional differences which could be taxonomically informative in this study, I grouped the specimens by taxon, and then performed ANOVA on each of the averaged measured variables (14 gametophytic and 3 sporophytic characters). I used the PROC ANOVA procedure in SAS to perform the analyses, and to output visualizations of the distributional data in the form of box-plots. To improve the statistical power of the ANOVAs, only the ten species under intensive study were included in the analysis.

Several taxa that were measured and included in the PCA (e.g., *R. confertum*) were not included in the ANOVA.

The number of specimens included in ANOVA varied depending on the dimensional variable. For the capsule characters, 27 specimens were included in the analysis; for leaf length, leaf width, leaf length-to-width ratio, and median cell length, 74 specimens were included; and for the other ten variables, 69 specimens were included. I then performed pairwise comparisons (Tukey's test) to identify significant dimensional differences among the ten species ($P < 0.05$). Preliminary t-tests of morphometric data (not shown) did not identify any significant dimensional differences between Southern Appalachian and Mexican populations of *P. pringlei*, so these populations were treated as a single species in ANOVA. Two unusually large specimens named *E. pringlei* [*Sharp 5250, Guatemala* (TENN); *Bryant 1682, Grand Canyon* (NY)] which were included in the PCA were excluded from ANOVA, due to their isolated position in the Principal Component plots.

For 69 specimens, the first three Principal Component Eigenvectors were also tested for significant differences between species, and for each the distribution of each Eigenvector was visualized as a box-plot like in the other ANOVAs.

B. Character-state data

For each of 88 specimens (Appendix 1), 35 gametophytic and 12 sporophytic characters were studied, scored, and entered into a data matrix. For 49 specimens sporophytic characters were totally lacking. Sterile specimens were not scored for character 6 (sexual condition) unless they belonged to a consistently sterile taxon, e.g.,

P. pringlei. [Note: late in the course of this study, fertile material of *P. pringlei* from India was actually discovered at NY; but these specimens were not included in the morphometric analysis.] In a very few instances a score was omitted due to character-state ambiguity. No polarity was implied by the coding (i.e., no phylogenetic distinction was made between “0” and “1”). The matrix of coded data is presented in Table 3.

An enumeration of the characters used in the analysis follow, with rationales for the delimitation of character-states. Leaf character-states (in particular leaf shape, acumen shape, and leaf margin type) were determined using the illustrations of Noguchi (1991), Flowers (1973) and Ireland & Bellolio-Trucco (1987). Since ecological characters may be expected to show variation that is not genetic in origin, only one ecological character were included in the morphometric study.

Ecological character

1. Habit. *Obligate aquatic = 0; not obligate aquatic = 1.* While many mosses favor moist or periodically inundated habitats (ex.: *E. hians*), obligate aquatic taxa are never found away from running water.

Gametophytic characters

2. Complanation. *Plants distinctly flattened = 0; most stems not flattened = 1.*

Rhynchostegium serrulatum is a good example of a truly complanate species. Most other species show more or less tendency toward complanation (*E. hians*, more; *R. murale*, less).

3. Heterophylly. *Plants distinctly heterophyllous = 0; plants isophyllous, or weakly heterophyllous = 1.* In most cases, differentiation between branch and stem leaves is mainly a function of the age and thickness of the stem (McFarland, pers. comm.). As the stem ages and thickens, the leaf base must expand to accommodate its growth. However, in some species (*E. praelongum*), the heterophyllous condition is quite striking (in that species, the alar cells of stem-leaves can become strongly inflated to accommodate the expanding stem). A clear distinction between “stem” and “branch” leaves can only be made when the branches off of a primary stem are determinate in growth (resulting in plants that are distinctly pinnate). True heterophylly of this type is rare and is presumably a derived condition.

4. Frequency of branching. *Branches many = 0; branches few = 1.* In some species (e.g., *P. riparioides*) the branches are widely spaced along a toughened, stoloniferous primary stem; whereas in others (e.g., *E. pulchellum*), the branches are close and frequent, overall producing a more compact, less straggly plant. It is never difficult to assign a specimen to one state or the other. Frequency of branching may be influenced by the aquatic environment.

5. Morphology of branch tips. *Branches spreading-crispate at tips = 0; branch tips not crispate = 1.* This character separates *P. muelleri* and *P. aquaticum* from the other taxa in this study. These taxa have broadly ovate leaves with pinched apices, which gives the branch tips a flared, spreading, crispate appearance.

6. Sexual condition. *Synoicous* = 0; *autoicous* = 1; *dioicous* = 2; *phylloidioicous* = 3; *constantly sterile* = 4. This is a very stable character at the species level. For sterile specimens this character was treated as missing datum, except for constantly-sterile taxa like *P. pringlei* and its allies. In some cases sexual condition was used to aid in the identification of species. Phylloidioicy was ranked as a morphological condition distinct from normal dioicy.

7. Rhizoid morphology. *Rhizoids papillose* = 0; *rhizoids smooth* = 1. The rhizoids in this group are mostly superficially smooth. Occasionally the surface of thick older rhizoids can become somewhat papillose. The hyaline tips of young rhizoids can also appear vaguely papillose. In some taxa, the rhizoid cell-contents appear rather granular, whereas in most taxa the rhizoids are translucent. In this study, papillosity of rhizoids was not constantly observed for any species. In the Brachytheciaceae this character appears to be of little diagnostic value at the species or genus level.

8. Pseudoparaphyllium shape. *Pseudoparaphyllia mostly rounded* = 0; *pseudoparaphyllia mostly acuminate* = 1. In the Brachytheciaceae pseudoparaphyllia are frequently encountered surrounding the branch buds and branch bases; they are analogous to the bud scales of flowering plants. They are consistently ecostate and hyaline, with erose margins, and swollen, \pm discolored basal cells. Their shape is quite plastic. Initially, I established five categories of pseudoparaphyllium shape (“rounded”, “rounded-erose”, “apiculate”, “cucullate”, and “acuminate”). But I soon realized that the shapes I had created were artificial categories imposed upon a continuous morphological

spectrum. As I was reluctant to entirely abandon the record of pseudoparaphyllium shape, I assigned each specimen the commoner one of two states. In the most general sense, broad-leaved plants have pseudoparaphyllia which are rounded in outline, and narrow-leaved plants have pseudoparaphyllia which are acuminate in outline. Unfortunately, the pattern is inconstant, even on a single plant. Also, pseudoparaphyllia which are somewhat intermediate in shape between the two states are frequently encountered (e.g., broadly acuminate; or oblong-truncate).

9. Disposition of leaves. *Leaves appressed = 0; leaves erect (diverging on average $<30^\circ$ from the stem) = 1; leaves erect-spreading (on average $<45^\circ$) = 2; leaves wide-spreading (on average $>45^\circ$) = 3.* The leaves of any single plant diverge from the stem at varying angles (often in response to their physical location on the stem); but overall the degree to which the leaves spread is a regular diagnostic feature. To accommodate many distinctive phenotypes, it seemed practical to use several categories to describe the disposition of the leaves.

10. Homomally. *Plants homomalous = 0; plants heteromalous = 1.* Although many species of Brachytheciaceae (e.g., *Brachytecium plumosum* (Hedw.) Schimp.) have their leaves \pm turned to one side, among the rostrate-operculate Brachytheciaceae included in this study it was rare. Plants were coded as homomalous only when the condition was noticeable and consistent.

11. Leaf texture. *Leaves striate = 0; leaves striolate = 1; leaves plicate = 2; leaves smooth = 3.* The leaves of many species of Brachytheciaceae have longitudinal wrinkles or pleats. I tried to distinguish between smooth leaves and those which were plicate (with broad folds), striate (strongly wrinkled, or with narrow folds), or striolate (weakly wrinkled). I am somewhat dubious about the distinctiveness of all four states. For example, I doubt whether there is a significant difference between smooth leaves and leaves which are striolate. Leaves which appear striolate when dry tend to become smooth when moistened. Therefore, I tried to code leaf texture based on observations of the dry state. Likewise, the difference between plicae and striae is a bit subjective. However, the presence of plicae may be correlated with the next character; whereas the presence of striae is a permanent feature of the leaf. Therefore I maintained all four states as distinct.

12. Concavity of leaves. *Leaves deeply concave = 0; leaves plane or somewhat concave = 1.* The leaves of all Brachytheciaceae are somewhat concave. However, those of species like *E. pulchellum* are rather rigidly erect, whereas species like *R. murale* and *Scleropodium obtusifolium* (Mitt.) Kindb. have leaves which are distinctly and deeply concave. In general I had no difficulty assigning the leaves of the specimens to one state or the other.

13. Dry habit of leaves. *Leaves twisted medially dry = 0; leaves variously contorted dry, or little changed, but not with a median spiral twist = 1.* The leaves of some species, particularly aquatic taxa, become diagonally twisted across the middle when dry; in some

cases even becoming subulate above. In other species the leaves are flat or variously wrinkled but not twisted.

14. Thickness of costa. *Costa slender = 0; costa thicker = 1.* A classic feature of *Eurhynchium* is the possession of a stout costa which may be roughened on the back and usually protrudes as a dorsal spine. In *Rhynchostegium* the costa is much weaker, and it hardly protrudes; in *Platyhypnidium* the costa is long but relatively slender.

15. Taper of costa. *Costa tapered to apex = 0; costa little tapered = 1.* This character was employed to distinguish between a costa which thins out until it disappears and one which vanishes abruptly, or protrudes from the lamina.

16. Surface of costa. *Costa toothed dorsally = 0; costa scabrous = 1; costa smooth = 2.* In some taxa the costa is toothed or prorulose on the dorsal surface. It would be quite unusual for a weak costa to be roughened dorsally; but there are many specimens with stout costae that are smooth on the back.

17. Costa apex. *Costa not protruding = 0; costa protruding as a small prickle = 1; costa protruding as a stout spine = 2.* The tendency of the costa tip to project as a spine from the dorsal surface of the leaf lamina is a character which has been heavily exploited in attempts to classify *Eurhynchium* and other rostrate-operculate Brachytheciaceae. In several species (e.g., *P. riparioides*) the costa is fairly strong and the tip has a tendency to lie above the plane of the leaf. I do not consider this condition equivalent to the stout

projecting spine observed in, for example, *E. striatum*. Therefore I maintained three distinct states for this character.

18. Leaf shape. *Cordate or triangular* = 0; *lanceolate* = 1; *ovate-lanceolate* = 2; *oblong-lanceolate* = 3; *circular* = 4; *elliptical* = 5; *ovate* = 6; *oblong* = 7; *oblong-ovate* = 8. Although I included a large number of states for this character, I could not see any reasonable way to collapse them into fewer states without arbitrarily losing some of the real variation this character provides. For specimens with a highly variable leaf shape, I chose the predominate character-state. For heterophyllous taxa, I coded the shape of the best-developed branch leaves, which are usually similar to stem leaves that are not overdeveloped.

19. Symmetry of leaf. *Leaves symmetrical* = 0; *leaves asymmetrical* = 1. Originally an attempt to separate leaves which are secund from those which are straight, I thought that that distinction might be correlated with homomally. Therefore I merely measured whether the leaves tended to have an equal or an unequal amount of lamina on each side of the costa.

20. Acumination of leaf. *Leaf apex obtuse* = 0; *apex apiculate* = 1; *apex acute* = 2; *apex short-acuminate* = 3; *apex long-acuminate* = 4. Like leaf shape, a large number of categories were established to reveal taxonomically useful differences. It is awkward to call apices which are distinctly apiculate “obtuse”, etc. This character is predicted to have differentiated in response to environmental pressures.

21. Leaf apex. *Apex consistently twisted = 0; apex occasionally twisted = 1; apex flat = 2.* Some species, like *R. serrulatum* or *Bryhnia novae-angliae*, have leaf apices which are consistently twisted. In other species, like *P. riparioides*, the leaf apex shows a tendency to twist but is usually too short to actually do so. The tendency to twist does not seem to be correlated with the length of the acumen.

22. Disposition of leaf margin. *Margins plane = 0; margins recurved below = 1; margins recurved above in parts of many leaves = 2.* In most specimens, the leaf margin is narrowly recurved in the alar region as a consequence of its insertion. However, the margins of broad-leaved taxa may be entirely plane. Other taxa have a margin which is ± narrowly recurved throughout. In specimens with sharply serrate margins (e.g., *E. hians* or *E. pulchellum*), distal recurvature often results in flaring teeth. This effect is particularly noticeable in branch leaves.

23. Leaf margin. *Margins entire = 0; margins weakly to sharply serrulate or denticulate = 1; margins serrate or coarsely toothed = 2.* The degree of serration varies somewhat depending on environment, but is plastic only to a certain degree. A plant with subentire margins will never be conspecific with one with coarsely serrate margins.

24. Marginal cell walls. *Lower marginal cells somewhat incrassate = 0; lower marginal cells not incrassate = 1.* In some species (e.g., *E. hians*, *P. pringlei*) a region of supra-alar cells is distinguished by walls thicker than those of the main lamina. In

P. pringlei in particular, these incrassate marginal cells give the suggestion of a leaf border (Crum & Anderson 1981).

25. Leaf decurrency. *Leaves not decurrent = 0; leaves noticeably decurrent = 1.* Stem leaves are usually much more decurrent than branch leaves in the Brachytheciaceae, and the presence of small decurrencies in stem leaves was not considered significant. However, in a few species, broad decurrencies are diagnostic (e.g., *Brachytecium rivulare* Schimp.; *E. praelongum*).

26. Demarcation of alar cells. *Outer alar cells abruptly delimited from basal cells = 0; outer alar cells confluent with basal cells = 1.* The alar cells are not a distinctive feature of the taxa included in this study. Mostly they are oblong and somewhat wider than adjacent cells; otherwise they are not much differentiated. The illustrations of the alar cells of *R. riparioides* (Hedw.) Cardot and *R. pringlei* Cardot in McFarland (1994) are typical. In most cases the outer alar cells grade imperceptibly into a region of somewhat incrassate, usually \pm porose basal leaf cells. But in some cases the outer alars are sharply distinct from the basal cells (and usually inflated, as in the stem leaves of *E. praelongum*).

27. Alar differentiation. *Alar cells not differentiated = 0; alar cells differentiated = 1.* Although the alar cells are poorly defined in most specimens, only one specimen showed an almost total lack of alar differentiation.

28. Alar cell walls. *Alar cells incrassate = 0; alar cells somewhat incrassate = 1; walls of alar cells not thickened = 2.* In general the walls of alar cells are less incrassate than those of adjoining basal cells; instead the alar cells are usually \pm enlarged. I investigated this character to see if any taxa consistently produce incrassate alar cells. The alar cells of older stem leaves invariably have thicker walls than those of 'typical' leaves. Although the distinctions are fine, three character-states were perceptible.

29. Porosity of alar cells. *Alar cells porose = 0; alar cells somewhat porose = 1; walls of alar cells not porose = 2.* A strongly porose condition seems more significant; whereas slight porosity is the natural effect of the cells being confluent with the basal cells, which are generally porose. However, I chose to maintain three distinct states for this character.

30. Relative size of alar cells. *Alar cells enlarged = 0; alar cells not enlarged = 1.*

Although the alars are usually enlarged to some extent, especially in breadth, I wanted to know if consistent enlargement might be taxonomically informative. Since many specimens had alar cells which were somewhat incrassate (and therefore distinct) though not particularly enlarged, I was able to assign characters to one state or the other with relative ease.

31. Appearance of alar cells. *Alar cells opaque-granular = 0; alar cells not opaque-granular = 1.* In some taxa (e.g., *Brachythecium laetum* (Brid.) Schimp.) the alar cells have a peculiar, grayish, granular, opaque appearance. This is a very difficult character

to assess and I have little confidence in its taxonomic utility. It is also possible that the opaque-granular condition is not well preserved in the herbarium.

32. Basal cell walls. *Basal cells somewhat incrassate = 0; basal cells not incrassate = 1.*

Incrassate basal cells were distinguished from basal cells without wall thickenings.

33. Porosity of basal cell walls. *Basal cell walls porose = 0; basal cell walls not distinctly porose = 1.* The porose nature of the basal and supra-basal cell walls is very distinctive in some species (e.g., *E. striatum*). Indeed, in some specimens all the laminal cells have a vaguely porose quality.

34. Apical laminal cells. *Apical cells truncate = 0; apical cells expanded = 1; apical cells not differentiated = 2.* In many species of Brachytheciaceae (e.g., *E. hians*, or *B. digastrum* Macoun & Kindb.) the apical cells of the leaf are abruptly short and broad. In other species the apical cells are short but not expanded (e.g., *P. riparioides*); and in still others they are basically undifferentiated (e.g., *R. serrulatum*).

Sporophytic characters

35. Seta surface. *Seta smooth = 0; seta roughened = 1.* This is one of the most reliable characters provided by the sporophyte. In some species, like *E. praelongum*, the seta is coarsely prorate. There was no ambiguity about this character for the specimens included in the morphometric study.

36. Operculum shape. *Operculum conic* = 0; *operculum short-rostrate* = 1; *operculum long-rostrate* = 2. All the main species included this study have a rostrum which is essentially long. Indeed, it is the single morphological feature that unites the species I included in my study. In the morphometric study a single specimen of *Hygrohypnum eugyrium* that was explicitly chosen as an outgroup had a conic operculum. I maintained three character-states so that any species showing plasticity in this respect would be identified.

37. Annulus. *Annulus strongly differentiated* = 0; *annulus poorly differentiated* = 1; *annulus not differentiated* = 2. In the Brachytheciaceae the absence of an annulus is apparently derived, most species having a well-developed annulus of 2-3 rows of cells (Huttunen & Ignatov 2004).

38. Disposition of capsule. *Capsule erect* = 0; *capsule slightly inclined* = 1; *capsule strongly inclined* = 2. The degree to which the capsules are inclined varies to some extent on a single specimen, but (like the disposition of the leaves) tends to be rather consistent and diagnostic overall for any particular species.

39. Exothecial cells. *Exothecial cells distinctly collenchymatous* = 0; *exothecial cells not or irregularly collenchymatous* = 1. In many species of Brachytheciaceae the exothecial cell walls are irregularly thickened, and those just below the capsule mouth can be ± collenchymatous. No species included in this study possesses exothecial cells as

strikingly collenchymatous as in *Sematophyllum* Mitt., but in some species the exothecial cells do have corner-thickenings.

40. Outer surface of endostome. *Endostome smooth* = 0; *endostome papillose* = 1.

The surface ornamentation of the endostome is very seldom mentioned in the literature, and then generally in reference to a particular species. In the publications that I have seen only Grout characterized the surface texture of the endostome for entire genera. He described the segments of *Brachythecium* (1897) and *Eurhynchium* (1898) as “granulose-roughened above”.

41. Length of endostome. *Endostome shorter than exostome* = 0; *endostome and*

exostome ± equal in length = 1; *endostome longer than exostome* = 2. For each

specimen, I evaluated whether the endostome teeth seemed to be shorter, equal to, or

longer than the exostome. The taxonomic utility of this character was not known, and

therefore the use of this character was experimental. In many mosses there is a tendency

for reduction of the exostome (Hedenäs 1995).

42. Perforation of endostome. *Segments narrowly perforate* = 0; *segments with gaping*

perforations = 1. Although there is some variability in this character, in some species the

endostome segments are much more widely perforate than in others.

43. Cilium length. *Cilia rudimentary* = 0; *cilia short* = 1; *cilia long* = 2. When well-

developed, well-preserved capsules are studied, cilium length is a reliable diagnostic

character. Unfortunately there is a tendency for the cilia to become broken in older capsules and herbarium material. Therefore, a record of the presence of long cilia may be considered more dependable than a record of their absence. I tried to observe fully-developed, undamaged cilia before assigning a specimen to one state or another. Endostome cilia were never entirely absent in the taxa included in this study.

44. Number of cilia. *Cilia mostly single = 0; cilia mostly paired = 1; cilia mostly in groups of three = 2.* In the rostrate-operculate Brachytheciaceae, two or three cilia are typically present between each endostome segment. The number of cilia between each segment varies in a single specimen. Because of the high variability of this character, in this study specimens were coded according to the state which was most prevalent. Solitary cilia (which were very unusual) seemed to arise by the reduction or physical degradation of adjacent cilia, or from the basal fusion of a pair of cilia (in which case the solitary cilium was extra stout). There seems to be a correlation between the number of cilia and the degree to which the endostome is developed generally. For example, *P. riparioides*, which has very long well-developed cilia, is the the only species in this study with the cilia frequently occurring in groups of four.

45. Development of projections at end walls of cilia. *Cilia not appendiculate = 0; appendiculate cilia present = 1.* The extent to which the end walls of cilia develop varies, but the possession of appendiculate cilia is distinctive. In some species (e.g., *P. aquaticum*), the cilia are never appendiculate. Thus two character-states may be distinguished: either a plant has the ability to produce appendiculate cilia (1) or it does

not (0). But since a species capable of producing appendiculate cilia may not always have them, this character may be undependable and is of questionable utility in a phylogenetic analysis. The difference between nodose and appendiculate cilia is very clearly rendered in McFarland (Figure 6, 1988).

Excluded characters

46. Surface of cilia. *Cilia smooth = 0; cilia papillose = 1.* This character seems to be correlated with character 40 and was therefore excluded.

47. Relative size of apical cell area. *Differentiated apical cells filling supracostal area = 1; filling about 1/2 the leaf length = 2; apical cells differentiated in more of a thin border = 3.* If differentiated apical cells are present, they occupy a different amount of the acumen depending on the species. However, the relative proportion of the supracostal area occupied by these distinctive apical cells may be diagnostic in itself, although the meaning of the character-state changes considerably depending on whether the costa is short or long.

Table 3. Data matrix of 45 morphological characters for 88 specimens included in phylogenetic analyses of *Platyhypnidium*. Characters in boldface, numbered as in text; question marks represent missing data.

Taxon	Coll. number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Brachythecium rivulare</i>	Buck 14068	0	1	2	1	1	?	1	1	1	0	0	0	0	0	0	2	0	2	1	3	2	0	1
<i>Bryhnia hultenii</i>	Schofield et al. 108026	1	1	2	0	1	?	1	0	0	1	0	0	1	0	0	2	1	0	0	2	2	1	1
<i>Eurhynchium angustirete</i>	Klaus s. n.	1	1	1	0	1	2	1	1	2	1	0	1	1	1	1	0	2	0	1	2	1	1	2
<i>E. fuegianum</i>	Buck 41017	0	0	1	0	1	1	1	0	2	1	1	0	0	1	1	0	2	0	1	2	2	1	1
<i>E. fuegianum</i>	Buck 41055	0	1	2	0	1	?	1	0	3	1	1	1	0	1	0	1	1	6	1	3	2	0	1
<i>E. fuegianum</i>	Buck 41073	0	1	2	0	1	1	0	0	2	1	1	1	0	1	1	0	1	2	0	2	2	1	1
<i>E. fuegianum</i>	Buck 41081	?	1	2	0	1	1	1	0	2	1	0	1	0	1	0	1	1	2	1	3	1	1	1
<i>E. fuegianum</i>	Buck 41162	0	1	2	0	1	?	1	1	2	1	1	1	0	1	1	1	1	6	1	0	1	1	1
<i>E. fuegianum</i>	Matteri 4202	0	1	2	0	1	1	1	0	2	1	1	1	0	1	0	1	0	2	1	2	1	1	1
<i>E. fuegianum</i>	Schäfer-Verwimp & Verwimp 8004	0	1	1	0	1	1	1	0	3	1	1	1	0	1	0	1	1	6	1	3	1	2	1
<i>E. hians</i>	Amtoft 2005b	1	1	0	0	1	?	1	1	3	1	1	1	1	1	1	0	2	2	1	2	1	2	2
<i>E. hians</i>	Gay s. n.	1	1	0	0	1	2	1	1	2	1	1	1	1	1	1	0	2	2	1	3	2	1	2
<i>E. hians</i>	Mosses of USSR 70	1	0	2	0	1	2	1	1	3	1	1	1	0	1	1	1	2	2	1	3	2	2	2
<i>E. hians</i>	Standley 5848	1	0	1	0	1	2	0	1	3	1	0	1	1	1	1	0	2	2	1	3	2	2	2
<i>E. hians</i>	Stebel 576/97	1	0	0	0	1	2	1	1	3	1	1	1	0	1	1	0	2	2	1	3	1	2	2
<i>E. hians</i>	Whitehouse 26870	0	1	0	1	1	2	1	0	2	1	1	1	1	1	1	0	2	2	1	2	2	1	2
<i>E. hians</i>	Wynns 326	1	1	2	0	1	2	0	1	3	1	1	1	1	1	1	0	2	2	0	2	2	2	2
<i>E. hians</i>	Wynns 622	1	1	0	0	1	2	1	1	2	1	1	1	0	1	1	0	2	2	1	2	2	1	2
<i>E. hians</i>	Zander 470	1	1	0	0	?	2	?	?	2	1	3	0	?	1	1	0	2	2	?	3	2	2	2
<i>E. praelongum</i>	Jenkins s. n.	1	1	0	0	1	2	1	1	2	1	1	1	0	1	1	0	2	0	1	3	1	1	2
<i>E. praelongum</i>	Wynns 646	1	1	0	0	1	2	1	1	2	1	1	1	0	1	1	0	2	0	1	3	1	1	2
<i>E. pulchellum</i>	Anderson 20865	1	1	0	0	1	?	1	1	1	1	0	1	1	?	1	1	1	1	?	3	1	2	2
<i>E. pulchellum</i>	Anderson 27753	1	1	0	0	1	?	1	1	1	1	0	1	1	1	1	0	2	1	1	3	2	2	2
<i>E. pulchellum</i>	Buck 15378	1	1	1	0	1	3	1	1	1	1	0	1	1	1	1	1	2	2	1	3	2	2	2
<i>E. pulchellum</i>	Hakelier s. n.	1	1	1	0	1	?	1	0	2	1	1	1	1	1	1	0	2	2	1	2	2	2	2
<i>E. pulchellum</i>	Pittillo 9804	1	1	0	0	1	?	0	?	1	1	0	1	1	1	1	1	2	1	1	?	2	2	2
<i>E. pulchellum</i>	Shevock 17526	1	1	2	0	1	?	1	1	2	1	0	1	1	1	1	0	2	1	1	4	1	2	2
<i>E. pulchellum</i>	Wynns 615	1	1	1	0	1	3	1	0	2	1	0	1	1	1	1	0	2	1	1	2	2	2	2
<i>E. pulchellum</i>	Zander 470	1	1	?	0	1	3	0	?	2	1	0	1	1	1	1	0	2	1	?	2	1	2	2
<i>E. pulchellum</i>	Zartman 1282	1	1	0	0	1	?	0	?	2	1	0	1	1	1	1	1	2	1	1	?	3	2	2
<i>E. selaginellifolium</i>	Hoe 3385	0	0	2	1	1	4	1	1	2	1	1	1	0	1	1	2	2	8	1	3	2	0	1
<i>E. selaginellifolium</i>	Hoe 4296	0	0	1	1	1	4	1	1	2	0	1	1	0	1	0	2	1	6	1	2	2	0	1
<i>E. striatum</i>	Buck 15078	?	1	1	0	1	2	0	1	2	1	0	1	1	1	1	0	2	0	1	3	1	1	2
<i>E. striatum</i>	Eggers et al. 21	1	1	1	0	1	?	1	1	2	1	2	1	1	1	1	0	2	0	1	3	1	1	2
<i>E. striatum</i>	Holmen 045	?	1	2	0	1	2	1	0	2	1	2	1	1	1	1	0	2	0	1	3	1	2	2
<i>E. striatum</i>	Schleicher s. n.	?	1	2	0	1	2	1	0	2	1	0	1	1	1	1	0	2	0	1	3	1	2	2
<i>E. striatum</i>	Schofield 104756	1	1	2	0	1	?	1	1	2	1	0	1	1	1	1	0	2	2	1	3	2	1	2
<i>E. striatum</i>	Seth s. n.	?	1	1	0	1	2	1	0	3	1	0	1	1	1	1	1	2	0	1	4	1	1	2
<i>E. striatum</i>	Vasak s. n.	?	1	2	0	1	2	1	0	3	1	2	1	1	1	1	0	2	0	1	4	1	2	2

Taxon	Coll. number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Hygrohypnum eugyrium</i>	Wynns 392	0	1	2	0	1	1	1	1	2	1	3	0	1	0	0	2	0	3	1	3	1	1	0
<i>Oxyrrhynchium</i> sp. 2	Buck 23824	0	1	2	1	1	4	1	1	2	1	1	1	0	1	0	2	0	2	1	2	2	0	1
<i>Platyhypnidium aquaticum</i>	Buck 39450	0	1	1	1	0	1	1	1	2	1	1	1	0	0	0	2	0	6	1	0	2	1	1
<i>P. aquaticum</i>	Buck 7962	0	0	2	1	0	1	1	1	2	1	1	1	0	0	0	1	1	6	1	0	2	0	1
<i>P. aquaticum</i>	Musci Amazonici et Andini 1422	0	1	2	1	0	1	1	1	2	1	1	1	0	0	0	2	0	6	1	0	1	0	1
<i>P. aquaticum</i>	Price et al. 1673	0	1	1	1	1	1	1	1	2	1	1	1	0	0	0	2	0	6	1	0	2	0	1
<i>P. aquaticum</i>	Ramirez P. 2760	0	1	2	1	0	1	1	0	2	1	2	1	1	0	0	2	0	6	1	2	1	0	1
<i>Platyhypnidium muelleri</i>	Motley 311	0	1	2	1	0	1	1	0	1	1	1	1	1	0	0	2	0	6	1	1	1	0	1
<i>P. muelleri</i>	Musci Frondosi Arch. Indici 95	0	1	1	1	0	1	1	1	3	1	3	1	0	0	0	2	0	6	1	1	2	1	1
<i>P. muelleri</i>	Musci Japonici 771	0	1	2	1	0	?	1	0	3	1	1	0	0	0	0	2	0	4	1	1	2	0	1
<i>P. muelleri</i>	Musci Japonici Exsic. 1316	0	1	2	1	0	?	1	1	2	1	3	1	0	0	0	2	0	6	0	2	2	0	1
<i>P. muelleri</i>	G. L. Smith J-951	0	1	2	0	0	1	1	0	2	1	1	1	1	0	0	2	0	6	1	2	1	0	1
<i>P. muelleri</i>	Wu 21163	0	1	2	1	0	?	1	1	3	1	1	1	0	0	0	2	1	6	1	0	2	0	1
<i>P. muelleri</i>	Yates 2992	0	0	2	1	0	?	1	0	2	1	1	1	0	0	0	2	1	6	1	1	0	1	1
<i>P. pringlei</i>	Bryant 1682	0	1	2	1	1	2	1	1	2	1	1	1	0	1	0	1	1	0	1	2	2	1	1
<i>P. pringlei</i>	Delgadillo 6044	0	1	2	1	1	4	1	1	2	1	1	1	0	1	0	2	1	2	1	2	1	1	1
<i>P. pringlei</i>	Delgadillo 6045	0	1	2	1	1	4	?	1	3	1	1	1	0	1	0	2	1	2	1	2	2	0	1
<i>P. pringlei</i>	Hill & Heaton 23469	0	0	1	1	1	4	1	1	1	0	2	1	1	1	0	2	6	1	2	2	2	1	1
<i>P. pringlei</i>	Pringle 10434	?	1	2	1	1	4	1	1	2	1	1	1	0	1	1	2	1	6	1	2	2	2	1
<i>P. pringlei</i>	Sharp 5250	0	1	2	1	1	4	1	1	2	1	0	1	1	1	0	1	1	6	1	2	0	1	1
<i>P. pringlei</i>	Wynns 488	0	0	1	1	1	4	1	1	2	0	1	1	0	1	1	0	2	2	1	3	2	1	2
<i>P. pringlei</i>	Wynns 546	0	1	1	1	1	4	1	0	2	0	1	1	0	1	1	1	1	2	1	2	2	1	1
<i>P. pringlei</i>	Wynns 568	0	1	2	1	1	4	1	1	1	0	1	1	0	1	1	1	1	2	1	3	1	1	1
<i>P. pringlei</i>	Zartman & Pittillo 240	0	1	2	1	1	4	1	0	1	0	1	1	0	1	1	2	1	6	1	3	2	1	1
<i>P. pringlei</i>	Zartman & Pittillo 454	0	1	1	1	1	4	1	1	1	0	1	1	0	1	1	2	1	2	1	3	2	1	1
<i>P. riparioides</i>	Allen 10659	0	1	2	1	1	1	1	0	2	1	2	1	0	0	0	2	0	6	1	2	2	0	1
<i>P. riparioides</i>	Anderson 24061	?	1	2	0	1	1	1	0	2	1	3	1	0	0	0	2	1	6	1	2	2	1	1
<i>P. riparioides</i>	Buck 35187	?	1	2	1	1	1	1	0	3	1	2	1	0	1	0	2	1	6	0	2	2	0	1
<i>P. riparioides</i>	Keith 4	0	1	2	1	1	?	1	0	2	1	3	0	0	0	0	2	1	6	1	1	2	0	1
<i>P. riparioides</i>	Matuda s. n.	?	1	2	1	1	1	1	0	2	1	3	1	1	0	0	2	1	6	1	2	2	0	1
<i>P. riparioides</i>	Small 74	?	0	1	0	1	1	1	1	2	1	2	1	0	0	0	1	1	6	1	2	2	1	1
<i>P. riparioides</i>	Wynns 240	0	1	2	1	1	?	1	0	2	1	1	1	0	0	0	2	0	6	0	2	2	0	1
<i>P. riparioides</i>	Wynns 241	0	1	2	1	1	?	1	0	3	1	1	1	0	0	0	2	0	5	0	2	1	0	1
<i>P. riparioides</i>	Wynns 274	0	1	2	1	1	1	1	0	3	1	2	1	0	0	0	2	0	6	0	2	2	0	1
<i>P. riparioides</i>	Wynns 574	0	1	2	1	1	1	1	0	1	1	1	0	0	0	0	2	1	6	0	2	2	0	1
<i>Rhynchostegium confertum</i>	Gradstein 853	1	1	2	0	1	1	1	1	1	1	3	0	0	0	0	2	0	3	1	2	2	0	1
<i>R. confertum</i>	Long 7448	1	1	2	0	1	1	1	1	1	1	2	1	0	0	0	2	0	2	1	3	1	1	1
<i>R. murale</i>	Aptroot 2849	1	1	2	0	1	1	1	0	1	1	2	0	1	0	0	2	1	5	1	1	2	1	0
<i>R. murale</i>	Aptroot 9745	?	1	2	0	1	1	1	0	2	1	1	0	1	0	0	2	0	5	1	2	2	1	1
<i>R. murale</i>	Musci Macr. Merid. Polon. Ex. 1091	1	0	2	0	1	1	1	0	1	1	2	0	1	0	0	2	0	8	0	1	2	1	1
<i>R. murale</i>	Musci Macr. Merid. Polon. Ex. 1137	1	1	2	0	1	1	0	0	1	1	3	0	0	0	0	2	0	8	0	1	2	1	1
<i>R. murale</i>	Ochyra 713/82	1	0	2	0	1	1	0	0	1	1	3	0	1	0	0	2	0	8	0	1	2	1	1
<i>R. rusciforme</i> var. <i>lutescens</i>	Schleicher s. n.	0	1	1	1	1	1	1	?	2	1	1	1	?	0	0	2	0	1	1	4	0	1	1

Taxon	Coll. number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Rhynchostegium serrulatum</i>	Buck 45007	?	0	2	0	1	1	1	1	3	1	3	1	1	0	0	1	1	2	1	4	0	1	1
<i>R. serrulatum</i>	D. K. Smith & Davison 194	1	0	2	1	1	1	1	1	3	1	3	1	0	0	0	0	1	2	1	4	0	2	1
<i>R. serrulatum</i>	Wynns 175	1	0	1	0	1	1	1	1	2	1	2	1	1	0	0	2	0	2	1	4	0	1	1
<i>R. serrulatum</i>	Wynns 296	1	0	2	0	1	1	1	1	3	1	1	1	1	0	0	2	0	1	1	4	0	1	1
<i>R. serrulatum</i>	Wynns 428	1	0	2	1	1	1	1	1	3	1	0	1	0	0	0	2	0	1	1	4	0	2	1
<i>Scleropodium obtusifolium</i>	Buck 30299	0	1	2	0	1	2	1	0	1	1	2	0	1	0	0	2	0	7	1	1	2	0	0

Taxon	Coll. number	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Brachythecium rivulare</i>	Buck 14068	1	1	1	1	2	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>Bryhnia hulthenii</i>	Schofield et al. 108026	1	1	0	1	2	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>Eurhynchium angustirete</i>	Klaus s. n.	0	0	0	1	1	1	0	1	0	0	0	0	2	0	2	1	1	1	1	2	2	1
<i>E. fuegianum</i>	Buck 41017	0	0	1	1	1	1	1	1	0	0	0	0	2	1	1	0	1	1	1	0	1	0
<i>E. fuegianum</i>	Buck 41055	0	0	1	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>E. fuegianum</i>	Buck 41073	0	0	1	1	0	1	1	1	0	0	0	0	2	1	0	0	?	1	1	?	?	?
<i>E. fuegianum</i>	Buck 41081	0	0	1	1	0	1	1	1	0	0	0	0	?	0	1	0	1	0	1	1	1	?
<i>E. fuegianum</i>	Buck 41162	0	0	1	1	1	1	1	1	0	0	2	0	?	?	?	?	?	?	?	?	?	?
<i>E. fuegianum</i>	Matteri 4202	0	0	0	1	0	1	0	1	0	0	0	0	2	0	?	0	1	1	0	1	2	0
<i>E. fuegianum</i>	Schäfer-Verwimp & Verwimp 8004	0	0	0	1	1	1	1	1	0	0	0	0	2	0	1	0	1	0	1	0	2	0
<i>E. hians</i>	Amtoft 2005b	1	0	1	1	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Gay s. n.	0	0	1	1	0	0	1	1	0	0	1	1	1	0	2	1	1	2	1	2	2	1
<i>E. hians</i>	Mosses of USSR 70	1	0	1	1	1	0	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Standley 5848	1	0	1	1	1	1	0	0	0	0	1	1	2	0	2	1	1	?	1	1	?	0
<i>E. hians</i>	Stebel 576/97	1	1	1	1	0	2	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Whitehouse 26870	1	0	1	1	2	2	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Wynns 326	0	0	0	1	0	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Wynns 622	1	0	1	1	0	1	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. hians</i>	Zander 470	0	1	?	1	0	1	?	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. praelongum</i>	Jenkins s.n.	1	1	1	1	2	2	0	1	1	1	1	1	?	0	2	1	1	1	1	2	1	0
<i>E. praelongum</i>	Wynns 646	1	1	1	1	1	1	0	1	0	1	1	1	?	0	2	1	1	1	0	1	1	0
<i>E. pulchellum</i>	Anderson 20865	0	0	1	1	0	?	?	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. pulchellum</i>	Anderson 27753	1	0	0	1	1	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. pulchellum</i>	Buck 15378	1	0	1	1	1	0	1	1	0	0	1	0	2	0	1	1	1	1	1	1	1	0
<i>E. pulchellum</i>	Hakelien s. n.	1	1	1	1	1	1	1	0	0	0	1	0	2	0	2	1	1	2	1	2	2	0
<i>E. pulchellum</i>	Pittillo 9804	0	0	?	1	?	0	?	0	?	0	1	0	2	0	1	1	1	?	?	?	?	?
<i>E. pulchellum</i>	Shevock 17526	0	1	1	1	1	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. pulchellum</i>	Wynns 615	1	0	1	1	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. pulchellum</i>	Zander 470	0	0	?	1	1	?	?	0	0	0	1	0	2	?	?	1	1	?	?	?	?	0
<i>E. pulchellum</i>	Zartman 1282	0	0	?	1	0	?	?	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. selaginellifolium</i>	Hoe 3385	0	0	1	1	1	2	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. selaginellifolium</i>	Hoe 4296	1	0	1	1	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?

Taxon	Coll. number	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>E. striatum</i>	Buck 15078	1	0	0	1	0	0	0	0	0	0	2	0	?	?	?	?	?	?	?	?	?	?
<i>E. striatum</i>	Eggers et al. 21	1	1	0	1	1	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>E. striatum</i>	Holmen 045	0	0	0	1	0	0	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>E. striatum</i>	Schleicher s. n.	0	0	0	1	1	2	0	1	0	0	1	0	2	0	1	1	1	1	1	2	2	1
<i>E. striatum</i>	Schofield 104756	1	0	0	1	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>E. striatum</i>	Seth s. n.	0	0	0	1	1	1	0	1	0	0	0	?	0	1	1	?	?	?	?	?	?	?
<i>E. striatum</i>	Vasak s. n.	1	0	0	1	0	0	0	0	1	0	2	?	?	?	?	?	?	?	?	?	?	?
<i>Hygrohypnum eugyrium</i>	Wynns 392	1	0	0	1	0	2	0	1	0	0	0	0	0	0	2	1	1	1	0	2	2	0
<i>Oxyrrhynchium</i> sp. 2	Buck 23824	1	0	0	1	2	2	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>Platyhypnidium aquaticum</i>	Buck 39450	1	0	0	1	2	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. aquaticum</i>	Buck 7962	1	0	0	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. aquaticum</i>	Musci Amazonici et Andini 1422	1	0	1	1	2	1	0	1	1	0	0	2	0	1	1	1	2	0	1	1	0	0
<i>P. aquaticum</i>	Price et al. 1673	1	0	0	1	2	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. aquaticum</i>	Ramirez P. 2760	1	0	0	1	2	1	0	1	0	0	0	?	0	1	1	1	2	0	1	1	0	0
<i>Platyhypnidium muelleri</i>	Motley 311	1	0	0	1	1	1	0	1	0	0	0	2	0	2	1	1	2	0	1	1	0	0
<i>P. muelleri</i>	Musci Frondosi Arch. Indici 95	1	0	0	1	0	1	0	1	0	0	0	?	?	?	1	1	1	1	0	2	0	0
<i>P. muelleri</i>	Musci Japonici 771	1	0	1	1	2	1	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>P. muelleri</i>	Musci Japonici Exsic. 1316	1	0	1	1	2	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. muelleri</i>	G. L. Smith J-951	1	0	1	1	1	2	0	1	0	1	0	2	0	1	1	1	1	0	1	1	0	0
<i>P. muelleri</i>	Wu 21163	1	0	1	1	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. muelleri</i>	Yates 2992	1	0	1	1	1	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Bryant 1682	1	0	1	1	2	2	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Delgadillo 6044	1	0	0	1	2	2	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Delgadillo 6045	1	0	0	1	2	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Hill & Heaton 23469	0	1	1	0	1	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Pringle 10434	0	1	1	1	1	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Sharp 5250	1	0	1	1	1	1	0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Wynns 488	0	1	1	1	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Wynns 546	0	1	1	1	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Wynns 568	0	0	1	1	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Zartman & Pittillo 240	0	1	1	1	0	2	0	1	0	1	2	?	?	?	?	?	?	?	?	?	?	?
<i>P. pringlei</i>	Zartman & Pittillo 454	0	1	1	1	1	2	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Allen 10659	0	0	0	1	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Anderson 24061	0	0	1	1	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Buck 35187	1	0	1	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Keith 4	0	0	1	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Matuda s. n.	1	0	1	1	1	1	0	1	0	1	0	2	0	1	1	1	1	1	2	2	1	1
<i>P. riparioides</i>	Small 74	1	0	1	1	1	0	0	1	0	0	0	2	0	2	1	?	?	?	?	?	?	?
<i>P. riparioides</i>	Wynns 240	1	0	1	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Wynns 241	1	0	1	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. riparioides</i>	Wynns 274	1	0	1	1	1	0	0	1	1	0	0	?	0	1	1	1	2	1	1	2	1	1
<i>P. riparioides</i>	Wynns 574	1	0	1	1	1	0	0	1	0	0	0	2	0	1	1	1	0	1	2	2	0	0

Taxon	Coll. number	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Rhynchostegium confertum</i>	Gradstein 853	1	0	1	1	1	1	0	1	0	0	0	0	2	0	1	1	1	1	1	2	1	0
<i>R. confertum</i>	Long 7448	0	0	1	1	1	1	0	0	0	0	2	0	2	0	2	1	1	1	0	2	2	0
<i>R. murale</i>	Aptroot 2849	1	0	1	1	1	0	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>R. murale</i>	Aptroot 9745	0	0	1	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	1	2	2	1
<i>R. murale</i>	Musci Macr. Merid. Polon. Ex. 1091	1	0	1	1	2	1	0	0	0	0	0	0	2	0	1	1	1	0	0	2	2	0
<i>R. murale</i>	Musci Macr. Merid. Polon. Ex. 1137	1	1	1	1	2	1	0	0	1	0	0	0	?	0	1	?	?	?	?	?	?	?
<i>R. murale</i>	Ochyra 713/82	1	0	1	1	1	1	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?
<i>R. rusciforme</i> var. <i>lutescens</i>	Schleicher s. n.	1	1	0	1	0	2	0	1	0	0	2	0	?	0	1	1	1	1	1	1	2	0
<i>R. serrulatum</i>	Buck 45007	1	0	1	1	1	1	0	1	0	0	2	0	2	0	2	1	1	1	0	2	1	0
<i>R. serrulatum</i>	D. K. Smith & Davison 194	1	0	1	1	1	0	0	0	0	0	0	0	2	0	2	1	1	1	0	2	2	0
<i>R. serrulatum</i>	Wynns 175	1	0	1	1	2	0	1	0	0	0	2	?	?	?	?	?	?	?	?	?	?	?
<i>R. serrulatum</i>	Wynns 296	1	0	0	1	1	1	1	0	0	0	2	?	?	?	?	?	?	?	?	?	?	?
<i>R. serrulatum</i>	Wynns 428	1	0	1	1	1	1	0	1	0	0	2	?	?	?	?	?	?	?	?	?	?	?
<i>Scleropodium obtusifolium</i>	Buck 30299	1	0	0	1	0	0	0	1	0	0	0	1	?	?	?	1	?	?	?	?	?	?

II. Molecular techniques

Seventy-four dried herbarium specimens of Brachytheciaceae were selected for DNA isolation. These specimens are listed in Appendix 2. One aim of this study was to assess the intraspecific variation present in the ITS region; therefore, several specimens of each species were chosen for DNA extraction. From each specimen, ca. 40 mg of green leafy branches were removed with forceps under a dissecting microscope, to exclude debris and other bryophytes growing intermixed in the specimen from the sample. Samples were ground in liquid nitrogen using a glazed ceramic mortar and pestle. DNA was isolated from the pulverized samples using a DNeasy Plant Mini extraction kit (Qiagen Inc., Valencia, Calif.) following the manufacturer's instructions, with the following modifications: a) 450 μ L of lysis buffer (AP1 buffer) were used instead of 400 μ L; b) the lysate was incubated at 65°C for 30 minutes instead of ten minutes; and c) DNA was incubated on the DNeasy Mini Spin column for ten minutes instead of five minutes before the final elution. These modifications for extracting DNA from dried plant material were suggested by Drábková et al. (2002). After some initial experimentation, DNA extracts of varying concentrations were obtained in a single 100 μ L elution step. The success of each extraction was verified by gel electrophoresis in 1% agarose gels. DNA concentration in the extract solutions was not quantified.

A region of nuclear ribosomal DNA (hereafter known as the ITS region) which includes the 3' end of the 18S RNA gene, the 5' end of the 26S RNA gene, the 5.8S RNA gene, and internal transcribed spacers 1 & 2 was amplified by polymerase chain reaction (PCR) using a GeneAmp PCR System 9700 thermocycler (Applied Biosystems, Foster City, Calif.). The protocol was modeled after Shaw (2000b). All PCR reactions were run

with a negative control as a check for contamination. An initial amplification was performed in a 25 μ L reaction volume containing 1 \times PCR buffer, 0.2 mM dNTPs in equimolar ratio, 2.5 mM MgCl₂, 0.5 units *Taq* polymerase, and 0.5 mM each of BMBC-R and LS4-R primers (Table 4). PCR buffer, salt solution, dNTPs and *Taq* polymerase were all obtained from a Sigma PCR CORE kit (Sigma-Aldrich, St. Louis, Mo.). Stock DNA (0.3 μ L) was added to each reaction as a template. Thirty cycles of amplification were performed with the following temperature profile: 95°C for one minute, 50°C for one minute, and 95°C for 45 seconds plus an additional five seconds for each successive cycle. A final seven-minute extension at 72°C was performed at the end. The amplification products were kept at 4°C until they could be screened on 1.2% agarose gels. In most cases a single PCR product was obtained, of about 1300 base pairs (bp) in length. When successful, PCR products were cleaned and concentrated into 20 μ L of Tris-EDTA (TE) buffer using Montage PCR filters (Millipore Corp., Bedford, Mass.). In a few cases more than one distinct product was obtained (Appendix 2); in such cases the products were frozen and stored for later purification. If little or no signal was obtained, 1 μ L of the reaction product was used as template in a second round of amplification. In some cases the same primers were used in this second round, yielding PCR products of the same length; but in other cases (Appendix 2), 0.5 μ M ITS1 and ITS4 primers (Table 4) were used in place of BMBC-R and LS4-R; the products of those reactions were about 800 bp in length. In a very few cases (Appendix 2), a third round of amplification was performed using 1 μ L of the second-round product as template and one or the other of the primer pairs. The longer products (i.e., those obtained by the first pair of primers) were preferentially sought (although this turned out not to matter, because the 18S and 26S

rDNA regions represented at the end of the amplification products were so highly conserved across all sequences). When the products of these amplifications were successful, these were also cleaned and concentrated in $1\times$ TE buffer to a volume of 20 μ L. All cleaned PCR products were screened again on 1.2% agarose gels prior to sequencing.

Table 4. Primer sequences used for amplifying the ITS1–5.8S–ITS2 rDNA region.

Forward	
BMBC-R	5'–GTACACACCGCCCGTCG–3'
ITS1	5'–TCCGTAGGTGAACCTGCGG–3'
Reverse	
LS4-R	5'–TCAAGCACTCTTTGACTCTC–3'
ITS4	5'–TCCTCCGCTTATTGATATGC–3'

D-rhodamine dye-terminator cycle sequencing was performed using the ABI Prism Big Dye Terminator cycle sequencing kit v. 3.1 (Applied Biosystems) and 5 μ L of clean PCR product as template. In some cases, less product was used, and replaced with micro-filtered PCR water (Appendix 2). Each 10- μ L reaction also contained 4 μ L of $0.75\times$ Big Dye reagent and 1 μ L of primer (0.625 μ M). The primers ITS1 and ITS4 were used in separate sequencing amplifications. In most cases (Appendix 2), replicate reactions were also performed for each PCR product, giving four or more replicate sequences per product overall. After the thermocycler was warmed to 80°C for five minutes, the following thermal profile was used to perform the sequencing reaction in 30 cycles: 96°C for ten seconds, followed by 50°C for five seconds, followed by 60°C for four minutes. Changes between critical temperatures were performed at a fixed rate of

1°C / sec. In most cases the sequencing products were cleaned by ethanol precipitation and dehydration, following the manufacturer's instructions. Sequencing products were run on an ABI Prism 3100 automated sequencer (Applied Biosystems) at the University of Tennessee Molecular Biology Research Facility.

Sequence chromatograms were compiled using ContigExpress software (a component of Vector NTI Suite 9.0.0, InforMax, Inc., Frederick, Md.) to produce consensus sequences based on replicate nucleotide identifications from both DNA strands. All consensus sequences were then aligned manually in MacClade v. 4.06 (Maddison & Maddison 2003). To reduce the possibility of misalignment due to ambiguity, an additional 45 ITS sequences from different species of Brachytheciaceae (Table 5) were obtained from GenBank (<http://www.ncbi.nih.gov>) and added to the MacClade data matrix. For most of the phylogenetic analyses these sequences were not used; however, their utility in resolving ambiguities in the alignment was appreciable. A majority of these sequences were available thanks to the recent study by Huttunen & Ignatov (2004). In addition, one sequence of *P. riparioides* var. *atlanticum* (Brid.) from a waterfall in Germany (Frahm s. n., Allerheiligen, Baden-Württemberg, 1 Sep 1997; BONN) was added to the matrix manually from a published sequence (Stech & Frahm 1999b). The total data matrix contained complete or partial sequences of the ITS region from 106 collections of Brachytheciaceae plus one collection of *Hygrohypnum luridum* (Hedw.) Jenn. (Amblystegiaceae), which was included as outgroup taxon in some analyses.

Table 5. ITS sequences from GenBank that were added to the primary data matrix for sequence alignment purposes. For species marked with an asterisk, a complete sequence was available.

Species	Accession number	Reference
<i>Aerobryum speciosum</i>	AF403619	Huttunen & Ignatov 2004
<i>Aerolindigia capillacea</i>	AF395634	Huttunen & Ignatov 2004
<i>Brachytheciastrum olympicum</i>	AY952446	Vanderpoorten et al. 2005
<i>Brachythecium acuminatum</i>	AF403654	Huttunen & Ignatov 2004
* <i>B. appleyardiae</i>	AY654619	Vanderpoorten et al. 2005
<i>B. geheebii</i>	AF403660	Huttunen & Ignatov 2004
<i>B. laetum</i>	AY166445	Huttunen & Ignatov 2004
* <i>B. salebrosum</i>	AY654609	Vanderpoorten et al. 2005
<i>B. velutinum</i>	AF403667	Huttunen & Ignatov 2004
<i>Bryhnia novae-angliae</i>	AF403588	Huttunen & Ignatov 2004
<i>B. novae-angliae</i>	AF403665	Huttunen & Ignatov 2004
<i>Bryoandersonia illecebra</i>	AF403626	Huttunen & Ignatov 2004
<i>Cirriphyllum cirrosum</i>	AF403641	Huttunen & Ignatov 2004
<i>C. piliferum</i>	AF403608	Huttunen & Ignatov 2004
<i>Clasmatodon parvulus</i>	AF403614	Huttunen & Ignatov 2004
<i>Donrichardsia macroneuron</i>	AF167350	Vanderpoorten et al. 2002b
<i>Eurhynchiopsis eustegium</i>	AF403602	Huttunen & Ignatov 2004
<i>Eurhynchium angustirete</i>	AF403621	Huttunen & Ignatov 2004
<i>E. crassinervium</i>	AF403668	Huttunen & Ignatov 2004
<i>E. pulchellum</i>	AF395635	Huttunen & Ignatov 2004
<i>E. pumilum</i>	AF230986; AF231001	Stech & Frahm 1999a
<i>E. striatulum</i>	AY166450	Huttunen & Ignatov 2004
<i>E. striatum</i>	AF230985; AF231000	Stech & Frahm 1999a
<i>Homalotheciella subcapillata</i>	AF403658	Huttunen & Ignatov 2004
<i>Homalothecium aureum</i>	AF403650	Huttunen & Ignatov 2004
<i>H. lutescens</i>	AF403642	Huttunen & Ignatov 2004
<i>H. sericeum</i>	AF403587	Huttunen & Ignatov 2004
* <i>Hygrohypnum luridum</i>	AF168137	Vanderpoorten et al. 2002b
<i>Kindbergia praelonga</i>	AY654610	Vanderpoorten et al. 2005
<i>Myuroclada maximowiczii</i>	AF403625	Huttunen & Ignatov 2004
* <i>Okamuraea hakoniensis</i>	AY568552	Li, Du & Wu unpublished
<i>Oxyrrhynchium vagans</i>	AF403652	Huttunen & Ignatov 2004
<i>Palamocladium euchloron</i>	AF403623	Huttunen & Ignatov 2004
<i>P. leskeoides</i>	AF403596	Huttunen & Ignatov 2004
<i>Platyhypnidium austrinum</i>	AY166449	Huttunen & Ignatov 2004
<i>P. riparioides</i>	AF403594	Huttunen & Ignatov 2004
<i>Pseudoscleropodium purum</i>	AF403663	Huttunen & Ignatov 2004
<i>Rhynchostegiella jacquinii</i>	AF403569	Huttunen & Ignatov 2004
<i>R. jacquinii</i>	AF230987; AF231002	Stech & Frahm 1999a
<i>Rhynchostegium psilopodium</i>	AF403643	Huttunen & Ignatov 2004
<i>R. rotundifolium</i>	AF230984; AF230999	Stech & Frahm 1999a
* <i>Scleropodium cespitans</i>	AY654614	Vanderpoorten et al. 2005
* <i>S. obtusifolium</i>	AY173520	Shaw et al. 2003
* <i>S. touretii</i>	AY173519	Shaw et al. 2003
* <i>S. touretii</i>	AY654611	Vanderpoorten et al. 2005
<i>Scorpiurium deflexifolium</i>	AF403599	Huttunen & Ignatov 2004

III. Cladistic analyses

Four cladistic analyses (heuristic search) were performed using PAUP* v. 4.0b10 software (Swofford 2002), on an iMac G5 personal computer. In three of the analyses, maximum parsimony (MP) was used as the optimization criterion; in the fourth, maximum likelihood (ML) was used. In all analyses, characters and character-states were unweighted.

First, I performed a MP analysis of the 45-character morphological data matrix for 85 taxa (Table 3). Preliminary analyses (not shown) revealed that inclusion of three specimens for which I had collected morphometric data [*Brachythecium rivulare* (Buck 14068; NY), *Bryhnia hultenii* (Schofield 108026; TENN), and *Hygrohypnum eugyrium* (Wynns 392; BOON)] significantly reduced the resolution of the resulting topologies; consequently, these three specimens were excluded. Bootstrap values (100 replicates) were generated and added to the strict consensus tree. No more than 20,000 equally-parsimonious trees were saved for any one replicate.

Next, I performed an MP analysis of a strictly molecular data set of 47 sequences from the entire ITS region (hereafter the ITS analysis), with *Hygrohypnum luridum* as outgroup. To obtain better resolution of the cladogram, eight GenBank sequences (as indicated by an asterisk in Table 5) plus one additional sequence of *P. riparioides* var. *atlanticum* (Frahm s. n., Allerheiligen) were added to a core set of 38 unique sequences obtained in the course of this study. Bootstrap values (1000 replicates) were generated and added to the strict consensus tree. No limit was placed on the number of equally-parsimonious trees saved, and branch swapping was allowed to proceed to completion.

For 45 specimens both morphological and molecular data were available; so a third MP analysis of combined morphological and molecular data was performed on that subset. The analysis of combined data was also bootstrapped (1000 replicates) and swapping went to completion.

Last, to survey the greater range of variation present in the family, I performed a ML analysis in PAUP* of only the 5.8S–ITS2 region (hereafter the ITS2 analysis) on a 70-taxon data set comprised of 41 GenBank sequences and 29 original sequences. Likelihood was chosen as the optimality criterion for the analysis of ITS2 after several parsimony analyses failed to proceed to completion (instead saving a steadily increasing number of equally parsimonious trees). In those tests, paring down the number of taxa included in the analysis from 70 to 50 had no effect. This may be because all three of the distinct but ambiguously-related clades found in the ITS analysis (Figure 6) were still well represented in the 50-taxon data set.

Based on the Akaike Information Criterion, the TIM+I+G model of sequence evolution was selected using Modeltest 3.7 (Posada & Crandall 1998), with base frequencies A = 0.1416, C = 0.3070, G = 0.3308, T = 0.2206; and substitution rate matrix $R(A-C) = 1.0000$, $R(A-G) = 1.5657$, $R(A-T) = 0.6269$, $R(C-G) = 0.6269$, $R(C-T) = 2.5326$, $R(G-T) = 1.0000$. The assumed proportion of invariable sites was set to 0.2995 and the rate heterogeneity among sites was assumed to follow a gamma distribution with a shape parameter (α) of 0.3203. The starting tree for the likelihood analysis was obtained by random stepwise addition in PAUP*.

RESULTS

I. Phenetic analyses

Two kinds of phenetic analyses were performed using measurement data from 87 specimens of Brachytheciaceae plus one specimen of *Hygrohypnum eugyrium*. Principal Components Analysis was performed on an 83-specimen data set to cluster specimens based on the similarity of their Principal Component scores (Eigenvectors), and Analysis of Variance was performed on a 60-specimen data set of only the ten main taxa (*Platyhypnidium riparioides*, *P. aquaticum*, *P. muelleri*, *P. pringlei*, *P. fuegianum*, *Eurhynchium striatum*, *E. hians*, *E. pulchellum*, *Rhynchostegium serrulatum*, and *R. murale*), to identify significant dimensional differences between them.

Principal Components Analysis

Eigenvectors generated by PCA are presented in Table 6. For each analysis, the cumulative variation accounted for by each successive Principal Component is also given.

For each OTU in PCA13, the first Principal Component score (PC 1) was plotted against both the second score (PC 2; Figure 1) and the third score (PC 3; Figure 2). For each OTU in PCA11, the same scores were plotted against each other (Figures 3 and 4). In both analyses, *P. riparioides*, *P. aquaticum* and *P. muelleri* formed a cluster (hereafter

Table 6. Eigenvectors generated by Principal Components Analysis. For each analysis, the cumulative variation accounted for by each successive Principal Component is indicated at the bottom of the column.

PCA 13															
species	number	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	
angustirete	Klaus s. n.	-0.159	2.599	0.077	0.415	-0.579	-1.093	-0.573	-0.271	0.162	-0.130	-0.119	0.214	-0.116	
aquaticum	Musci Amazonici et Andini 1422	-0.589	-0.280	-0.805	-0.418	-1.532	-0.421	0.437	0.167	0.457	-0.126	-0.351	-0.088	-0.013	
aquaticum	Ramírez P. 2760	0.567	2.353	0.774	0.015	-0.922	-0.352	0.412	-0.088	0.389	-0.130	0.028	0.181	0.094	
confertum	Gradstein 853	0.391	-2.568	0.793	1.072	0.085	0.511	0.653	1.242	0.088	-0.057	0.404	0.226	0.010	
confertum	Long 7448	-0.075	-2.038	-0.934	0.933	-1.668	-0.786	-0.516	-0.714	-1.130	-0.173	-0.160	-0.041	0.052	
fuegianum	Buck 41017	-1.591	1.196	-0.245	-1.237	0.695	-0.420	-0.310	0.388	-1.063	0.237	-0.229	-0.044	0.032	
fuegianum	Buck 41073	-1.915	0.267	0.240	-0.653	-0.338	-0.559	-0.294	0.854	0.839	-0.383	-0.335	-0.072	-0.023	
fuegianum	Buck 41081	-1.822	-0.535	0.566	-0.092	-0.824	-0.119	-0.586	0.636	0.899	0.512	-0.228	0.076	0.128	
fuegianum	Matteri 4202	-1.492	0.086	-0.403	-0.387	0.822	-0.231	0.211	0.250	-0.665	0.179	-0.093	-0.110	0.015	
fuegianum	Schäfer-Verwimp & Verwimp 8004	-0.694	0.662	0.200	-0.297	1.732	0.560	0.287	0.338	0.363	0.275	0.352	-0.017	0.096	
hians	Gay s. n.	-0.931	0.632	-0.003	-0.315	1.722	0.341	0.320	-0.300	0.141	0.303	-0.276	-0.047	0.097	
hians	Standley 5848	-2.083	-0.061	-0.107	1.175	-0.008	0.432	0.080	-0.031	0.155	0.373	-0.044	-0.007	0.008	
Hygrohypnum eugyrium	Wynns 392	-1.158	-1.363	3.993	-2.906	0.425	0.660	-0.900	-1.091	-0.367	-0.726	0.116	0.037	0.023	
muelleri	Motley 311	2.590	1.408	-1.740	-1.168	1.296	-0.060	0.581	0.424	0.055	-0.884	0.372	-0.034	0.000	
muelleri	Musci Frondosi Arch. Indici 95	2.397	0.509	-2.359	-2.405	-1.219	-0.034	0.834	0.049	-0.577	0.253	0.126	0.114	-0.044	
muelleri	G. L. Smith J-951	-0.199	1.081	0.210	0.773	-1.387	1.846	1.480	-0.576	-0.654	0.054	0.425	-0.057	0.068	
murale	Aptroot 9745	0.231	-2.098	0.430	-0.521	-0.327	1.923	-0.136	0.680	-0.005	0.164	-0.104	0.061	-0.158	
murale	Musci Merid. Macr. Polon. Ex. 1091	0.192	-1.829	-0.675	-1.121	-0.975	0.304	0.273	-1.338	1.436	0.199	0.144	-0.079	0.096	
praelongum	Jenkins s. n.	-2.255	-2.546	-1.716	-0.491	0.525	-1.425	-0.227	-0.064	0.358	0.278	0.399	0.078	-0.047	
praelongum	Wynns 646	-4.430	-0.317	-0.480	1.243	0.126	-0.357	0.905	-0.537	-0.110	-0.189	0.115	-0.137	-0.148	
pulchellum	Buck 15378	-1.934	-0.096	0.150	1.222	1.301	0.760	-0.220	0.248	0.052	-0.197	0.082	0.022	-0.141	
pulchellum	Hakelier s. n.	-2.089	-0.545	0.361	0.814	0.312	-0.252	0.758	-0.288	-0.353	-0.310	-0.750	0.051	0.005	
riparioides	Matuda s. n.	1.503	0.589	-2.270	0.984	0.804	0.759	-0.282	-0.003	0.287	-0.828	-0.554	0.059	0.137	
riparioides	Small 74	0.410	0.323	-0.199	-1.408	-1.412	0.275	-0.929	1.568	-0.361	-0.025	0.086	-0.202	-0.001	
riparioides	Wynns 274	1.115	0.682	-2.276	0.417	1.132	0.464	-1.647	-0.793	0.112	0.429	0.390	-0.038	-0.010	
riparioides	Wynns 574	1.326	1.270	-0.502	0.126	-0.459	1.031	-0.840	-0.765	-0.256	0.288	-0.265	0.109	-0.144	
ruscifforme var. lutescens	Schleicher s. n.	5.265	-0.456	1.665	-0.988	1.189	-1.089	1.134	-0.263	0.407	0.515	-0.436	-0.076	-0.139	
serrulatum	Buck 45007	3.380	-3.269	0.172	1.268	0.432	-1.399	-0.222	-0.016	-0.659	-0.268	0.294	0.017	0.069	
serrulatum	G. L. Smith & Davison 194	4.640	-0.101	1.632	2.417	-0.290	0.564	-0.541	0.203	0.120	0.170	-0.240	-0.139	0.022	
striatum	Schleicher s. n.	0.229	2.376	1.568	1.192	-0.856	-0.908	-0.190	-0.069	0.649	-0.403	0.669	-0.110	-0.077	
striatum	Seth s. n.	-0.819	2.070	1.881	0.340	0.196	-0.926	0.045	0.159	-0.769	0.600	0.180	0.054	0.109	
cumulative variation		0.338	0.515	0.654	0.758	0.833	0.887	0.923	0.953	0.979	0.990	0.999	0.999	1.000	

PCA 11

species	number	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
angustirete	Klaus s.n.	0.189	-0.974	1.520	0.861	-0.551	-0.894	-0.406	0.023	-0.144	-0.015	0.180
aquaticum	Buck 39450	0.329	-1.011	0.442	-1.607	-1.320	-0.174	-0.076	0.364	0.838	-0.059	0.041
aquaticum	Buck 7962	5.804	-2.437	-0.772	-0.833	0.434	-0.953	-0.593	-0.971	-0.085	0.412	0.432
aquaticum	Musci Amazonici et Andini 1422	-0.439	-0.092	-0.505	-0.573	-1.349	-0.172	0.379	-0.095	-0.328	-0.072	-0.073
aquaticum	Price et al. 1673	2.204	-0.983	-0.331	0.414	0.220	0.850	0.055	-0.326	-1.077	0.018	-0.059
aquaticum	Ramírez P. 2760	1.022	-0.464	1.393	-0.262	-0.495	-0.530	0.123	-0.135	-0.163	0.101	0.076
Brachythecium rivulare	Buck 14068	-0.399	-1.151	-2.361	0.442	-1.187	0.440	-0.933	0.083	0.912	0.428	-0.256
Bryhnia hultenii	Schofield et al. 108026	-0.076	-2.040	-1.067	-2.760	0.227	-1.339	-0.875	-0.469	-0.329	0.119	0.049
confertum	Gradstein 853	0.160	2.322	-1.642	0.079	0.592	0.597	1.021	-0.475	-0.102	0.046	0.238
confertum	Long 7448	-0.210	0.951	-1.859	0.329	-1.050	-0.923	-1.438	-0.091	-0.052	0.125	-0.111
fuegianum	Buck 41017	-1.495	-0.509	1.972	-0.462	0.429	-0.449	0.114	0.176	-0.026	0.077	-0.108
fuegianum	Buck 41055	-1.609	-0.324	1.106	0.485	-0.587	-0.136	-0.180	0.038	-0.632	0.158	-0.098
fuegianum	Buck 41073	-1.867	0.240	0.638	-0.119	-0.373	0.177	0.588	-0.534	-0.324	-0.056	-0.064
fuegianum	Buck 41081	-1.849	1.032	0.204	0.152	-0.761	0.643	0.140	0.160	0.054	0.090	0.054
fuegianum	Buck 41162	-1.070	1.555	2.503	0.326	-0.440	-0.759	1.113	0.225	-0.413	0.322	-0.206
fuegianum	Matteri 4202	-1.465	-0.172	0.554	-0.324	0.592	-0.299	0.329	0.299	-0.083	-0.022	-0.100
fuegianum	Schäfer-Verwimp & Verwimp 8004	-0.616	-0.047	0.884	-0.382	1.193	0.730	0.863	0.418	0.148	0.001	0.022
hians	Amtoft 2005b	-1.951	0.056	1.154	-0.453	0.848	-0.263	-0.199	0.153	-0.310	0.045	-0.099
hians	Gay s. B110n.	-0.835	-0.125	0.716	-0.625	1.131	0.311	0.278	0.836	-0.308	0.004	-0.077
hians	Mosses of USSR 70	-1.718	0.224	-1.865	0.019	1.001	-0.169	0.667	-0.116	0.069	-0.006	0.091
hians	Standley 5848	-1.934	-0.178	-0.338	0.512	-0.046	0.382	-0.192	0.551	-0.220	-0.035	0.062
hians	Stebel 576/97	-1.248	0.512	-0.811	-0.555	0.358	-0.160	0.483	0.130	0.249	-0.139	0.038
hians	Whitehouse 26870	-2.365	-1.506	-0.554	-0.700	0.971	-0.259	-0.312	0.060	-0.185	-0.197	-0.065
hians	Wynns 326	-1.542	-1.417	0.027	0.126	0.938	0.115	-0.550	1.192	0.164	0.057	-0.046
hians	Wynns 622	-1.882	-0.158	-0.591	0.575	0.605	-0.179	-0.139	0.030	-0.358	-0.057	0.018
Hygrohypnum eugyrium	Wynns 392	-1.301	3.789	1.400	-3.769	1.656	0.487	-2.352	-1.131	0.611	0.157	-0.050
muelleri	Motley 311	2.725	-1.201	0.710	-0.638	0.519	0.138	1.607	-0.476	-0.244	-0.008	-0.069
muelleri	Musci Frondosi Arch. Indici 95	2.593	-0.957	0.530	-1.897	-1.524	-0.100	1.092	0.218	0.230	0.025	0.101
muelleri	Musci Japonici 771	2.440	-2.415	-0.813	-1.671	1.456	-0.632	1.401	0.376	0.220	-0.076	0.008
muelleri	Musci Japonici Ex. 1316	0.892	0.193	1.340	-1.411	0.817	0.958	0.177	0.304	-0.397	-0.044	-0.118
muelleri	G. L. Smith J-951	0.430	-0.883	0.035	-1.204	-0.539	0.444	-0.465	0.126	-0.243	0.023	-0.013
muelleri	Wu 21163	3.249	-1.934	0.368	0.072	-0.013	-0.408	0.528	0.266	-0.113	0.190	0.239
muelleri	Yates 2992	1.759	-0.945	1.307	-1.160	-1.236	-0.654	0.172	-0.600	-0.298	0.072	0.183
murale	Aptroot 2849	-0.286	-1.182	-2.878	0.286	0.727	0.306	-0.043	0.173	0.146	0.340	-0.227
murale	Aptroot 9745	0.115	2.022	-0.567	-1.218	-0.135	1.958	0.009	-0.187	-0.336	-0.086	0.144

species	number	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
murale	Musci Merid. Macr. Polon. Ex. 1091	0.166	0.967	-1.748	-1.983	-1.050	0.839	-0.440	0.556	0.508	-0.044	0.014
murale	Musci Merid. Macr. Polon. Ex. 1137	-2.081	1.053	-0.900	-1.809	-0.229	0.281	-0.058	-0.727	-0.654	-0.053	0.003
murale	Ochyra 713/82	-1.863	-0.042	-1.363	-1.268	-0.580	0.363	-0.759	-0.334	-0.745	-0.014	-0.077
Oxyrrhynchium sp 2	Buck 23824	-0.733	0.005	-1.755	-0.434	0.373	-0.308	-0.058	0.350	0.407	-0.095	-0.008
praelongum	Jenkins s. n.	-2.663	0.454	-1.790	-0.025	-0.066	-0.381	0.512	0.424	0.831	-0.034	0.225
praelongum	Wynns 646	-4.211	-1.100	-1.102	0.078	0.322	-0.733	-0.313	0.304	-0.138	-0.200	0.063
pringlei (Mex.)	Delgadillo 6044	-2.604	-0.979	-0.292	0.243	-0.769	0.387	0.530	-0.418	-0.082	-0.098	-0.022
pringlei (Mex.)	Delgadillo 6045	-2.261	-1.159	-0.938	0.107	-1.538	-0.623	-0.016	0.022	-0.454	0.045	-0.074
pringlei (Mex.)	Pringle 10434	-1.637	-1.840	-0.352	0.305	-0.790	-0.259	-0.066	0.198	0.139	0.002	-0.065
pringlei (US)	Hill & Heaton 23469	-1.744	-1.151	1.068	-0.108	0.209	-0.008	0.917	-0.090	-0.353	0.018	-0.147
pringlei (US)	Wynns 488	-2.105	-0.294	-0.841	0.572	0.172	-0.074	0.509	-0.026	-0.037	-0.089	0.109
pringlei (US)	Wynns 546	-2.521	0.664	0.916	0.909	0.102	0.138	0.772	-0.539	0.753	-0.005	0.072
pringlei (US)	Wynns 568	-1.079	-0.337	0.239	0.865	-0.926	-0.024	0.224	-0.355	0.098	0.004	-0.056
pringlei (US)	Zartman & Pittillo 240	-1.168	-0.385	-0.419	0.516	-0.375	-0.657	0.730	0.541	0.537	-0.006	-0.059
pringlei (US)	Zartman & Pittillo 454	-1.779	0.367	-1.125	1.519	-0.664	-0.487	1.510	-1.553	-0.312	-0.065	0.059
"pringlei"	Sharp 5250	0.959	-0.537	-0.187	0.025	-0.297	0.138	0.202	0.731	0.812	0.060	-0.057
"pringlei"	Bryant 1682	1.197	-2.236	0.325	0.782	0.928	-0.317	0.045	0.780	0.263	-0.037	0.166
pulchellum	Anderson 27753	-1.684	3.212	1.703	1.240	1.193	1.413	0.749	-0.047	0.851	0.654	0.204
pulchellum	Buck 15378	-1.890	0.031	-0.136	0.671	1.040	0.773	-0.095	0.077	-0.421	-0.105	0.128
pulchellum	Hakelner s. n.	-1.991	0.396	-0.667	-0.332	0.626	-0.718	-0.327	0.226	-0.970	0.029	-0.035
pulchellum	Shevock 17526	-2.880	1.511	-0.668	1.172	-0.881	-0.044	-0.345	-0.140	-0.199	-0.097	0.341
pulchellum	Wynns 615	-1.881	-0.079	1.144	-0.118	0.924	0.611	0.162	0.302	0.723	-0.135	0.027
riparioides	Allen 10659	3.283	-1.421	0.036	1.883	0.859	0.565	-1.083	-0.464	0.333	-0.102	-0.080
riparioides	Anderson 24061	0.229	-1.643	-0.071	0.130	0.460	0.905	-0.721	0.322	-0.157	0.039	-0.002
riparioides	Buck 35187	2.814	-0.948	2.126	0.444	-0.211	0.973	-0.392	-0.527	0.359	-0.150	0.089
riparioides	Keith 4	1.171	-1.960	-0.433	0.691	0.529	1.619	-0.752	0.162	0.035	-0.138	0.053
riparioides	Matuda s. n.	1.604	-1.183	-0.643	0.927	-0.134	0.961	0.347	0.074	-1.357	0.198	-0.116
riparioides	Small 74	0.444	0.523	1.539	-0.209	-1.248	0.823	0.560	-0.924	0.109	-0.006	-0.203
riparioides	Wynns 240	3.260	-1.121	-0.305	0.699	-0.304	1.045	0.187	0.139	-0.556	0.026	-0.037
riparioides	Wynns 241	2.551	0.172	0.276	0.800	-0.108	0.499	-0.451	-0.689	0.718	-0.277	-0.168
riparioides	Wynns 274	1.073	-1.058	0.149	1.200	-0.195	1.174	-0.616	0.961	0.374	-0.004	0.046
riparioides	Wynns 574	1.593	-0.286	0.869	-0.055	-0.691	0.865	-1.122	0.570	-0.364	-0.041	0.114
ruscifforme var. lutescens	Schleicher s. n.	5.127	3.076	0.177	-1.619	1.274	-1.028	1.107	0.725	-0.104	-0.393	-0.107
Scleropodium obtusifolium	Buck 30299	-0.749	0.201	0.717	-0.925	-1.906	0.891	0.267	-0.254	0.826	-0.293	0.014
selaginellifolium	Hoe 3385	0.965	-0.177	-2.794	1.438	2.431	-0.369	0.210	-1.243	0.393	-0.072	-0.077
selaginellifolium	Hoe 4296	2.456	-0.059	-1.109	0.497	-1.161	-0.183	0.267	0.074	1.036	0.032	-0.185

species	number	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
serrulatum	Buck 45007	2.832	3.178	-2.482	0.670	0.833	-1.077	-0.051	-0.276	0.235	0.032	-0.076
serrulatum	D. K. Smith & Davison 194	4.660	2.550	-0.382	1.418	0.206	0.449	-0.434	0.086	-0.694	-0.150	-0.227
serrulatum	Wynns 175	1.643	2.115	-0.112	0.668	-0.860	-1.607	-1.197	0.926	-0.228	-0.016	-0.014
serrulatum	Wynns 296	2.233	5.265	-0.824	0.784	-1.088	-0.205	-0.062	1.177	-0.692	-0.064	0.305
serrulatum	Wynns 428	2.613	2.943	-0.833	-0.201	-0.934	-0.302	0.991	-0.027	0.434	0.134	-0.221
striatum	Buck 15078	-0.308	1.541	2.321	1.076	0.432	-1.005	-0.489	0.358	-0.228	0.132	-0.105
striatum	Eggers et al. 21	-0.162	-0.824	1.725	0.325	-0.123	-0.658	0.210	-0.338	0.101	-0.056	0.006
striatum	Holmen 045	0.115	-0.329	1.645	0.767	0.607	-1.162	-0.877	-0.396	0.298	-0.053	0.008
striatum	Schleicher s. n.	0.637	-0.141	1.123	0.915	-0.150	-0.818	-0.294	-0.639	0.384	-0.194	-0.014
striatum	Schofield 104756	-1.034	1.253	1.143	1.094	0.185	0.010	-0.892	-0.496	-0.403	-0.075	0.031
striatum	Seth s. n.	-0.545	0.338	2.189	0.292	0.750	-1.296	-0.200	0.277	0.357	0.061	-0.023
striatum	Vasak s. n.	0.193	-0.318	0.993	1.314	-0.284	-0.464	-1.282	-0.458	0.361	-0.241	0.041
cumulative variation		0.368	0.565	0.701	0.793	0.859	0.906	0.951	0.975	0.996	0.999	1.000

Platyhypnidium s. str.) that was close to and sometimes overlapped *Rhynchostegium*. *Rhynchostegium serrulatum* was usually resolved in an isolated position (Figures 1-3). In the plot of PC 1 vs. PC 3 for PCA11 (Figure 4), some specimens of *R. serrulatum* were resolved near *Platyhypnidium*. A collection named *R. rusciforme* var. *lutescens* Schimp. (*Schleicher s. n.*, near Saillon, Switzerland; DUKE) was always very close to *R. serrulatum*. *Rhynchostegium murale* and *R. confertum*, which always clustered together, were never found close to *R. serrulatum*. In some plots (Figures 2 and 3), they overlapped with *Platyhypnidium s. str.*, but in others (Figures 1 and 4), they did not. In PCA11, some specimens of *R. murale* fell in a cluster of *Eurhynchium* species (Figures 3 and 4).

Eurhynchium striatum appeared to be an intermediate taxon between *Platyhypnidium s. str./Rhynchostegium* and the other species of *Eurhynchium*. *Platyhypnidium fuegianum* always clustered with *E. pulchellum* & *E. hians*. When the sporophyte data were excluded (Figures 3 and 4), *P. fuegianum* was also close to *E. striatum*. One specimen of *E. angustirete* that was included in the study was not clearly separated from *E. striatum* (Figures 1 and 4).

Platyhypnidium pringlei and *E. hians* were not separated in PCA11 (Figures 3 & 4). Neither were Mexican and Appalachian populations of *P. pringlei* separated in PCA11. However, *Bryant 1682* (*Grand Canyon*; NY) and *Sharp 5250* (*Guatemala*; TENN), both identified as *E. pringlei*, did not appear to be correctly named. Based on PCA11, it is more likely that these specimens belong to *Platyhypnidium s. str.* However, since *Bryant 1682* is dioicous, its placement in *Platyhypnidium s. str.* is problematic.

Two specimens of the Hawaiian endemic moss *E. selaginellifolium* (Müll. Hal.) E. B. Bartram (*Hoe 3385*, TENN; *Hoe 4296*, NY) that were previously identified as *P. muelleri* could not be separated from *Platyhypnidium* in PCA11.

Schofield et al. 108026 (Alaska; TENN), identified as *E. pulchellum*, does not belong to that species based on PCA11. I have named the specimen *Bryhnia hultenii*.

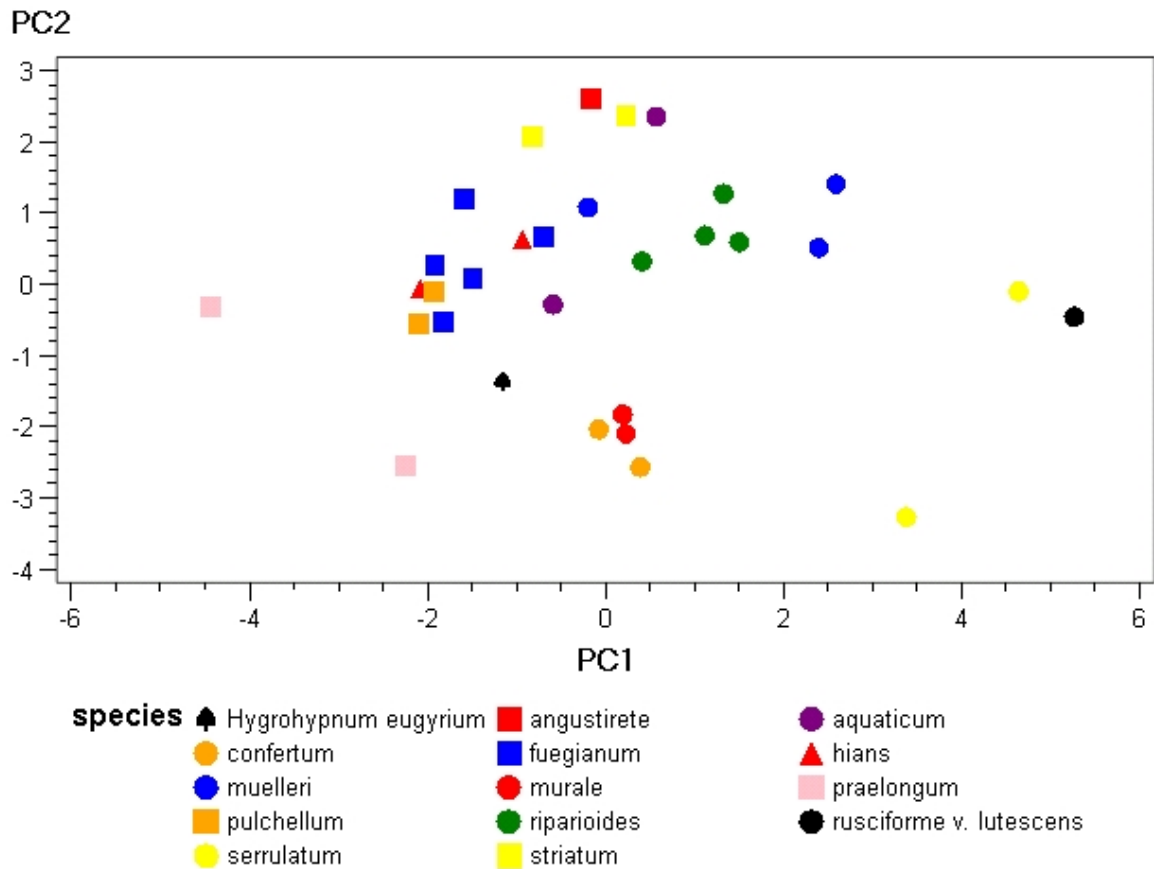


Figure 1. Plot of PC 1 vs. PC 2 for the 31 OTUs included in PCA13.

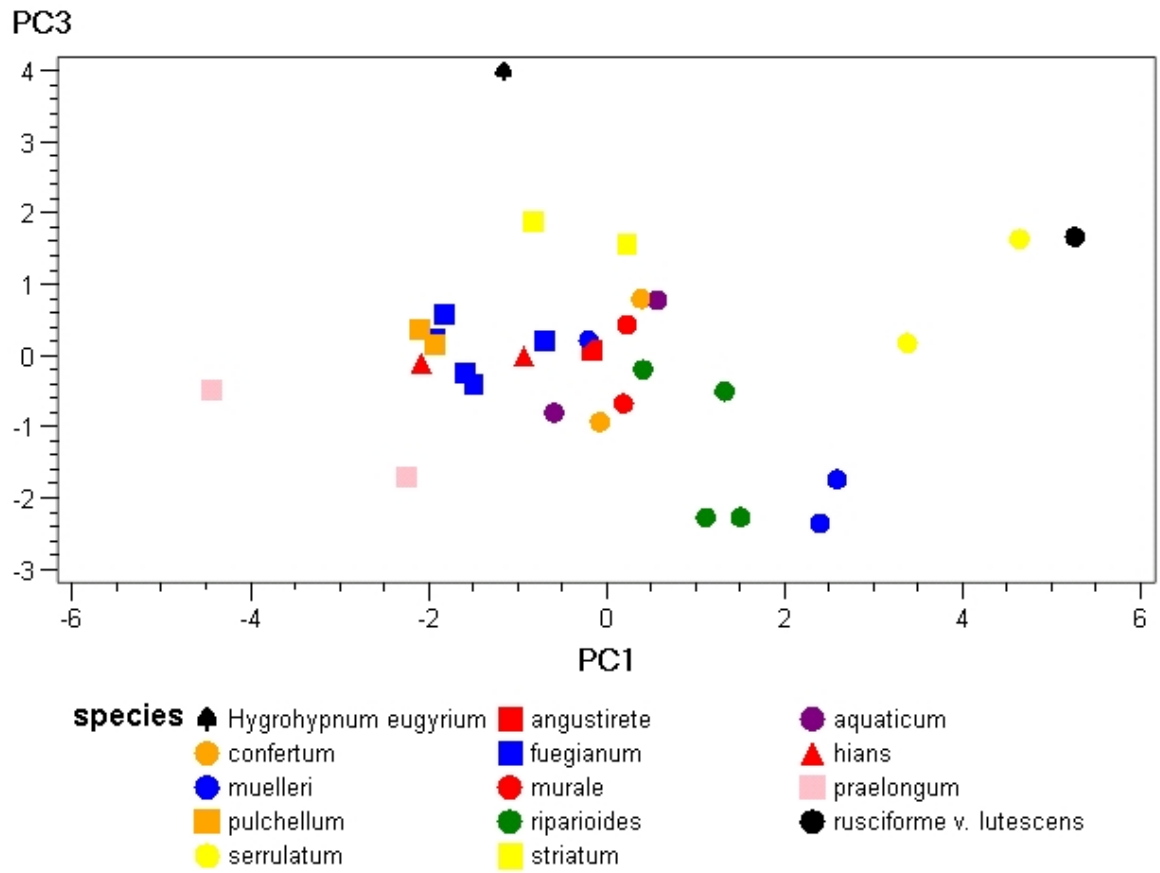


Figure 2. Plot of PC 1 vs. PC 3 for the 31 OTUs included in PCA13.

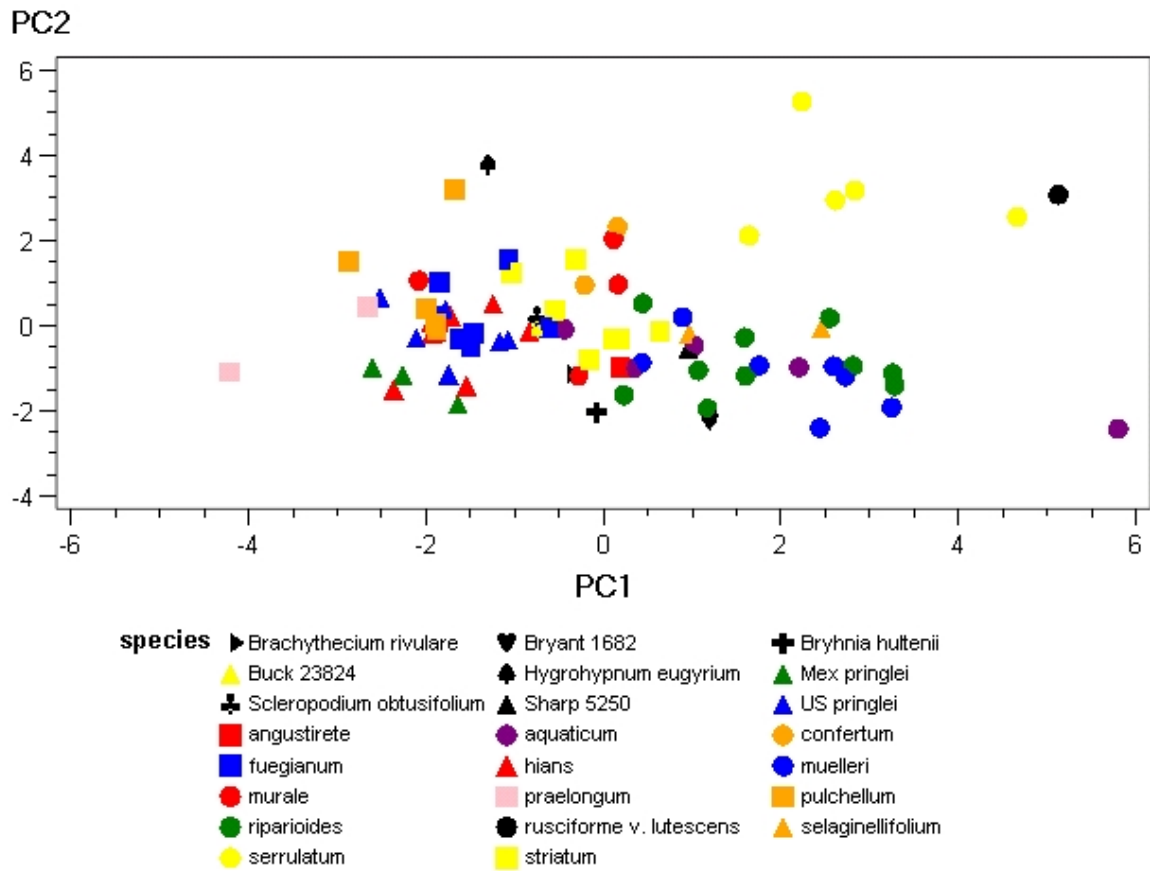


Figure 3. Plot of PC 1 vs. PC 2 for the 83 OTUs included in PCA11.

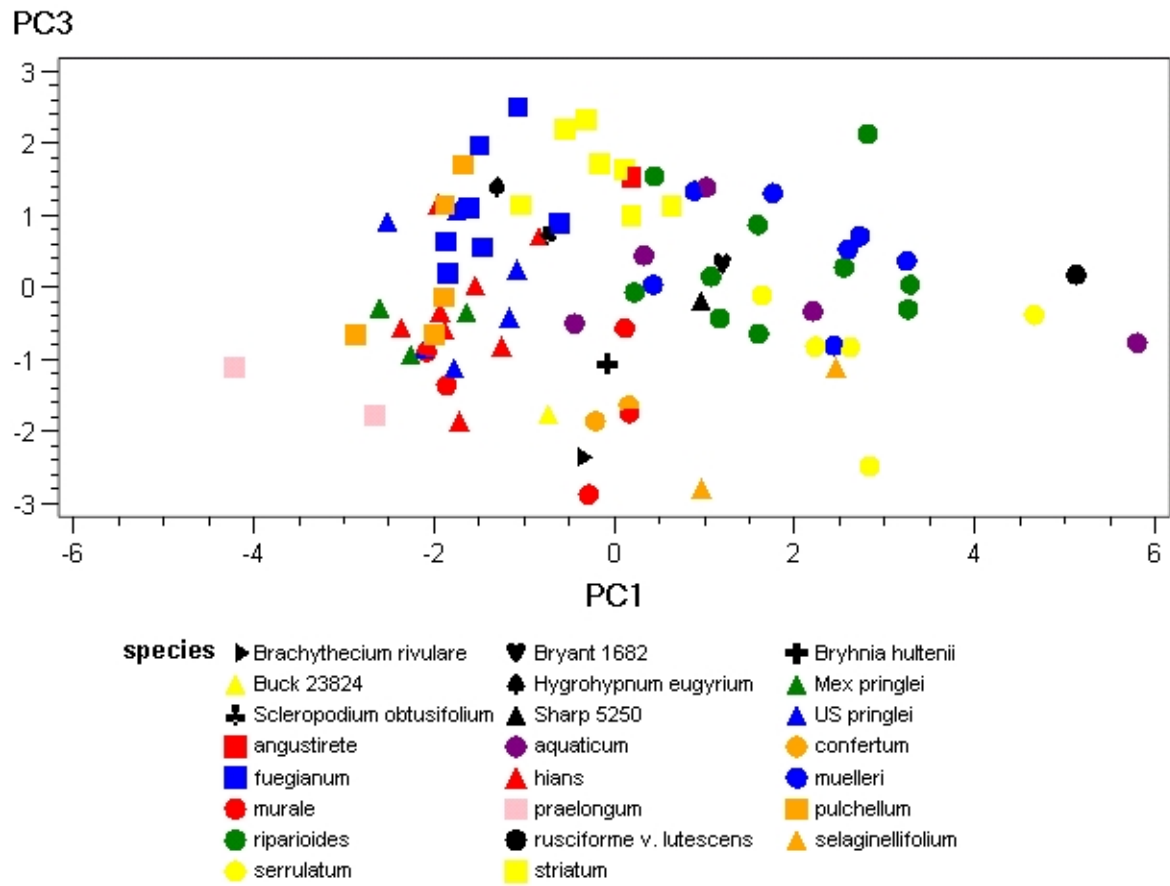


Figure 4. Plot of PC 1 vs. PC 3 for the 83 OTUs included in PCA11.

Analysis of variance

Descriptive statistics (mean, median, standard deviation and standard error) were calculated for each of the averaged variables treated with ANOVA for each of the ten species that were closely studied. These statistics are presented in Table 7. Significant dimensional differences between the ten taxa were identified by pairwise comparison (Tukey's test) and are listed in Table 8. A large number of significant dimensional relationships were resolved among the species tested. No significant difference in capsule width or capsule length-to-width ratio was found in any species. Box-plots were generated for each dimensional variable and also for the first three Principal Components for each species (Figures B1–B20). For each species, the shaded box represents the middle 50% of the distribution for that variable. The “whiskers” on the boxes were drawn to the first data point falling within 1.5 times the range of the middle 50%.

In general, large-leaved species were well separated from small-leaved species by ANOVA. In terms of leaf length itself (Figure B4), two groups were clearly distinguished: one group (with large leaves) included *Platyhypnidium s. str.*, *R. serrulatum* and *E. striatum*; the other (with smaller leaves) included *P. pringlei*, *E. hians*, *E. pulchellum*, *P. fuegianum* and *R. murale*. *Eurhynchium hians* had the shortest leaves. Leaf width (Figure B5) followed a similar pattern: in *Platyhypnidium s. str.* and *E. striatum* the leaves were significantly wider than in *E. hians*, *E. pulchellum*, *P. fuegianum* & *R. murale*. A similar pattern was reflected in the PC 1 scores, where *Platyhypnidium s. str.* and *R. serrulatum* formed a group that was distinct from the other six species (Figure B18).

Not surprisingly, cell size was also somewhat correlated with leaf size: in *Platyhypnidium s. str.* and *R. serrulatum*, the basal cells were significantly longer than in the other species (Figure B9); and basal cell width appeared to be a useful feature for separating *Platyhypnidium s. str.* + *Rhynchostegium* from *Eurhynchium* + *P. pringlei* (Figure B10). The median leaf cells were longest in the large-leaved species *P. riparioides* and *R. serrulatum*; and they were shortest in the small-leaved *E. hians* (Figure B12). They were widest in *P. muelleri*, and narrowest in *E. pulchellum* and *E. striatum* (Figure B13). The subapical cells were elongate in *R. serrulatum* and *E. striatum*; in other taxa they were truncate (Figure B15). The subapical cells were widest in *P. riparioides* (Figure B16).

Rhynchostegium serrulatum and *E. pulchellum* were distinguished by leaves with a high length-to-width ratio (Figure B6), and these two species were also well separated from all others in terms of PC 2 (Figure B19). *Platyhypnidium pringlei* had the longest costa in relation to the length of the leaf. This ratio was significantly lower in the two species of *Rhynchostegium* that were included than in the other species, so this character may be useful for separating *Platyhypnidium* and *Rhynchostegium* (Figure B8).

There were very few significant dimensional differences among sporophytes. *Eurhynchium striatum* had the largest capsules, and *P. riparioides* and *P. muelleri* had the smallest (Figure B1).

Table 7. Descriptive statistics based on dimensional measurements of ten species of rostrate-operculate Brachytheceaceae. All values were calculated from averaged measurements except for minimum and maximum values.

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Capsule length							
<i>aquaticum</i>	2	2.24	2.24	0.45	0.32	1.36	3.13
<i>fuegianum</i>	5	1.98	2.08	0.24	0.11	1.59	2.47
<i>hians</i>	2	2.04	2.04	0.02	0.01	1.64	2.58
<i>muelleri</i>	3	1.68	1.75	0.35	0.20	1.29	2.17
<i>murale</i>	2	1.72	1.72	0.35	0.25	1.29	2.25
<i>pringlei</i>	0						
<i>pulchellum</i>	4	1.85	1.92	0.19	0.10	1.52	2.30
<i>riparioides</i>	4	1.72	1.68	0.14	0.07	1.39	2.05
<i>serrulatum</i>	2	1.76	1.76	0.56	0.40	1.14	2.26
<i>striatum</i>	3	2.58	2.49	0.24	0.14	1.92	3.16
Capsule width							
<i>aquaticum</i>	2	1.06	1.06	0.13	0.09	0.71	1.44
<i>fuegianum</i>	5	1.02	1.03	0.13	0.06	0.83	1.44
<i>hians</i>	2	0.98	0.98	0.15	0.10	0.66	1.29
<i>muelleri</i>	3	0.91	0.81	0.28	0.16	0.53	1.51
<i>murale</i>	2	0.92	0.92	0.36	0.26	0.53	1.39
<i>pringlei</i>	0						
<i>pulchellum</i>	4	0.79	0.80	0.11	0.06	0.63	1.01
<i>riparioides</i>	4	0.98	0.97	0.13	0.07	0.83	1.14
<i>serrulatum</i>	2	0.81	0.81	0.08	0.05	0.63	0.93
<i>striatum</i>	3	1.16	1.19	0.13	0.07	0.76	1.71
Capsule length : width							
<i>aquaticum</i>	2	2.12	2.12	0.21	0.15	1.72	2.79
<i>fuegianum</i>	5	1.94	1.95	0.10	0.05	1.58	2.22
<i>hians</i>	2	2.13	2.13	0.33	0.23	1.69	2.83
<i>muelleri</i>	3	1.98	1.56	0.84	0.49	1.28	4.00
<i>murale</i>	2	1.96	1.96	0.41	0.29	1.53	2.72
<i>pringlei</i>	0						
<i>pulchellum</i>	4	2.39	2.26	0.28	0.14	2.00	2.80
<i>riparioides</i>	4	1.78	1.82	0.27	0.13	1.45	2.22
<i>serrulatum</i>	2	2.15	2.15	0.50	0.35	1.70	2.76
<i>striatum</i>	3	2.27	2.40	0.25	0.14	1.84	3.59

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Leaf length							
<i>aquaticum</i>	5	1.60	1.59	0.40	0.18	1.01	2.32
<i>fuegianum</i>	7	1.15	1.13	0.07	0.03	0.98	1.36
<i>hians</i>	9	0.98	1.02	0.08	0.03	0.79	1.21
<i>muelleri</i>	7	1.49	1.45	0.19	0.07	1.09	1.92
<i>murale</i>	5	1.04	1.07	0.15	0.07	0.72	1.41
<i>pringlei</i>	9	1.12	1.11	0.14	0.05	0.81	1.52
<i>pulchellum</i>	9	1.09	1.14	0.12	0.04	0.69	1.59
<i>riparioides</i>	10	1.84	1.70	0.32	0.10	1.31	2.60
<i>serrulatum</i>	5	1.80	1.72	0.30	0.14	1.16	2.85
<i>striatum</i>	8	1.69	1.63	0.16	0.06	1.19	2.35
Leaf width							
<i>aquaticum</i>	5	1.21	1.12	0.44	0.19	0.59	2.05
<i>fuegianum</i>	7	0.71	0.68	0.11	0.04	0.49	1.14
<i>hians</i>	9	0.61	0.62	0.09	0.03	0.40	0.81
<i>muelleri</i>	7	1.17	1.19	0.21	0.08	0.81	1.72
<i>murale</i>	5	0.56	0.56	0.07	0.03	0.40	0.78
<i>pringlei</i>	9	0.67	0.67	0.10	0.03	0.42	1.06
<i>pulchellum</i>	9	0.53	0.55	0.07	0.02	0.32	0.88
<i>riparioides</i>	10	1.15	1.11	0.18	0.06	0.87	1.78
<i>serrulatum</i>	5	0.85	0.77	0.19	0.09	0.55	1.36
<i>striatum</i>	8	1.07	1.12	0.14	0.05	0.71	1.47
Leaf length : width							
<i>aquaticum</i>	5	1.39	1.38	0.17	0.08	1.05	1.77
<i>fuegianum</i>	7	1.67	1.67	0.19	0.07	1.18	2.21
<i>hians</i>	9	1.66	1.58	0.22	0.07	1.14	2.14
<i>muelleri</i>	7	1.30	1.20	0.15	0.06	1.06	1.78
<i>murale</i>	5	1.89	1.85	0.20	0.09	1.41	2.56
<i>pringlei</i>	9	1.72	1.70	0.28	0.09	1.15	2.63
<i>pulchellum</i>	9	2.13	2.04	0.38	0.13	1.56	3.64
<i>riparioides</i>	10	1.62	1.57	0.14	0.04	1.22	2.22
<i>serrulatum</i>	5	2.18	2.18	0.30	0.13	1.62	2.90
<i>striatum</i>	8	1.61	1.60	0.20	0.07	1.16	2.27

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Basal cell length							
<i>aquaticum</i>	5	48.52	44.60	7.14	3.19	30	70
<i>fuegianum</i>	7	35.14	35.00	3.74	1.41	23	45
<i>hians</i>	8	34.28	33.50	3.99	1.41	24	53
<i>muelleri</i>	7	53.03	53.80	5.62	2.12	23	75
<i>murale</i>	5	41.20	36.60	8.77	3.92	23	75
<i>pringlei</i>	9	32.29	31.80	3.21	1.07	23	48
<i>pulchellum</i>	5	31.36	30.40	3.84	1.72	20	50
<i>riparioides</i>	10	45.60	45.80	4.54	1.43	29	63
<i>serrulatum</i>	5	52.44	54.20	4.39	1.96	23	75
<i>striatum</i>	8	35.90	36.40	3.07	1.09	24	49
Basal cell width							
<i>aquaticum</i>	5	13.44	13.00	2.53	1.13	8	24
<i>fuegianum</i>	7	8.71	8.80	1.04	0.39	5	15
<i>hians</i>	8	10.05	10.10	1.26	0.45	6	15
<i>muelleri</i>	7	12.94	12.60	1.77	0.67	9	20
<i>murale</i>	5	12.96	11.80	2.60	1.16	8	20
<i>pringlei</i>	9	10.38	10.40	1.44	0.48	5	18
<i>pulchellum</i>	5	8.72	8.80	0.76	0.34	5	13
<i>riparioides</i>	10	12.92	13.40	1.34	0.42	8	18
<i>serrulatum</i>	5	14.52	14.60	1.12	0.50	9	25
<i>striatum</i>	8	8.88	8.90	1.26	0.40	6	12
Basal cell length : width							
<i>aquaticum</i>	5	3.74	3.49	0.43	0.19	2.31	7.00
<i>fuegianum</i>	7	4.28	4.06	0.49	0.19	1.77	6.67
<i>hians</i>	8	3.58	3.44	0.51	0.18	2.09	6.67
<i>muelleri</i>	7	4.25	4.25	0.42	0.16	2.15	6.67
<i>murale</i>	5	3.34	3.53	0.64	0.29	1.70	5.63
<i>pringlei</i>	9	3.29	3.16	0.54	0.18	2.11	6.00
<i>pulchellum</i>	5	3.91	3.52	1.01	0.45	1.69	9.60
<i>riparioides</i>	10	3.70	3.55	0.52	0.17	2.07	6.25
<i>serrulatum</i>	5	3.75	3.87	0.36	0.16	1.53	6.64
<i>striatum</i>	8	4.13	4.03	0.42	0.15	2.45	6.33

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Median cell length							
<i>aquaticum</i>	5	72.20	70.00	14.28	6.39	40	110
<i>fuegianum</i>	7	61.57	62.80	7.87	2.97	45	83
<i>hians</i>	9	51.22	52.00	7.89	2.63	33	74
<i>muelleri</i>	7	71.94	76.40	9.71	3.67	38	103
<i>murale</i>	5	67.32	60.80	14.96	6.69	48	103
<i>pringlei</i>	9	51.89	51.00	4.64	1.55	30	74
<i>pulchellum</i>	9	59.58	58.40	7.19	2.40	32	86
<i>riparioides</i>	10	84.00	80.80	9.55	3.02	53	131
<i>serrulatum</i>	5	98.68	90.60	19.94	8.92	63	153
<i>striatum</i>	8	60.55	60.70	7.79	2.75	43	118
Median cell width							
<i>aquaticum</i>	5	7.76	7.00	1.87	0.84	6	14
<i>fuegianum</i>	7	5.85	6.20	0.60	0.23	5	9
<i>hians</i>	8	5.98	6.00	0.86	0.31	4	9
<i>muelleri</i>	7	8.31	8.40	1.38	0.52	5	13
<i>murale</i>	5	6.60	6.60	0.55	0.24	5	9
<i>pringlei</i>	9	6.07	5.80	0.81	0.27	4	10
<i>pulchellum</i>	5	5.32	5.00	0.70	0.31	4	7
<i>riparioides</i>	10	6.56	6.60	1.01	0.32	4	10
<i>serrulatum</i>	5	8.04	8.60	1.40	0.62	6	11
<i>striatum</i>	8	5.80	5.80	0.52	0.19	4	9
Median cell length : width							
<i>aquaticum</i>	5	9.82	10.09	1.94	0.87	4.86	18.33
<i>fuegianum</i>	7	10.80	10.02	1.91	0.72	6.63	16.60
<i>hians</i>	8	8.98	9.23	2.03	0.72	4.44	16.25
<i>muelleri</i>	7	9.16	9.54	2.16	0.82	3.92	15.00
<i>murale</i>	5	10.48	10.32	2.50	1.19	6.11	19.00
<i>pringlei</i>	9	8.82	8.79	0.99	0.33	4.78	16.00
<i>pulchellum</i>	5	11.73	11.22	2.70	1.21	8.00	21.25
<i>riparioides</i>	10	13.20	12.66	1.91	0.60	8.13	19.60
<i>serrulatum</i>	5	12.71	13.11	3.32	1.49	6.18	23.00
<i>striatum</i>	8	10.77	10.17	2.13	0.75	6.25	23.60

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Apical cell length							
<i>aquaticum</i>	5	24.84	24.60	4.13	1.85	13	48
<i>fuegianum</i>	7	27.94	26.80	5.46	2.07	19	50
<i>hians</i>	8	26.65	27.80	3.27	1.15	14	38
<i>muelleri</i>	7	23.46	23.20	3.83	1.45	13	45
<i>murale</i>	5	19.16	20.00	3.43	1.53	10	31
<i>pringlei</i>	9	24.29	26.00	5.06	1.69	12	45
<i>pulchellum</i>	5	30.44	31.20	5.55	2.48	14	50
<i>riparioides</i>	10	25.48	26.00	4.77	1.51	13	40
<i>serrulatum</i>	5	52.68	53.80	6.11	2.73	30	85
<i>striatum</i>	8	36.25	34.80	5.52	1.95	24	60
Apical cell width							
<i>aquaticum</i>	5	9.08	8.20	2.10	0.94	5	14
<i>fuegianum</i>	7	8.06	7.80	1.32	0.50	6	13
<i>hians</i>	8	9.63	9.50	0.80	0.28	5	14
<i>muelleri</i>	7	9.54	10.00	1.66	0.63	5	14
<i>murale</i>	5	8.52	8.00	1.56	0.70	5	12
<i>pringlei</i>	9	7.91	7.80	0.74	0.25	5	11
<i>pulchellum</i>	5	8.72	8.80	1.38	0.62	5	12
<i>riparioides</i>	10	10.38	10.70	1.60	0.51	5	16
<i>serrulatum</i>	5	7.72	7.20	1.62	0.72	4	13
<i>striatum</i>	8	8.50	8.40	0.37	0.13	4	12
Apical cell length : width							
<i>aquaticum</i>	5	2.97	2.61	0.78	0.35	1.63	9.60
<i>fuegianum</i>	7	3.67	3.13	1.28	0.48	1.77	8.33
<i>hians</i>	8	2.89	3.02	0.49	0.17	1.56	5.00
<i>muelleri</i>	7	2.55	2.45	0.46	0.17	1.36	4.60
<i>murale</i>	5	2.35	2.34	0.27	0.12	1.00	4.14
<i>pringlei</i>	9	3.20	3.14	0.80	0.27	1.50	9.00
<i>pulchellum</i>	5	3.94	4.05	1.31	0.58	1.27	8.60
<i>riparioides</i>	10	2.59	2.60	0.54	0.17	0.81	5.00
<i>serrulatum</i>	5	7.22	7.22	1.82	0.81	3.75	12.14
<i>striatum</i>	8	4.43	4.19	0.76	0.27	2.50	8.57

Character, by species	n	Mean	Median	Std Dev	SE	Min	Max
Costa length							
<i>aquaticum</i>	5	1.21	1.26	0.26	0.11	0.70	1.89
<i>fuegianum</i>	7	0.93	0.92	0.08	0.03	0.76	1.20
<i>hians</i>	8	0.76	0.78	0.07	0.03	0.52	0.99
<i>muelleri</i>	7	1.17	1.13	0.22	0.08	0.51	1.70
<i>murale</i>	5	0.67	0.62	0.14	0.06	0.25	0.98
<i>pringlei</i>	9	0.98	0.97	0.14	0.05	0.68	1.33
<i>pulchellum</i>	5	0.84	0.86	0.16	0.07	0.46	1.16
<i>riparioides</i>	10	1.52	1.44	0.27	0.09	0.93	2.27
<i>serrulatum</i>	5	1.12	1.07	0.25	0.11	0.76	1.87
<i>striatum</i>	8	1.35	1.37	0.15	0.05	0.94	1.85
Costa length : Leaf length							
<i>aquaticum</i>	5	0.76	0.77	0.04	0.02	0.58	0.90
<i>fuegianum</i>	7	0.81	0.81	0.02	0.01	0.73	0.89
<i>hians</i>	8	0.77	0.76	0.03	0.01	0.56	0.87
<i>muelleri</i>	7	0.78	0.78	0.06	0.02	0.42	0.91
<i>murale</i>	5	0.64	0.62	0.07	0.03	0.29	0.84
<i>pringlei</i>	9	0.87	0.88	0.03	0.01	0.76	0.94
<i>pulchellum</i>	5	0.78	0.80	0.06	0.03	0.61	0.88
<i>riparioides</i>	10	0.82	0.84	0.04	0.01	0.71	1.01
<i>serrulatum</i>	5	0.62	0.63	0.05	0.02	0.44	0.72
<i>striatum</i>	8	0.80	0.79	0.04	0.02	0.67	0.93

Table 8. Significant differences between taxa, by character, as identified by Tukey's test in ANOVA ($P < 0.05$).

CHARACTER	<i>SPECIES 1</i>	<i>SPECIES 2</i>	CHARACTER	<i>SPECIES 1</i>	<i>SPECIES 2</i>
leaf length (Figure B4)	<i>aquaticum</i>	<i>fuegianum</i>	leaf length : width (Figure B6)	<i>muelleri</i>	<i>pringlei</i>
	<i>aquaticum</i>	<i>hians</i>		<i>murale</i>	<i>aquaticum</i>
	<i>aquaticum</i>	<i>murale</i>		<i>murale</i>	<i>muelleri</i>
	<i>aquaticum</i>	<i>pringlei</i>		<i>pulchellum</i>	<i>aquaticum</i>
	<i>aquaticum</i>	<i>pulchellum</i>		<i>pulchellum</i>	<i>fuegianum</i>
	<i>muelleri</i>	<i>hians</i>		<i>pulchellum</i>	<i>hians</i>
	<i>muelleri</i>	<i>murale</i>		<i>pulchellum</i>	<i>muelleri</i>
	<i>muelleri</i>	<i>pringlei</i>		<i>pulchellum</i>	<i>pringlei</i>
	<i>muelleri</i>	<i>pulchellum</i>		<i>pulchellum</i>	<i>riparioides</i>
	<i>riparioides</i>	<i>fuegianum</i>		<i>pulchellum</i>	<i>striatum</i>
	<i>riparioides</i>	<i>hians</i>		<i>serrulatum</i>	<i>aquaticum</i>
	<i>riparioides</i>	<i>muelleri</i>		<i>serrulatum</i>	<i>fuegianum</i>
	<i>riparioides</i>	<i>murale</i>		<i>serrulatum</i>	<i>hians</i>
	<i>riparioides</i>	<i>pringlei</i>		<i>serrulatum</i>	<i>muelleri</i>
	<i>riparioides</i>	<i>pulchellum</i>		<i>serrulatum</i>	<i>pringlei</i>
	<i>serrulatum</i>	<i>fuegianum</i>		<i>serrulatum</i>	<i>riparioides</i>
	<i>serrulatum</i>	<i>hians</i>		<i>serrulatum</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>murale</i>			
	<i>serrulatum</i>	<i>pringlei</i>			
	<i>serrulatum</i>	<i>pulchellum</i>			
	<i>striatum</i>	<i>fuegianum</i>			
	<i>striatum</i>	<i>hians</i>			
	<i>striatum</i>	<i>murale</i>			
<i>striatum</i>	<i>pringlei</i>				
<i>striatum</i>	<i>pulchellum</i>				
leaf width (Figure B5)	<i>aquaticum</i>	<i>fuegianum</i>	capsule length (Figure B1)	<i>striatum</i>	<i>riparioides</i>
	<i>aquaticum</i>	<i>hians</i>		<i>striatum</i>	<i>muelleri</i>
	<i>aquaticum</i>	<i>murale</i>			
	<i>aquaticum</i>	<i>pringlei</i>			
	<i>aquaticum</i>	<i>pulchellum</i>			
	<i>aquaticum</i>	<i>serrulatum</i>			
	<i>muelleri</i>	<i>fuegianum</i>			
	<i>muelleri</i>	<i>hians</i>			
	<i>muelleri</i>	<i>murale</i>			
	<i>muelleri</i>	<i>pringlei</i>			
	<i>muelleri</i>	<i>pulchellum</i>			
	<i>riparioides</i>	<i>fuegianum</i>			
	<i>riparioides</i>	<i>hians</i>			
	<i>riparioides</i>	<i>murale</i>			
	<i>riparioides</i>	<i>pringlei</i>			
	<i>riparioides</i>	<i>pulchellum</i>			
<i>serrulatum</i>	<i>pulchellum</i>				
<i>striatum</i>	<i>fuegianum</i>				
<i>striatum</i>	<i>hians</i>				
<i>striatum</i>	<i>murale</i>				
<i>striatum</i>	<i>pringlei</i>				
<i>striatum</i>	<i>pulchellum</i>				

CHARACTER	SPECIES 1	SPECIES 2	CHARACTER	SPECIES 1	SPECIES 2
costa length (Figure B7)	<i>aquaticum</i>	<i>hians</i>	basal cell length (Figure B9)	<i>aquaticum</i>	<i>fuegianum</i>
	<i>aquaticum</i>	<i>murale</i>		<i>aquaticum</i>	<i>hians</i>
	<i>muelleri</i>	<i>hians</i>		<i>aquaticum</i>	<i>pringlei</i>
	<i>muelleri</i>	<i>murale</i>		<i>aquaticum</i>	<i>pulchellu.m</i>
	<i>riparioides</i>	<i>fuegianum</i>		<i>aquaticum</i>	<i>striatum</i>
	<i>riparioides</i>	<i>hians</i>		<i>muelleri</i>	<i>fuegianum</i>
	<i>riparioides</i>	<i>muelleri</i>		<i>muelleri</i>	<i>hians</i>
	<i>riparioides</i>	<i>murale</i>		<i>muelleri</i>	<i>murale</i>
	<i>riparioides</i>	<i>pringlei</i>		<i>muelleri</i>	<i>pringlei</i>
	<i>riparioides</i>	<i>pulchellum</i>		<i>muelleri</i>	<i>pulchellum</i>
	<i>riparioides</i>	<i>serrulatum</i>		<i>muelleri</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>hians</i>		<i>murale</i>	<i>pringlei</i>
	<i>serrulatum</i>	<i>murale</i>		<i>riparioides</i>	<i>fuegianum</i>
	<i>striatum</i>	<i>fuegianum</i>		<i>riparioides</i>	<i>hians</i>
	<i>striatum</i>	<i>hians</i>		<i>riparioides</i>	<i>pringlei</i>
	<i>striatum</i>	<i>murale</i>		<i>riparioides</i>	<i>pulchellum</i>
	<i>striatum</i>	<i>pringlei</i>		<i>riparioides</i>	<i>striatum</i>
<i>striatum</i>	<i>pulchellum</i>	<i>serrulatum</i>	<i>fuegianum</i>		
<i>serrulatum</i>	<i>hians</i>	<i>serrulatum</i>	<i>hians</i>		
<i>serrulatum</i>	<i>murale</i>	<i>serrulatum</i>	<i>murale</i>		
<i>serrulatum</i>	<i>pringlei</i>	<i>serrulatum</i>	<i>pringlei</i>		
<i>serrulatum</i>	<i>pulchellum</i>	<i>serrulatum</i>	<i>pulchellum</i>		
<i>serrulatum</i>	<i>striatum</i>	<i>serrulatum</i>	<i>striatum</i>		
costa length : leaf length (Figure B8)	<i>murale</i>	<i>aquaticum</i>	basal cell width (Figure B10)	<i>aquaticum</i>	<i>fuegianum</i>
	<i>murale</i>	<i>fuegianum</i>		<i>aquaticum</i>	<i>hians</i>
	<i>murale</i>	<i>hians</i>		<i>aquaticum</i>	<i>pringlei</i>
	<i>murale</i>	<i>muelleri</i>		<i>aquaticum</i>	<i>pulchellum</i>
	<i>murale</i>	<i>pringlei</i>		<i>aquaticum</i>	<i>striatum</i>
	<i>murale</i>	<i>pulchellum</i>		<i>muelleri</i>	<i>fuegianum</i>
	<i>murale</i>	<i>riparioides</i>		<i>muelleri</i>	<i>hians</i>
	<i>murale</i>	<i>striatum</i>		<i>muelleri</i>	<i>pringlei</i>
	<i>pringlei</i>	<i>aquaticum</i>		<i>muelleri</i>	<i>pulchellum</i>
	<i>pringlei</i>	<i>hians</i>		<i>muelleri</i>	<i>striatum</i>
	<i>pringlei</i>	<i>muelleri</i>		<i>murale</i>	<i>fuegianum</i>
	<i>pringlei</i>	<i>pulchellum</i>		<i>murale</i>	<i>hians</i>
	<i>pringlei</i>	<i>serrulatum</i>		<i>murale</i>	<i>pulchellum</i>
	<i>pringlei</i>	<i>striatum</i>		<i>murale</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>aquaticum</i>		<i>riparioides</i>	<i>fuegianum</i>
	<i>serrulatum</i>	<i>fuegianum</i>		<i>riparioides</i>	<i>hians</i>
	<i>serrulatum</i>	<i>hians</i>		<i>riparioides</i>	<i>pringlei</i>
<i>serrulatum</i>	<i>muelleri</i>	<i>riparioides</i>	<i>pulchellum</i>		
<i>serrulatum</i>	<i>pulchellum</i>	<i>riparioides</i>	<i>striatum</i>		
<i>serrulatum</i>	<i>riparioides</i>	<i>serrulatum</i>	<i>fuegianum</i>		
<i>serrulatum</i>	<i>striatum</i>	<i>serrulatum</i>	<i>hians</i>		
		<i>serrulatum</i>	<i>pringlei</i>		
		<i>serrulatum</i>	<i>pulchellum</i>		
		<i>serrulatum</i>	<i>striatum</i>		
		basal cell length : width (Figure B11)	<i>pringlei</i>	<i>fuegianum</i>	
			<i>pringlei</i>	<i>muelleri</i>	

CHARACTER	SPECIES 1	SPECIES 2	CHARACTER	SPECIES 1	SPECIES 2
median cell length (Figure B12)	<i>aquaticum</i>	<i>hians</i>	apical cell length (Figure B15)	<i>murale</i>	<i>pulchellum</i>
	<i>aquaticum</i>	<i>pringlei</i>		<i>murale</i>	<i>serrulatum</i>
	<i>muelleri</i>	<i>hians</i>		<i>murale</i>	<i>striatum</i>
	<i>muelleri</i>	<i>pringlei</i>		<i>serrulatum</i>	<i>aquaticum</i>
	<i>riparioides</i>	<i>fuegianum</i>		<i>serrulatum</i>	<i>fuegianum</i>
	<i>riparioides</i>	<i>hians</i>		<i>serrulatum</i>	<i>hians</i>
	<i>riparioides</i>	<i>pringlei</i>		<i>serrulatum</i>	<i>muelleri</i>
	<i>riparioides</i>	<i>pulchellum</i>		<i>serrulatum</i>	<i>pringlei</i>
	<i>riparioides</i>	<i>striatum</i>		<i>serrulatum</i>	<i>pulchellum</i>
	<i>serrulatum</i>	<i>aquaticum</i>		<i>serrulatum</i>	<i>riparioides</i>
	<i>serrulatum</i>	<i>fuegianum</i>		<i>serrulatum</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>hians</i>		<i>striatum</i>	<i>aquaticum</i>
	<i>serrulatum</i>	<i>muelleri</i>		<i>striatum</i>	<i>fuegianum</i>
	<i>serrulatum</i>	<i>murale</i>		<i>striatum</i>	<i>hians</i>
	<i>serrulatum</i>	<i>pringlei</i>		<i>striatum</i>	<i>muelleri</i>
	<i>serrulatum</i>	<i>pulchellum</i>		<i>striatum</i>	<i>pringlei</i>
<i>serrulatum</i>	<i>striatum</i>	<i>striatum</i>	<i>riparioides</i>		
median cell width (Figure B13)	<i>aquaticum</i>	<i>pulchellum</i>	apical cell width (Figure B16)	<i>riparioides</i>	<i>fuegianum</i>
	<i>aquaticum</i>	<i>striatum</i>		<i>riparioides</i>	<i>pringlei</i>
	<i>muelleri</i>	<i>riparioides</i>		<i>riparioides</i>	<i>serrulatum</i>
	<i>muelleri</i>	<i>pringlei</i>			
	<i>muelleri</i>	<i>hians</i>			
	<i>muelleri</i>	<i>fuegianum</i>			
	<i>muelleri</i>	<i>striatum</i>			
	<i>muelleri</i>	<i>pulchellum</i>			
	<i>serrulatum</i>	<i>hians</i>			
	<i>serrulatum</i>	<i>fuegianum</i>			
	<i>serrulatum</i>	<i>striatum</i>			
	<i>serrulatum</i>	<i>pringlei</i>			
<i>serrulatum</i>	<i>pulchellum</i>				
median cell length : width (Figure B14)	<i>pringlei</i>	<i>riparioides</i>	apical cell length : width (Figure B17)	<i>serrulatum</i>	<i>aquaticum</i>
	<i>pringlei</i>	<i>serrulatum</i>		<i>serrulatum</i>	<i>fuegianum</i>
	<i>riparioides</i>	<i>hians</i>		<i>serrulatum</i>	<i>hians</i>
	<i>riparioides</i>	<i>muelleri</i>		<i>serrulatum</i>	<i>muelleri</i>
				<i>serrulatum</i>	<i>murale</i>
		<i>serrulatum</i>	<i>pringlei</i>		
		<i>serrulatum</i>	<i>pulchellum</i>		
		<i>serrulatum</i>	<i>riparioides</i>		
		<i>serrulatum</i>	<i>striatum</i>		
		<i>striatum</i>	<i>hians</i>		
		<i>striatum</i>	<i>muelleri</i>		
		<i>striatum</i>	<i>murale</i>		
		<i>striatum</i>	<i>riparioides</i>		

CHARACTER	SPECIES 1	SPECIES 2
Principal Component 1 (Figure B18)	<i>aquaticum</i>	<i>fuegianum</i>
	<i>aquaticum</i>	<i>hians</i>
	<i>aquaticum</i>	<i>murale</i>
	<i>aquaticum</i>	<i>pringlei</i>
	<i>aquaticum</i>	<i>pulchellum</i>
	<i>aquaticum</i>	<i>striatum</i>
	<i>muelleri</i>	<i>fuegianum</i>
	<i>muelleri</i>	<i>hians</i>
	<i>muelleri</i>	<i>murale</i>
	<i>muelleri</i>	<i>pringlei</i>
	<i>muelleri</i>	<i>pulchellum</i>
	<i>muelleri</i>	<i>striatum</i>
	<i>riparioides</i>	<i>fuegianum</i>
	<i>riparioides</i>	<i>hians</i>
	<i>riparioides</i>	<i>murale</i>
	<i>riparioides</i>	<i>pringlei</i>
	<i>riparioides</i>	<i>pulchellum</i>
	<i>riparioides</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>fuegianum</i>
	<i>serrulatum</i>	<i>hians</i>
<i>serrulatum</i>	<i>murale</i>	
<i>serrulatum</i>	<i>pringlei</i>	
<i>serrulatum</i>	<i>pulchellum</i>	
<i>serrulatum</i>	<i>striatum</i>	
<i>striatum</i>	<i>pringlei</i>	
<i>striatum</i>	<i>pulchellum</i>	
Principal Component 2 (Figure B19)	<i>pulchellum</i>	<i>aquaticum</i>
	<i>pulchellum</i>	<i>muelleri</i>
	<i>pulchellum</i>	<i>riparioides</i>
	<i>pulchellum</i>	<i>serrulatum</i>
	<i>serrulatum</i>	<i>aquaticum</i>
	<i>serrulatum</i>	<i>fuegianum</i>
	<i>serrulatum</i>	<i>hians</i>
	<i>serrulatum</i>	<i>muelleri</i>
	<i>serrulatum</i>	<i>murale</i>
	<i>serrulatum</i>	<i>pringlei</i>
	<i>serrulatum</i>	<i>riparioides</i>
	<i>serrulatum</i>	<i>striatum</i>
Principal Component 3 (Figure B20)	<i>murale</i>	<i>fuegianum</i>
	<i>murale</i>	<i>muelleri</i>
	<i>murale</i>	<i>pulchellum</i>
	<i>murale</i>	<i>riparioides</i>
	<i>murale</i>	<i>striatum</i>
	<i>serrulatum</i>	<i>aquaticum</i>
	<i>serrulatum</i>	<i>fuegianum</i>
	<i>serrulatum</i>	<i>muelleri</i>
	<i>serrulatum</i>	<i>riparioides</i>
	<i>serrulatum</i>	<i>striatum</i>
	<i>striatum</i>	<i>hians</i>
<i>striatum</i>	<i>pringlei</i>	

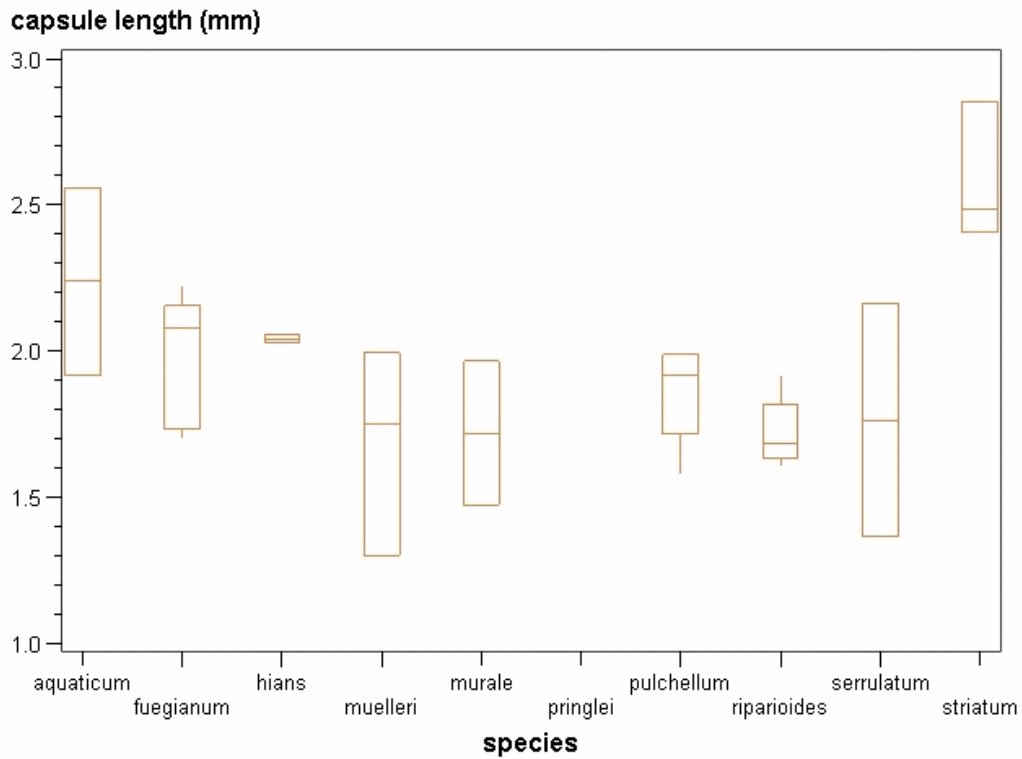


Figure B1. By-species comparison of average capsule length.

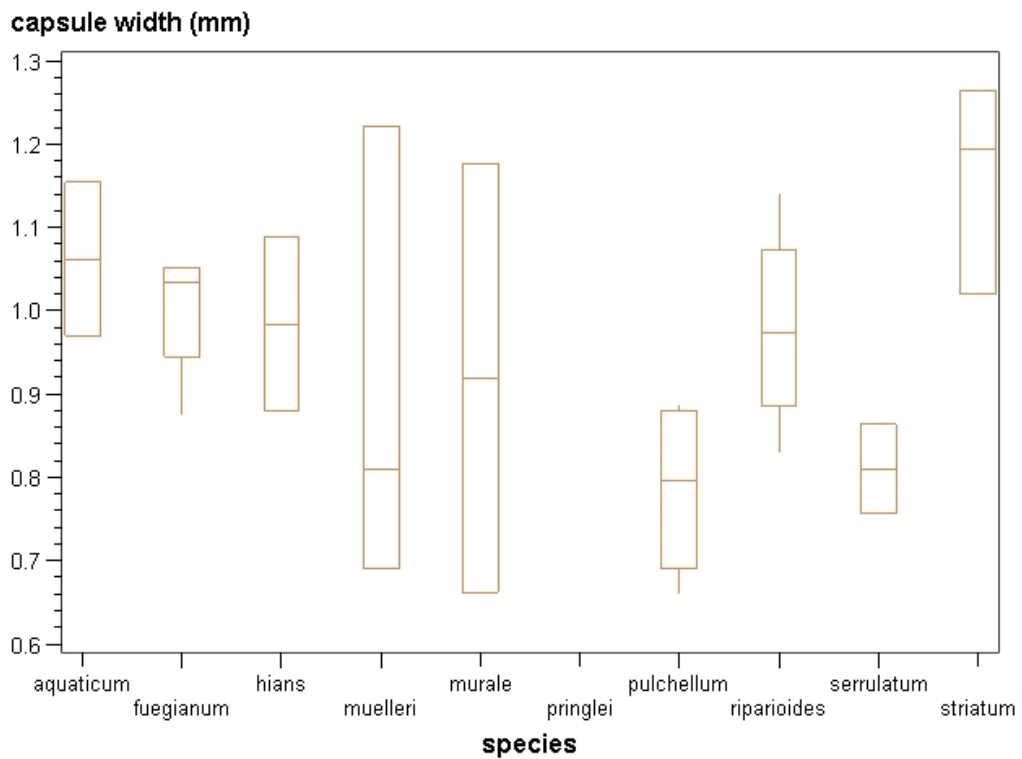


Figure B2. By-species comparison of average capsule width.

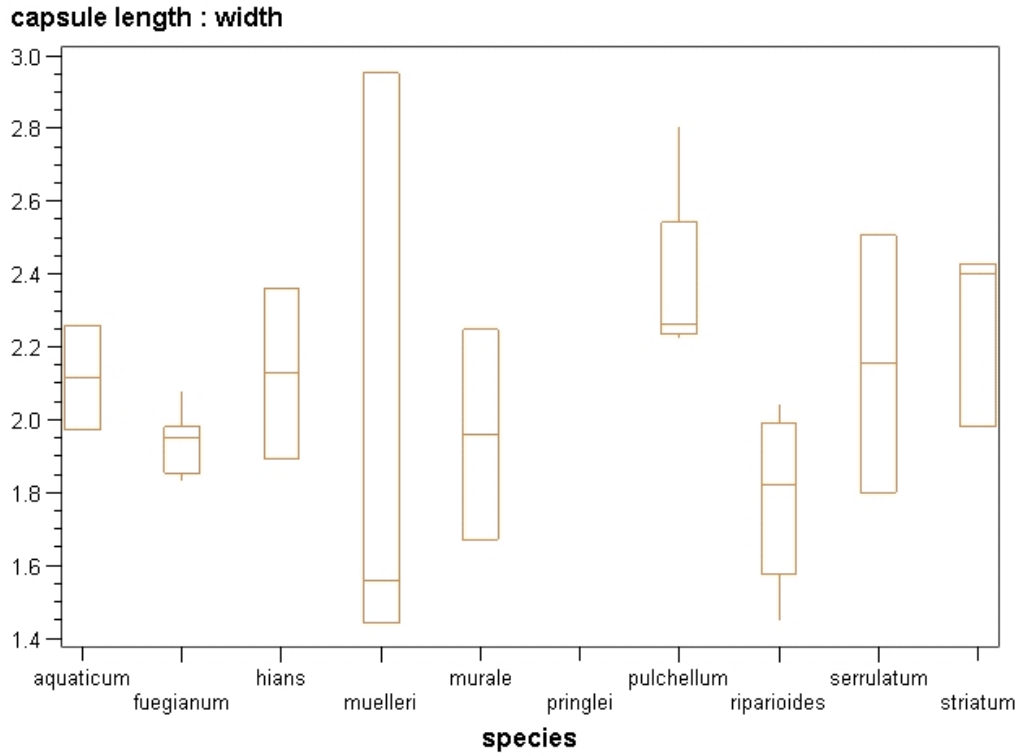


Figure B3. By-species comparison of average capsule length-to-width ratio.

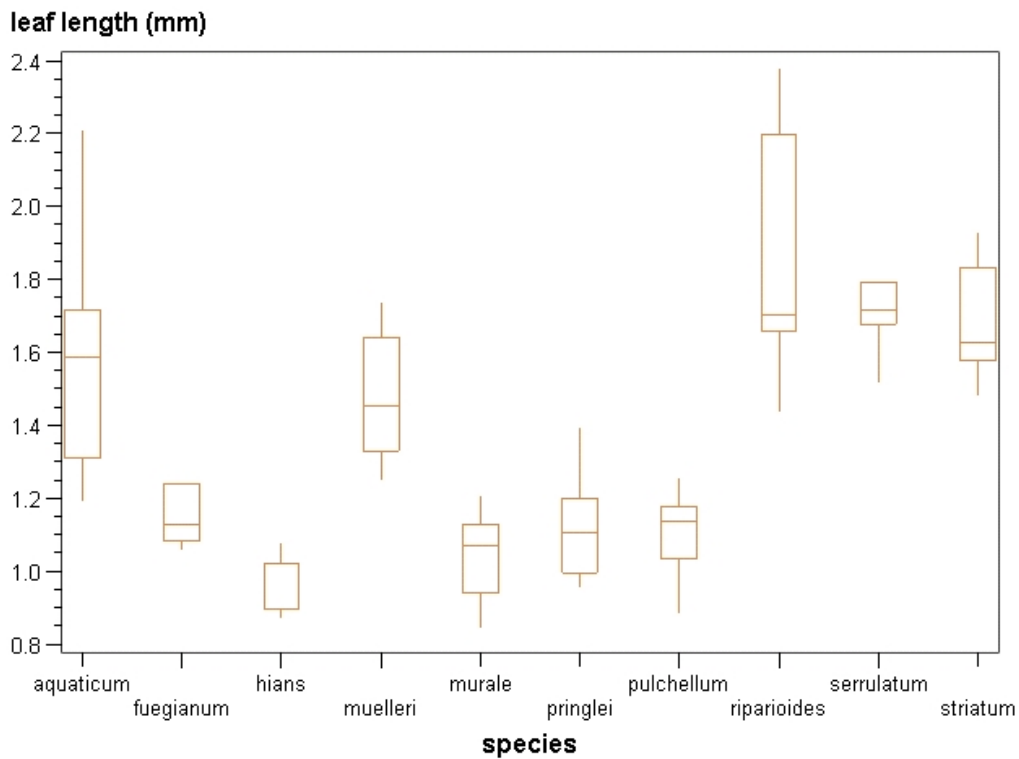


Figure B4. By-species comparison of average leaf length.

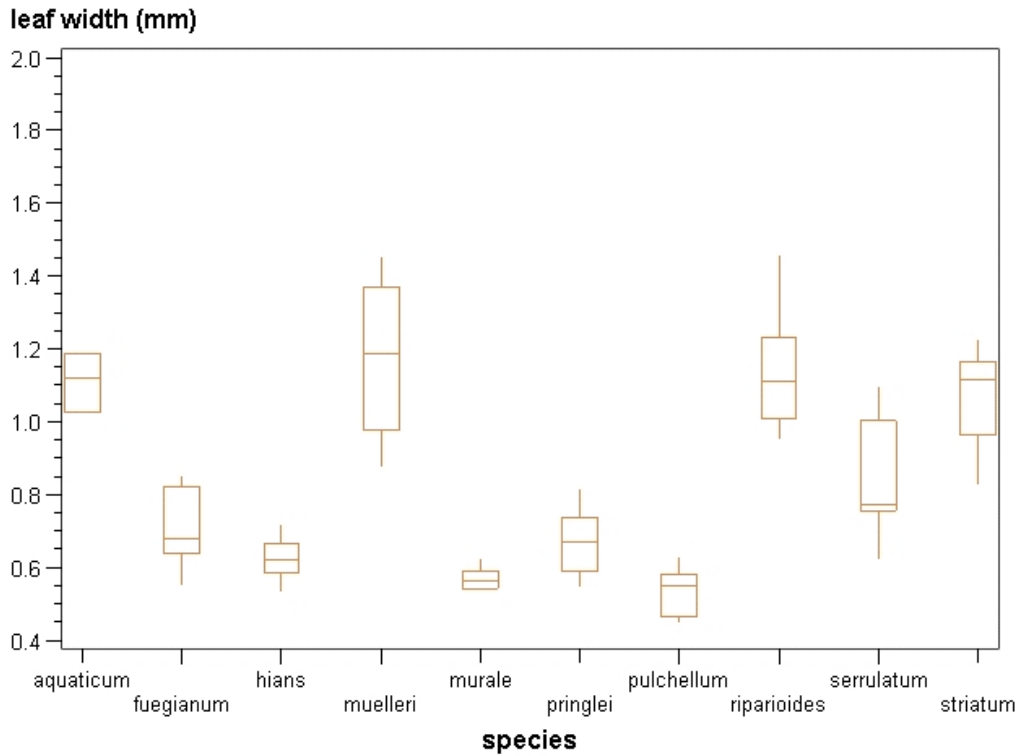


Figure B5. By-species comparison of average leaf width.

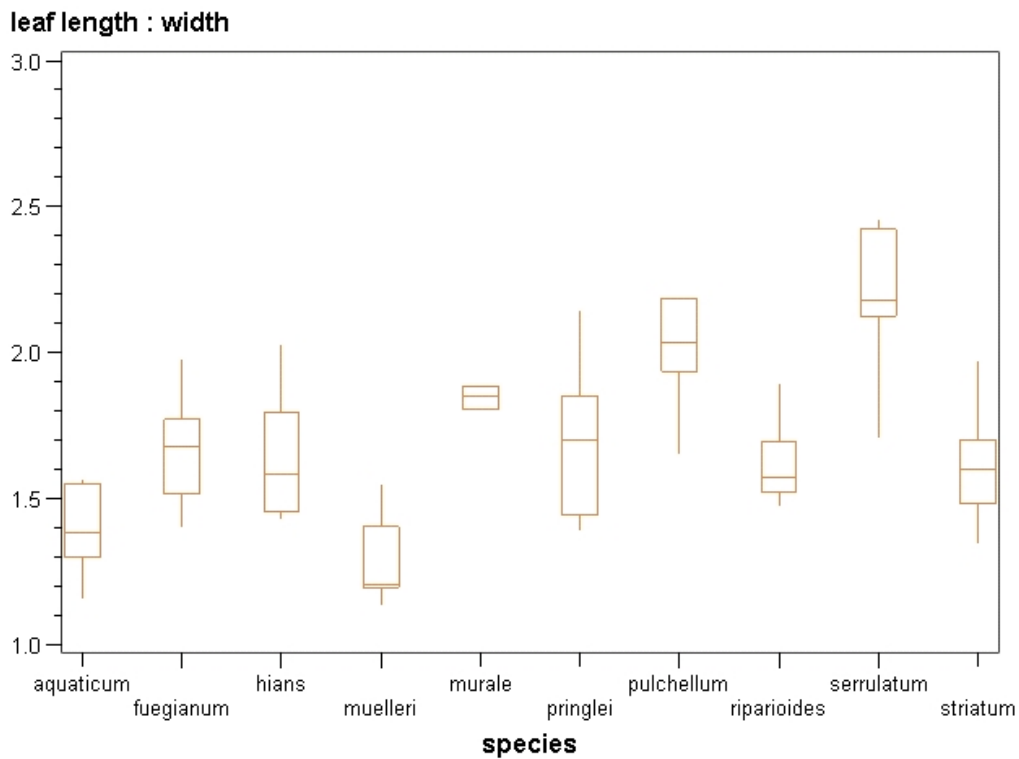


Figure B6. By-species comparison of average leaf length-to-width ratio.

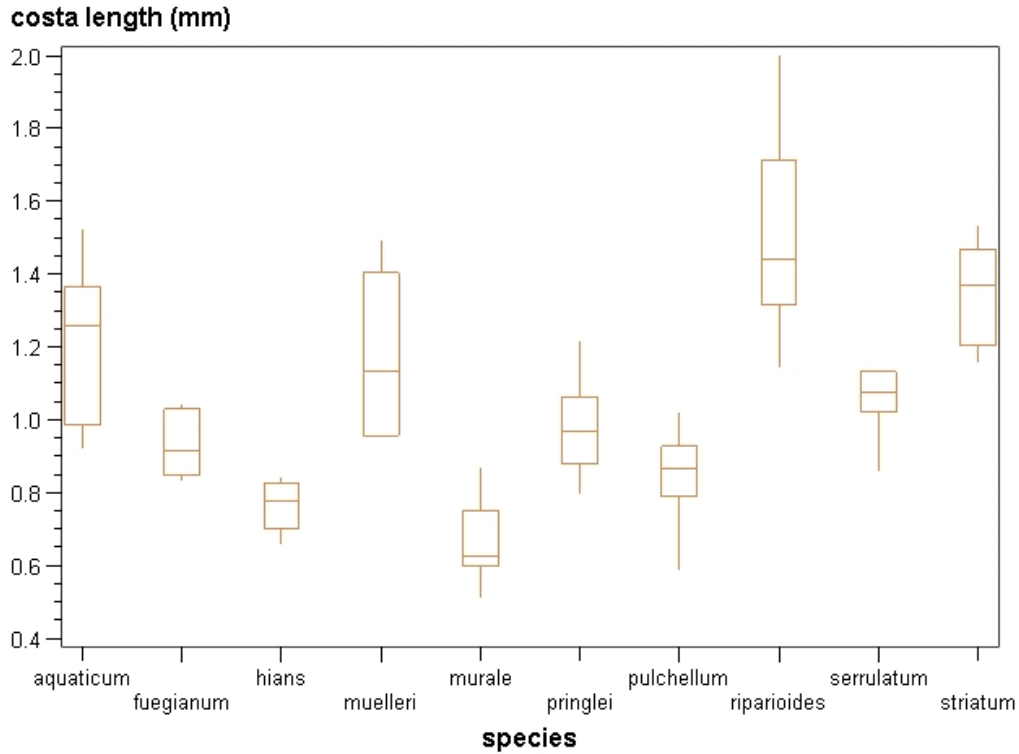


Figure B7. By-species comparison of average costa length.

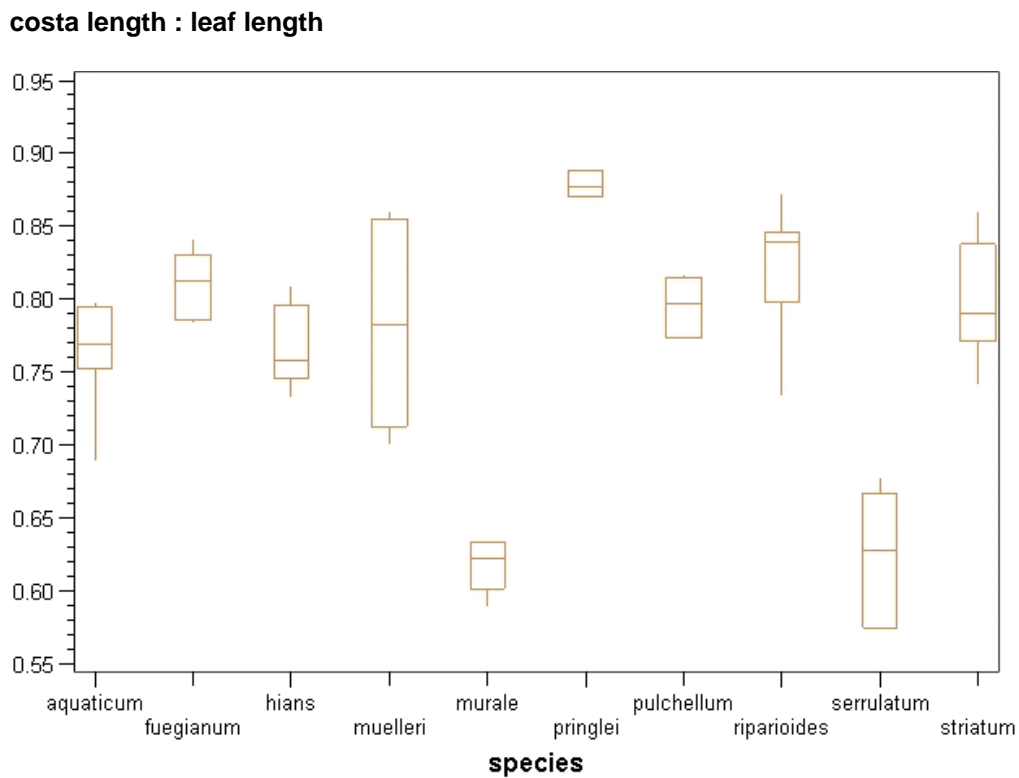


Figure B8. By-species comparison of average costa-to-leaf length ratio.

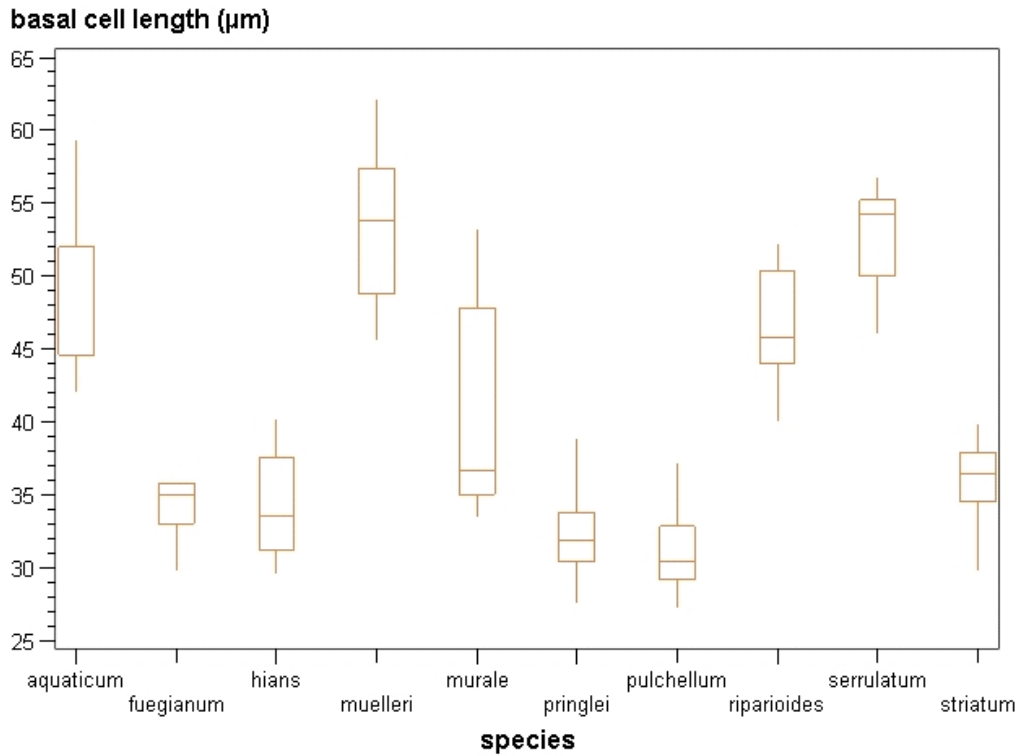


Figure B9. By-species comparison of average basal cell length.

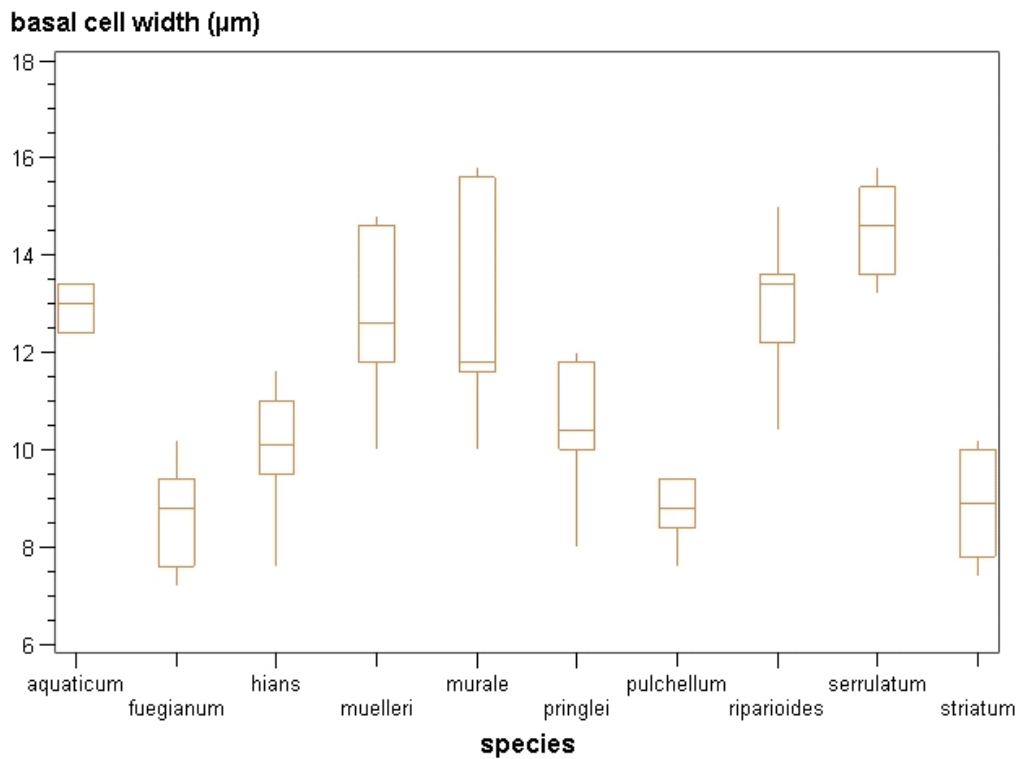


Figure B10. By-species comparison of average basal cell width.

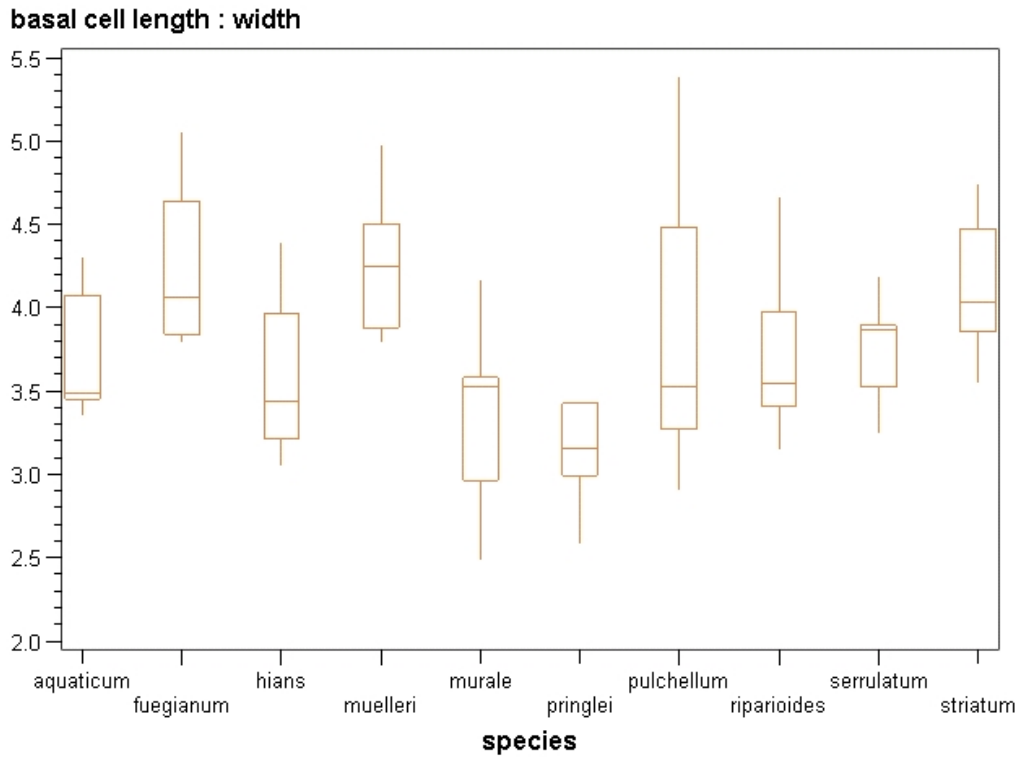


Figure B11. By-species comparison of average basal cell length-to-width ratio.

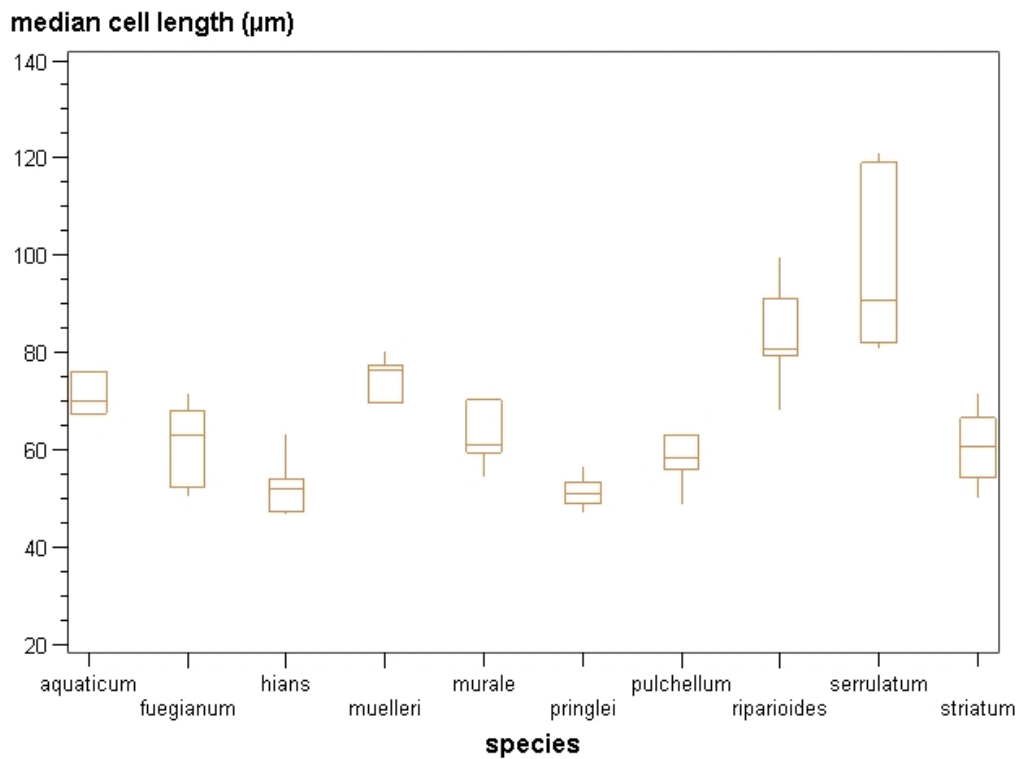


Figure B12. By-species comparison of average median cell length.

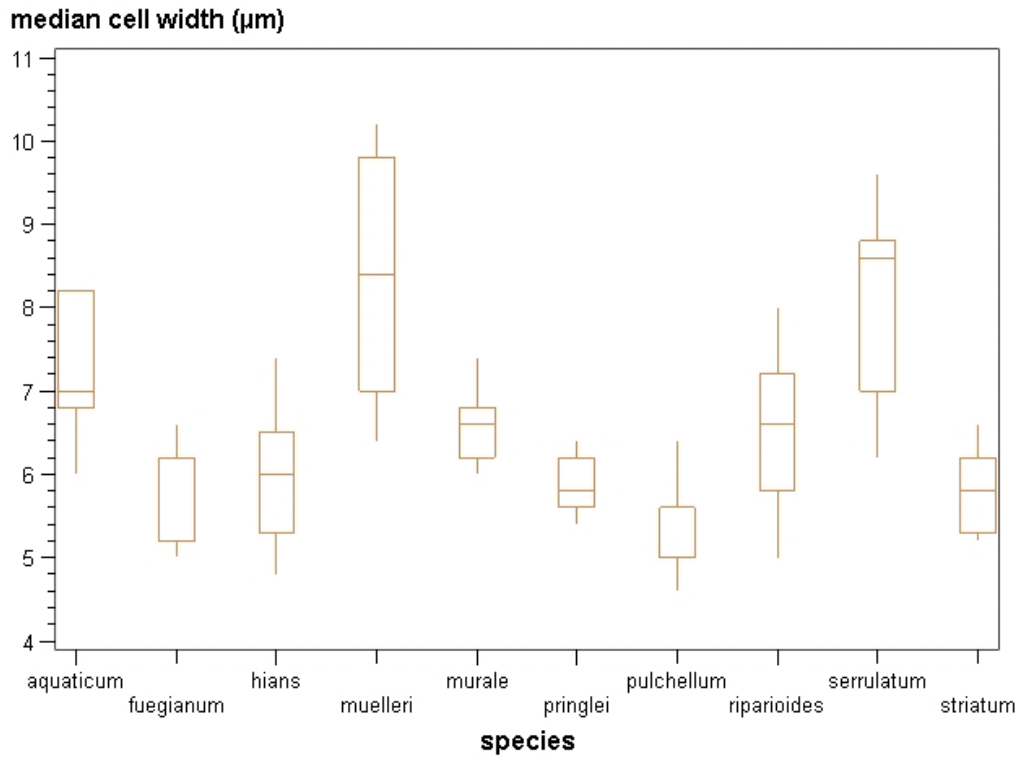


Figure B13. By-species comparison of average median cell width.

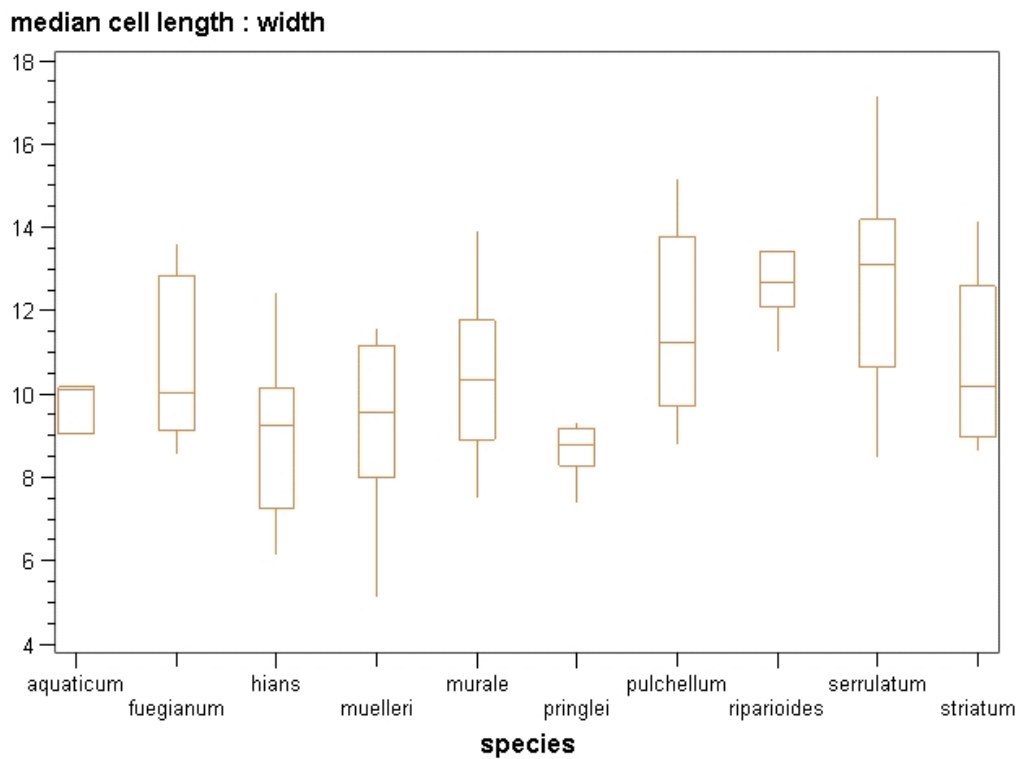


Figure B14. By-species comparison of average median cell length-to-width ratio.

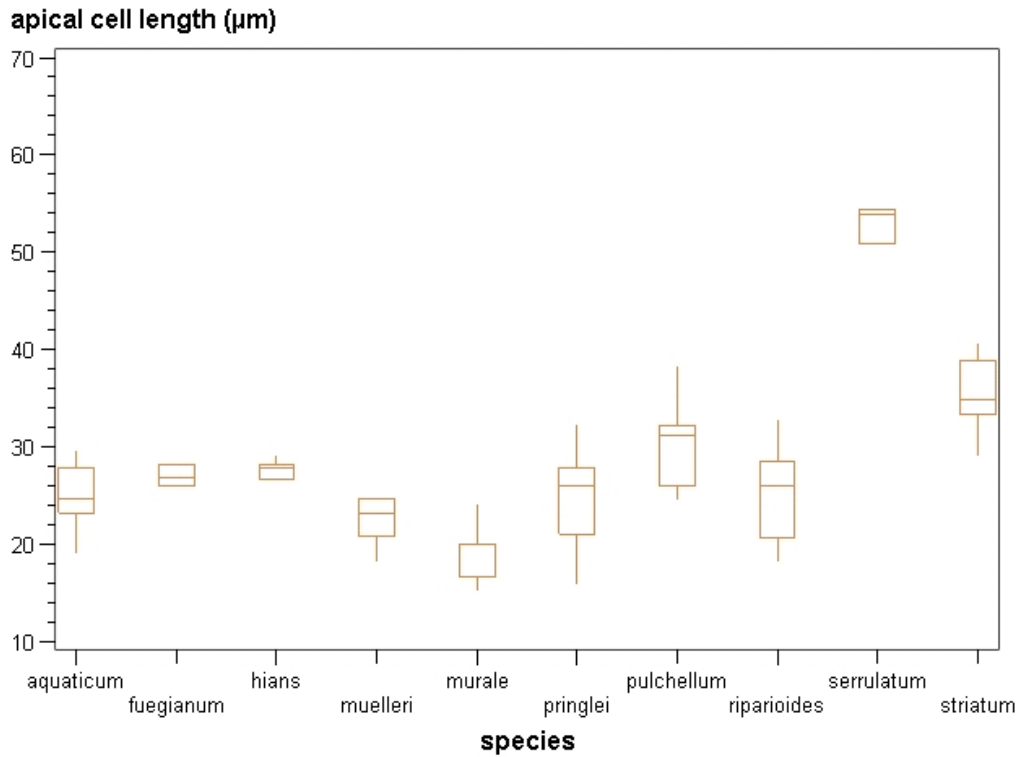


Figure B15. By-species comparison of average subapical cell length.

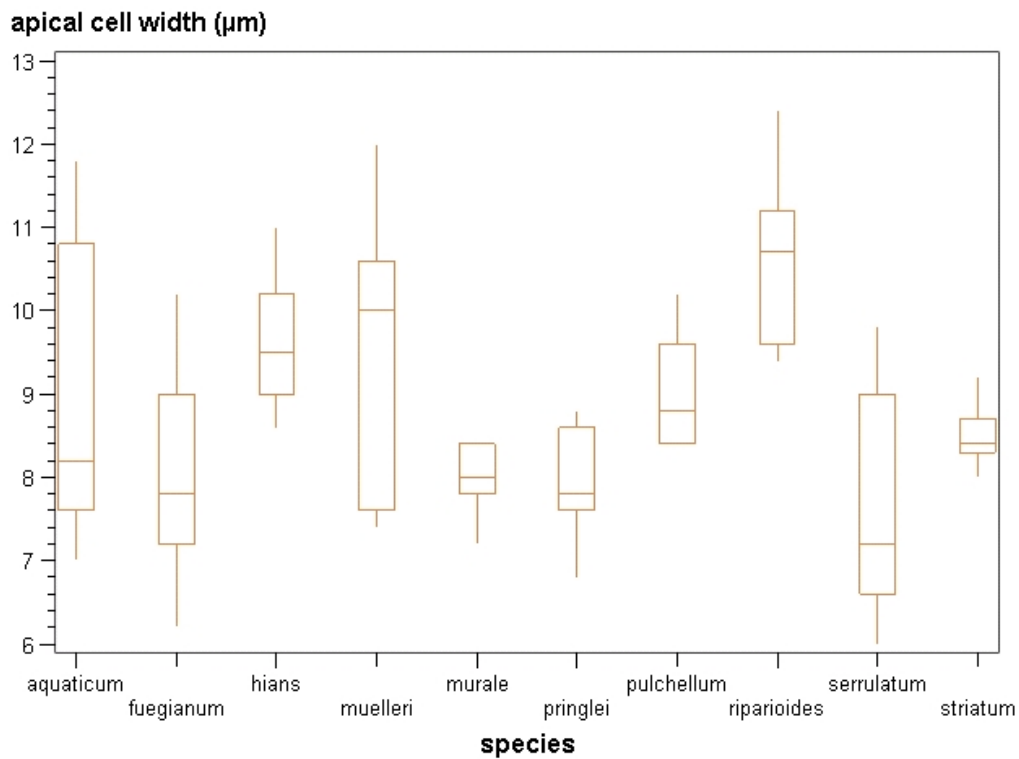


Figure B16. By-species comparison of average subapical cell width.

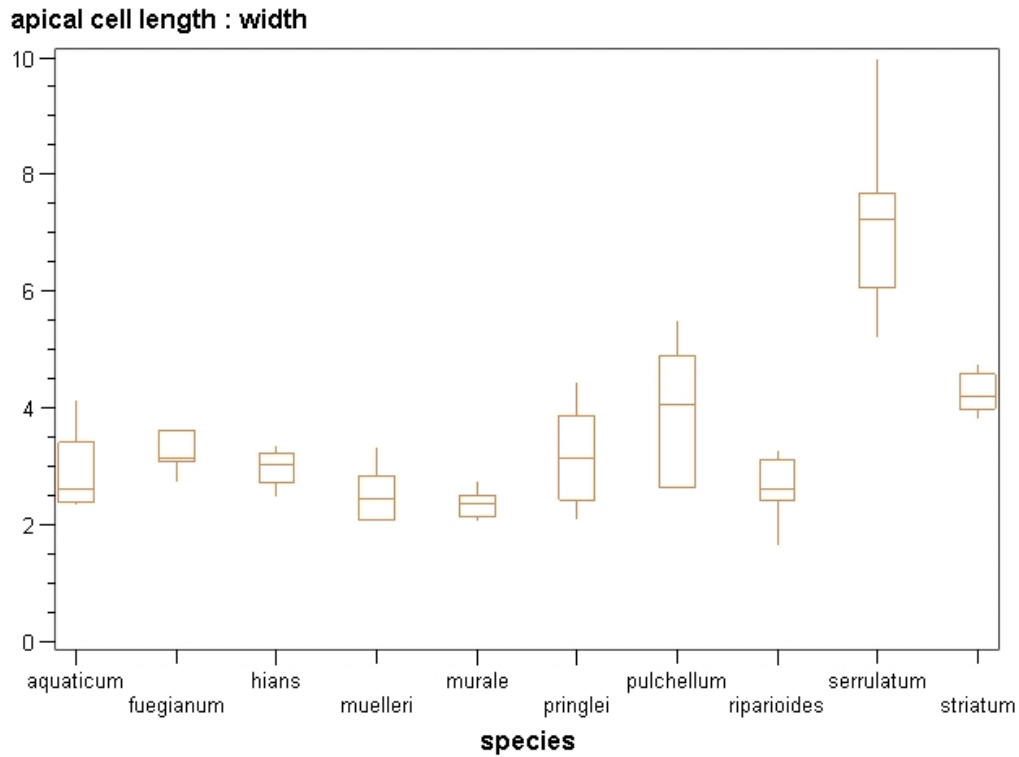


Figure B17. By-species comparison of average subapical cell length-to-width ratio.

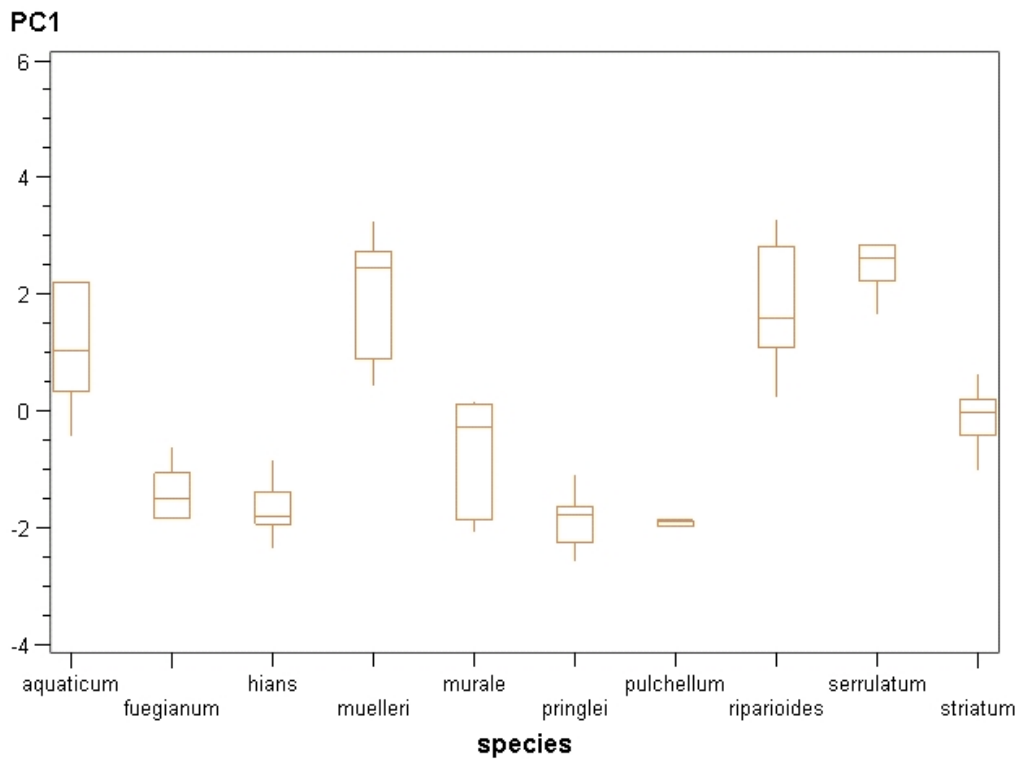


Figure B18. By-species comparison of Principal Component 1 score for PCA11.

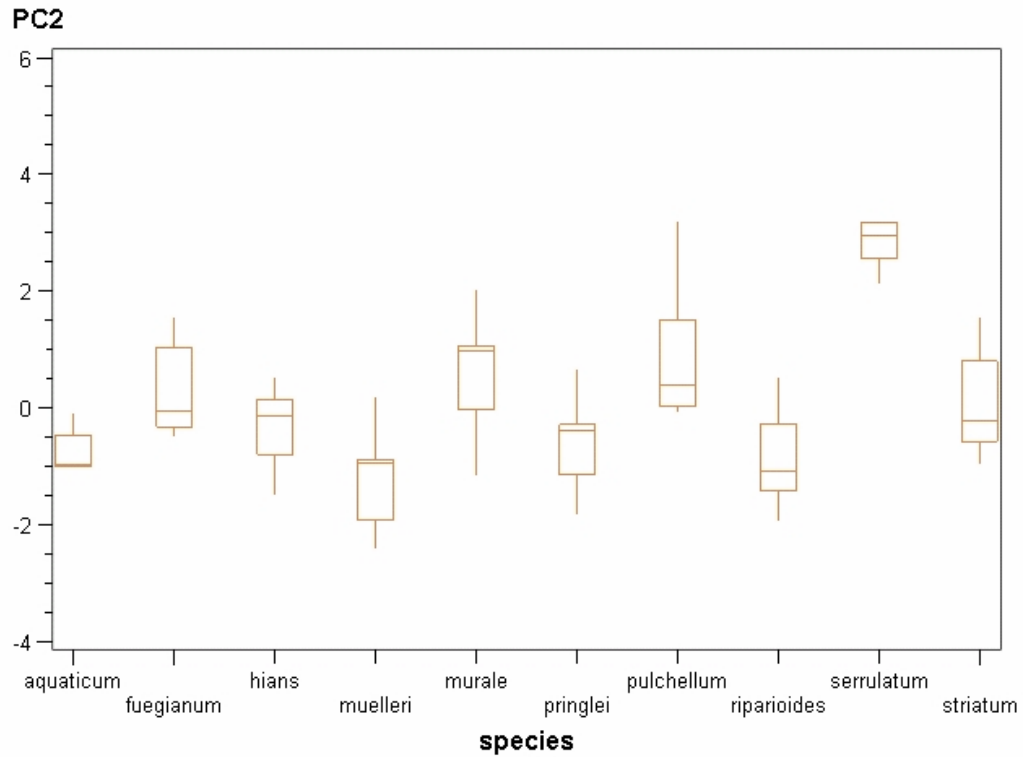


Figure B19. By-species comparison of Principal Component 2 score for PCA11.

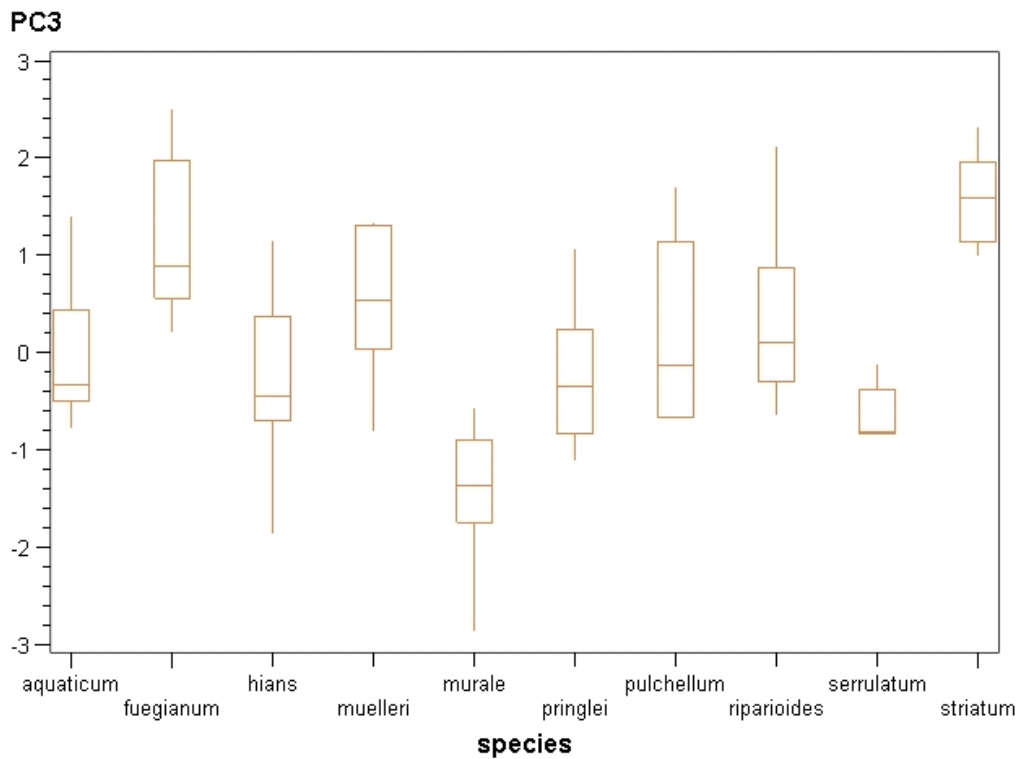


Figure B20. By-species comparison of Principal Component 3 score for PCA11.

II. Cladistic analyses

1. Morphological data

Morphometric methods were applied to a number of odd collections in addition to the ten species of *Platyhypnidium*, *Rhynchostegium*, and *Eurhynchium* under close study. The parsimony analysis of morphological data included 85 collections of Brachytheciaceae (Appendix 1). Based on preliminary analyses that included different/multiple outgroup taxa, *Scleropodium obtusifolium* was chosen as outgroup taxon, and it was the only OTU in the analysis that lacked a long-beaked operculum. Of the 45 characters included in the analysis, 42 were parsimony-informative, 2 variable characters were parsimony-uninformative, and 1 was constant. The strict consensus tree of 736 equally-parsimonious trees is shown in Figure 5. Tree length = 434; CI = 0.1636; RI = 0.6395. Bootstrap values (100 replicates) are superimposed on the branches of the cladogram. Here and hereafter, “*Oxyrrhynchium* sp. 1” denotes *E. selaginellifolium*.

2. Molecular data

The ITS region was successfully sequenced for 60 specimens of Brachytheciaceae. Several of the herbarium specimens I selected for DNA extraction were formerly misidentified, and therefore an even broader sampling of Brachytheciaceae was achieved, including three conic-operculate species (*Brachythecium rivulare*, *Bryhnia hultenii*, and *Scleropodium obtusifolium*). Although the sequence of the ITS region varied greatly between taxa in this study, in some species it was highly conserved. For example, the ITS sequence was identical in collections of *P. riparioides* from New York State and the Southern Appalachians, in spite of growing in different watersheds separated by over

seven hundred miles. Redundant sequences were excluded from the analyses; these were found in greater numbers in the ITS2 analysis. Both analyses based exclusively on ITS data were rooted with *Hygrohypnum luridum* (Figures 6 and 7).

A parsimony analysis of 47 nuclear ribosomal DNA sequences spanning both ITS regions was performed. Of 705 characters included in the analysis, 141 were parsimony-informative, 82 variable characters were parsimony-uninformative, and 482 were constant. The strict consensus of 108 equally-parsimonious trees yielded the topography shown in Figure 6. Tree length = 392; CI = 0.7551; RI = 0.9093. Bootstrap values (1000 replicates) are superimposed on the branches of the cladogram.

To survey the overall variation present in the sequence alignment, a likelihood analysis of the 5.8S–ITS2 region was performed on a 70-taxon data set that included 41 of the GenBank sequences listed in Table 5. Out of 444 included characters, heuristic searches under ML resulted in 18 equally-likely trees ($-\ln L = 2617.57201$; Figure 7).

3. Combined data

For 45 specimens, both molecular and morphological data were available. Another maximum parsimony search was performed on a matrix of this group of sequences. Of 951 characters included in the analysis, 169 were parsimony-informative, 36 variable characters were parsimony-uninformative, and 746 were constant. The strict consensus of 72 equally-parsimonious trees yielded the topography shown in Figure 8. The tree is rooted by *Brachythecium rivulare* and *Bryhnia hultenii*. Tree length = 545; CI = 0.4899; RI = 0.8130. Bootstrap values (1000 replicates) are superimposed on the branches of the cladogram.

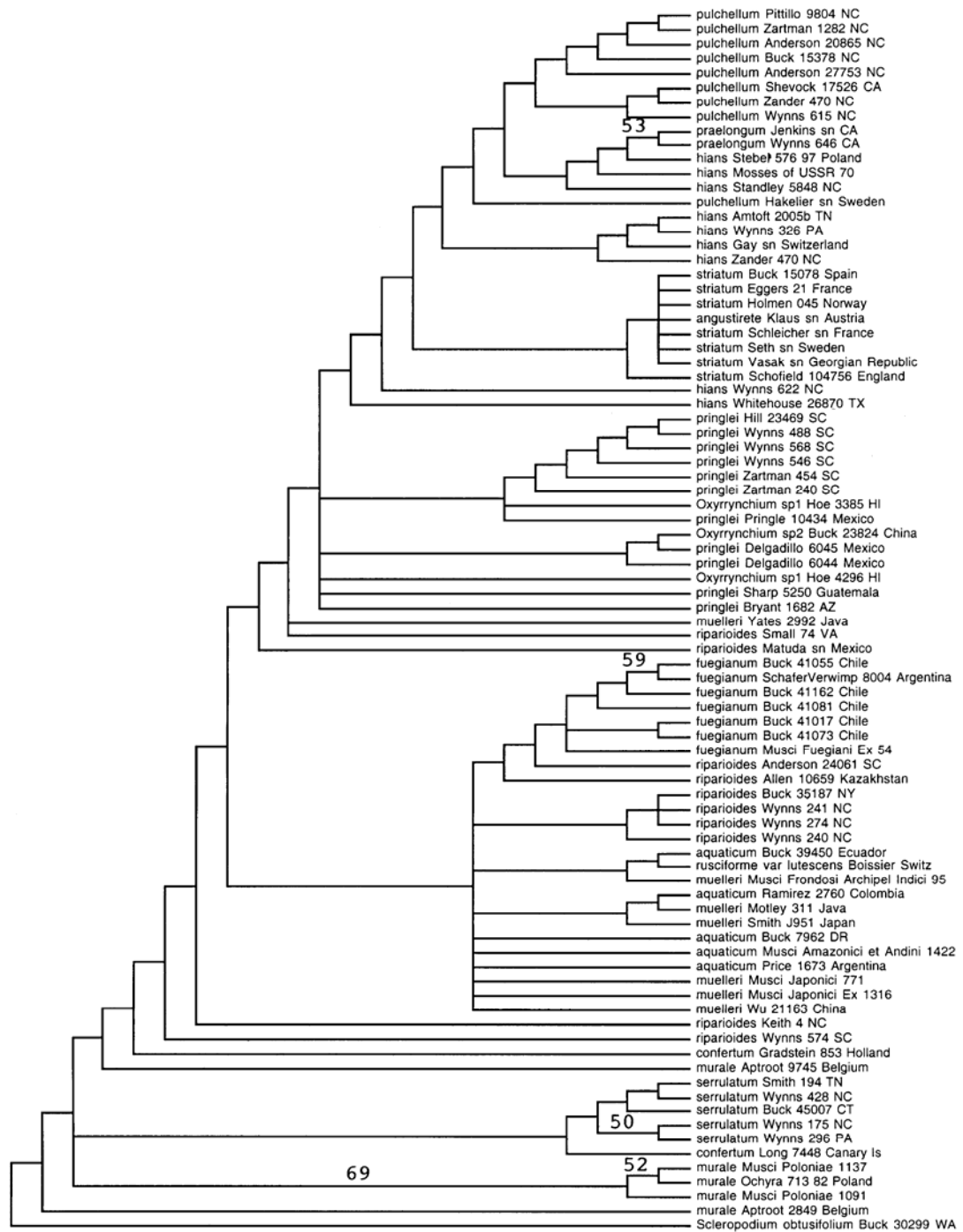


Figure 5. Strict consensus of 736 equally-parsimonious trees based on 45 morphological characters for 85 specimens. Bootstrap values (100 replicates) are indicated.

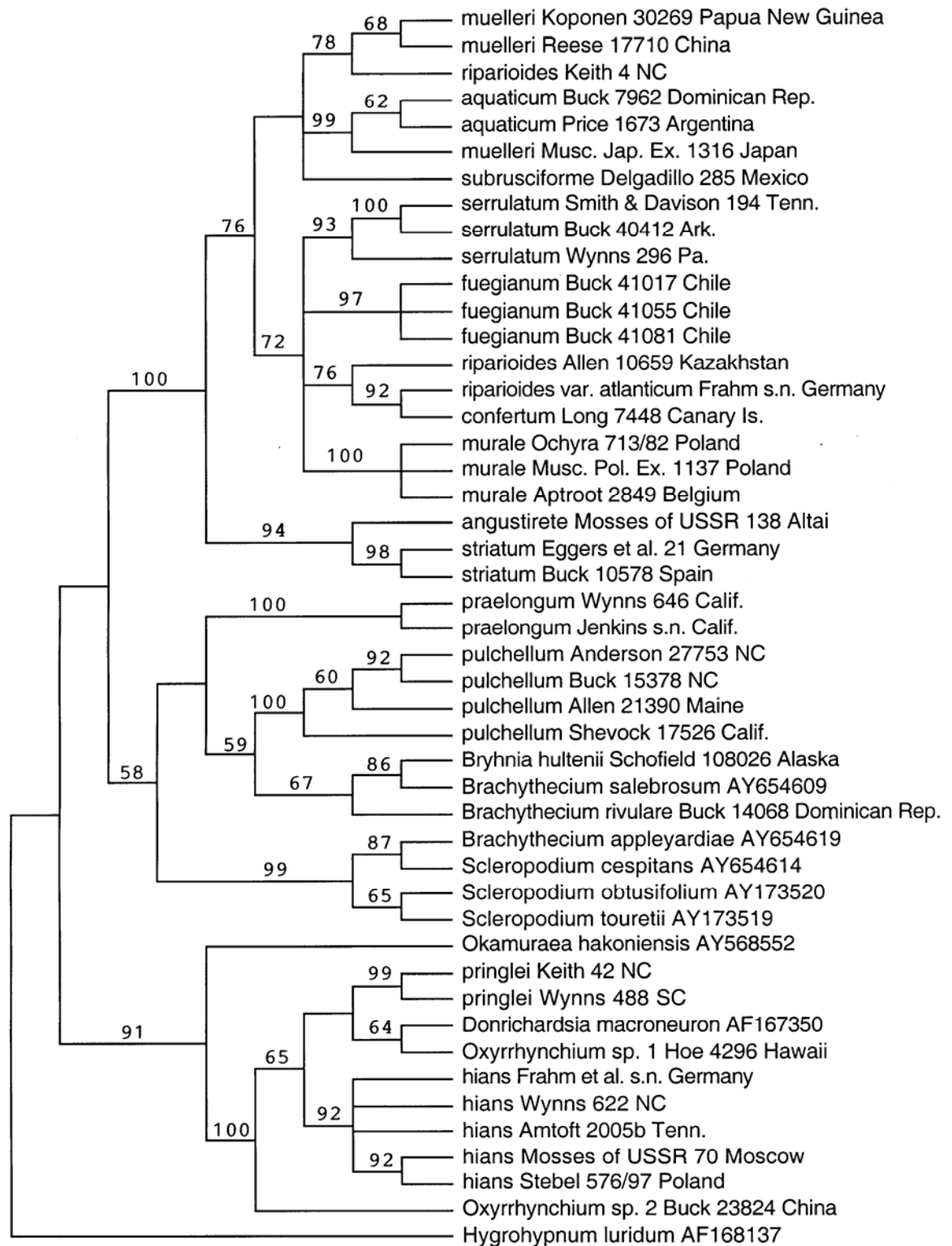


Figure 6. Strict consensus of 108 equally-parsimonious trees based on 47 complete ITS rDNA sequences. Bootstrap values (1000 replicates) are indicated.

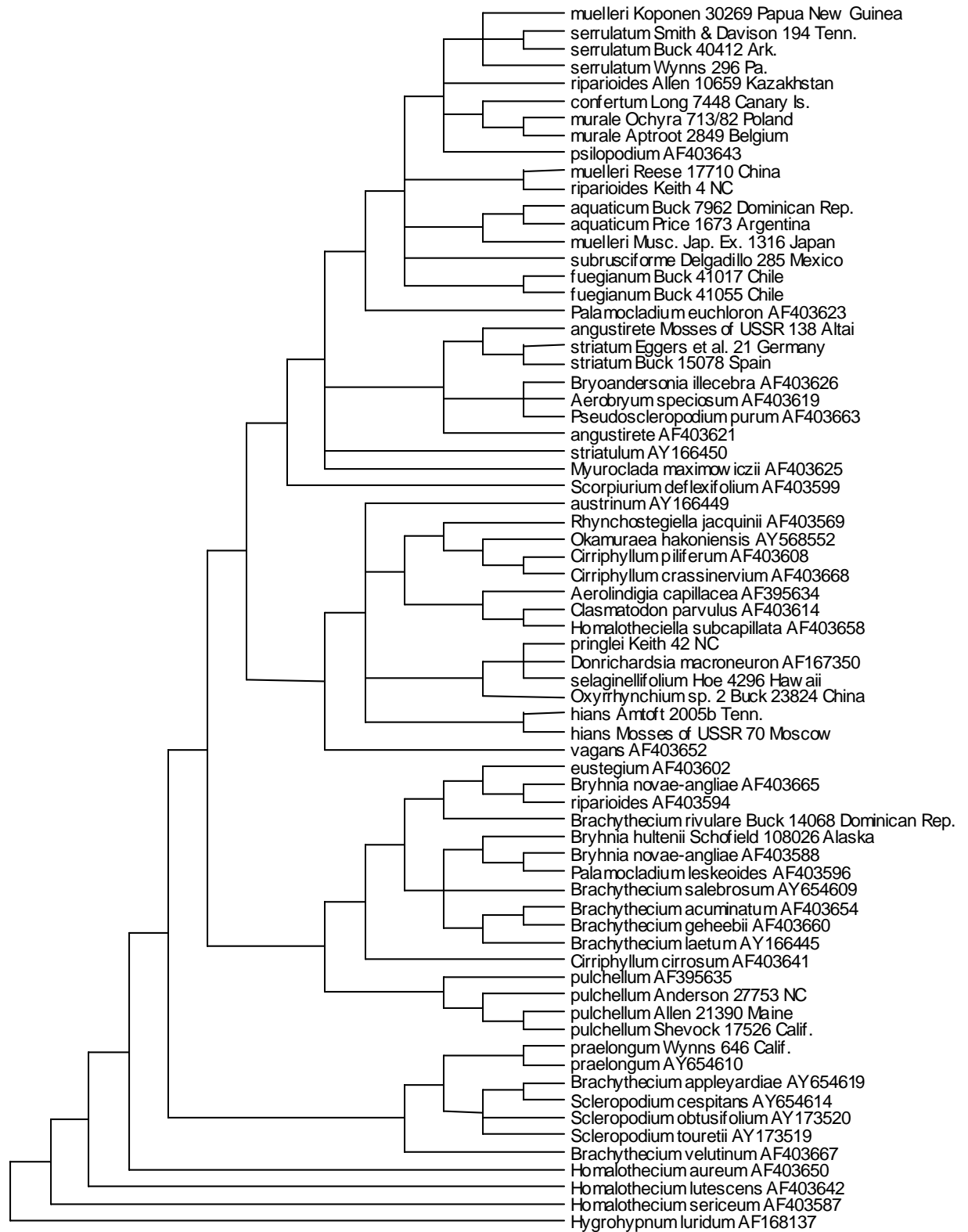


Figure 7. Consensus of 18 equally-likely trees based on 5.8S-ITS2 data for 70 specimens.

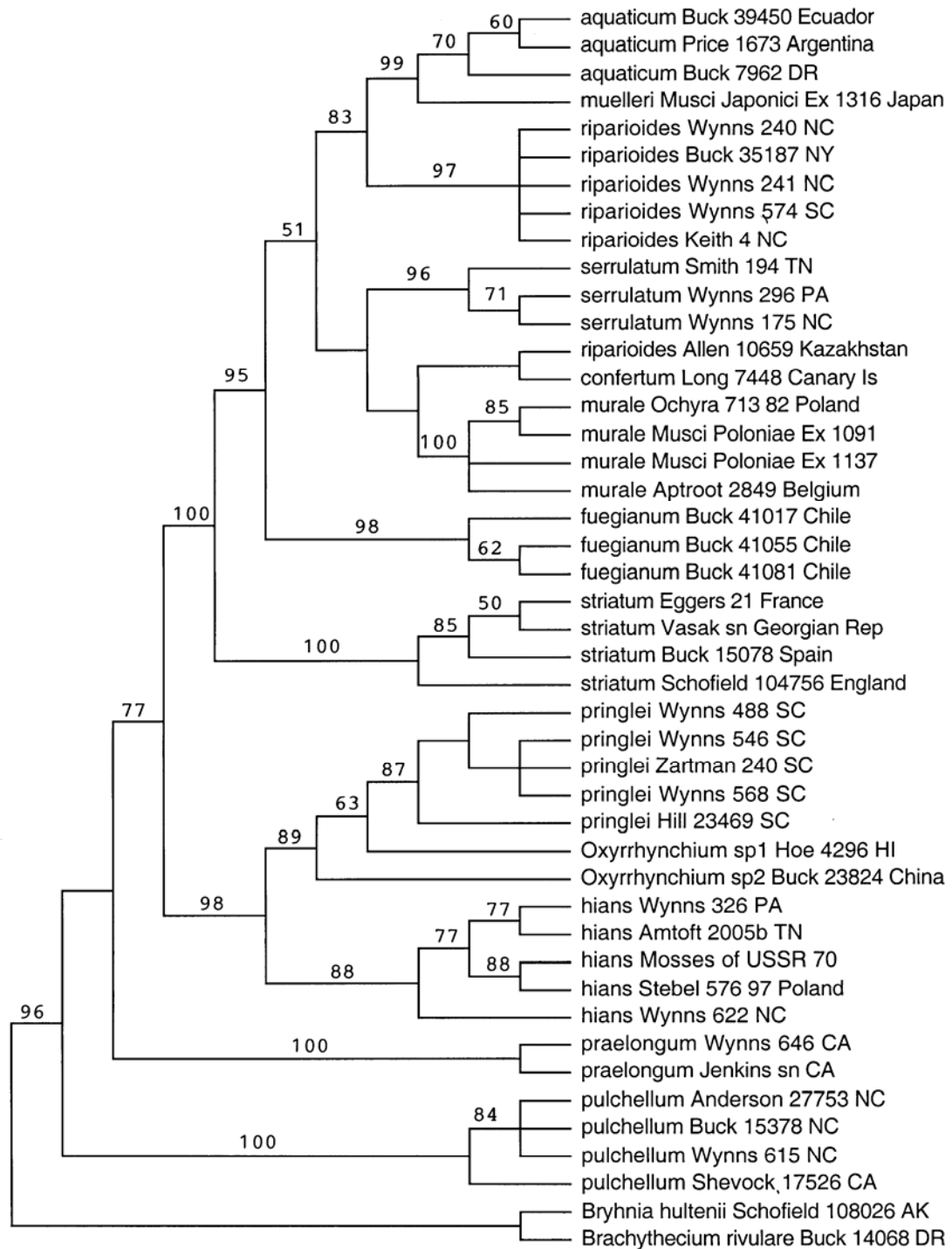


Figure 8. Strict consensus of 72 equally-parsimonious trees based on combined morphological and molecular (ITS) data for 45 specimens. Bootstrap values (1000 replicates) are indicated.

DISCUSSION

The single synapomorphy for the main taxa under study (a long-beaked operculum) is evidently not a reliable character for the delimitation of monophyletic groups in the Brachytheciaceae. In some genera (e.g., *Homalothecium* Schimp.) both conic and rostrate opercula are known. In other genera (e.g., *Rhynchostegiella*, *Bryhnia* Kaurin, or *Scleropodium* Bruch & Schimp.) intermediate forms are present (operculum long-conic, conic-apiculate, or short-rostrate). It should not therefore have come as a surprise that different groups of rostrate-operculate taxa included in this study were resolved in widely divergent parts of the family.

As a consequence of the apparently polyphyletic natures of both *Platyhypnidium* and *Eurhynchium*, the specimens included in this study represented a rather broad sampling of Brachytheciaceae. However, the study was not designed to evaluate phylogenetic relationships within the entire family, and the data set is not large enough (in number of characters, or taxa) to be useful for classification above the genus level. For suprageneric classification of the Brachytheciaceae, reference should be made to the phylogeny presented in Ignatov & Huttunen (2002).

The cladograms generated from DNA sequence data were suggestive of many interesting relationships. Although bootstrap values should be viewed with skepticism as being possible overestimates or underestimates of the confidence one can place in a clade

(Swofford & Begle 1993), very high bootstrap values certainly lend a putative clade credibility. In the ITS analysis, two distinct lineages with complete bootstrap support (100) were found: one which included *P. aquaticum*, *P. muelleri*, *P. riparioides*, *P. fuegianum*, all species of *Rhynchostegium*, and *E. striatum* (including *E. angustirete*); and one which I have called the “*Oxyrrhynchium* lineage,” that included *E. hians*, *P. pringlei*, *E. selaginellifolium*, and other aquatic taxa.

ITS data appear to be quite appropriate for phylogeny reconstruction in the rostrate-operculate Brachytheciaceae, especially when ITS1 data are included (Stech & Frahm 1999a). However, two broadly-distributed species (*P. riparioides* and *P. muelleri*) were not resolved as monophyletic entities in the ITS-based analyses. Apparently, in some species geographically-isolated populations have become strongly differentiated in terms of their ITS sequences. Since the ITS region is mostly non-coding (although not necessarily non-functional), variation in ITS among geographically-isolated conspecific populations is not surprising. In fact, a lack of variation in widely-separated populations would be more surprising.

It is unfortunate that I was not able to sequence a second locus (of chloroplast DNA) to increase the resolution of the cladogram based on molecular data. However, ITS data typically provide more resolution than other loci (Huttunen & Ignatov 2004). Therefore, clades of ITS sequences which are very strongly supported probably do represent natural groups of taxa.

The topology of the tree based on morphology alone conflicted seriously with the cladograms based on ITS data. Since the morphological characters used in the phylogenetic analyses were exceedingly homoplastic, it might be unwise to place too

much confidence in the relationships suggested in Figure 5. However, the three traditional genera *Rhynchostegium*, *Platyhypnidium*, and *Eurhynchium* could be broadly distinguished. This result was gratifying because it showed that the traditional classification of this group based on morphology (alpha-taxonomy) was also found by cladistic analysis of morphological characters. A phylogenetic approach to morphological analysis should therefore be justifiable whenever homoplastic characters can be identified and excluded. Unfortunately, in the case of pleurocarpous mosses, nearly all the characters seem to be potentially homoplastic (cf. Hedenäs 1997). Therefore one may expect that phylogenies of pleurocarpous mosses based strictly on morphology will not accurately reflect natural relationships. In short, morphometric data are really quite inappropriate for the reconstruction of pleurocarp phylogenies.

To find relationships which were supported by both kinds of data (morphological and molecular), I performed a combined analysis of 45 OTUs. Although the tree produced by this analysis should be viewed with more skepticism than the tree based on ITS alone, it did in some ways suggest a more satisfactory systematic arrangement. For example, this analysis resolved *P. fuegianum* in an intermediate evolutionary position between *E. striatum* and *Rhynchostegium* / *Platyhypnidium s. str.*

The phenetic analyses were suggestive of many relationships, including some which seemed to be natural. In particular, dimensional differences at the cellular level appeared to be useful for separating some taxa; e.g., median cell length-to-width ratio could be used to separate *P. muelleri* and *P. riparioides*; and the basal cells appeared to be consistently wider in *Rhynchostegium* and *Platyhypnidium s. str.* than in *P. pringlei* or any species of *Eurhynchium sensu lato*. However, many other significant dimensional

differences revealed by ANOVA were suggestive of artificial relationships. In particular, leaf size tended to cluster species which are not really closely related, e.g., *R. murale* and *E. hians*. There is not much similarity between the gametophytes of these species, other than that they both have rather small leaves.

Principal Components Analysis supported some of the relationships identified in the phylogenetic analyses; e.g., the close relationship between *P. pringlei* and *E. hians*. It also supported the separation of *E. praelongum* from other species of *Eurhynchium*. However, the separation of *R. serrulatum* from other species of *Rhynchostegium* was also well supported by PCA, although the placement of *R. serrulatum* in *Rhynchostegium* is now widely accepted (cf. Buck 1998). All phylogenetic analyses also supported the generic identity of *R. serrulatum*. So, phenetic data could also be highly misleading. From this study, it appears that phenetic clusters generated by PCA can be good indicators of evolutionary kinship between taxa, but relationships suggested by PCA should be corroborated with other kinds of data (i.e., molecular data) before they are accepted.

In general, the taxonomic patterns revealed in the phenetic analyses better reflected the molecular phylogeny than did the phylogenetic analysis based on morphology. These results suggest that morphological data from pleurocarpous mosses are better treated with phenetic analysis than with phylogenetic analysis. Therefore, future morphometric studies of pleurocarpous mosses should probably focus on the collection of continuous-variable (measurement) data, rather than on the collection of discrete character-state data. This is convenient, because the assignment of characters to discrete states in pleurocarpous mosses can be quite arbitrary, and is often confounded by

the discovery of specimens having a phenotype intermediate between two supposedly distinct states.

The importance of including more than one representative of each species in a statistical analysis was highlighted by this study. For example, the apparent polyphyly of *P. riparioides* found by the molecular analyses would not have been identified if only one specimen had been used to represent the species. Also, since misidentification of pleurocarpous mosses in the herbarium is very common, comparison of multiple representatives of a single species should reduce the number of misnamed taxa included in pleurocarp phylogenies.

Platyhypnidium

In the phenetic analyses, the segregation of *Platyhypnidium* from *Rhynchostegium* was generally supported. In both Principal Component analyses, a *Platyhypnidium s. str.* [= *P. riparioides*, *P. muelleri* and *P. aquaticum*] cluster was perceptible; sometimes encroaching on *E. striatum*, and sometimes on terrestrial species of *Rhynchostegium*. Although ANOVA identified a few characters which could be used to separate *P. muelleri* and *P. riparioides* (leaf length, costa length, median cell width, and median cell length-to-width ratio), *P. aquaticum* was in no respect significantly different from either species. In ANOVA, costa length-to-leaf length ratio and Principal Component 3 could be used to separate *Platyhypnidium* and *Rhynchostegium*; (the latter variable accounting for about 13% of the variation in the Principal Components data set). The phylogenetic analysis based on morphology also supported the distinctiveness of *Platyhypnidium*.

In contrast, the analyses of molecular data alone strongly supported the inclusion of *Platyhypnidium* in *Rhynchostegium*. In the ITS analysis, two clades that included all species of *Platyhypnidium* and *Rhynchostegium* were identified: one mainly-aquatic clade that included *P. riparioides* from eastern North America, *P. aquaticum*, *P. muelleri*, and *R. subrusciforme* (Müll. Hal.) A. Jaeger; and one mainly-terrestrial clade that included all other species of *Rhynchostegium*, plus *P. fuegianum* and two Old World collections of *P. riparioides*. In the analysis of ITS2 alone, *R. murale*, *R. confertum*, *R. serrulatum*, *R. psilopodium* Ignatov & Huttunen, one specimen of *P. riparioides* from Kazakhstan (Allen 10659, DUKE), and one specimen of *P. muelleri* from Papua New Guinea (Koponen 30269, NY) formed a clade sister to the other collections of *Platyhypnidium* s. str., *P. fuegianum* and *R. subrusciforme*.

One explanation for the apparently polyphyletic natures of both *P. riparioides* and *P. muelleri* in the molecular analyses is that each species is composed of more than one unrelated but morphologically inseparable aquatic lineage related to *Rhynchostegium*. Another explanation is that either or both are good species, but *Platyhypnidium* cannot be neatly separated from *Rhynchostegium* using ITS data. The degree of infraspecific molecular polymorphism seen in the ITS sequences of geographically-separated populations of *P. riparioides* and *P. muelleri* is comparable to the degree of variation observed between terrestrial species of *Rhynchostegium*. Based on the grouping of *P. fuegianum* and some other *Platyhypnidium* collections with the terrestrial species of *Rhynchostegium* in the molecular analyses, it does not appear that the terrestrial habit may be used to separate *Rhynchostegium* from *Platyhypnidium*.

Both *Platyhypnidium* and *Rhynchostegium* have smooth, glossy, concave leaves with relatively weak costae. Even in robust taxa, the leaves have a somewhat delicate quality. Sometimes the plants are bronzed or reddish. The capsules are like those of *Brachythecium*, except the operculum is rostrate; and in *Platyhypnidium* they tend to be plump (resembling *B. plumosum*). All species of *Rhynchostegium* and *Platyhypnidium* are autoicous and have smooth setae. I consider *Platyhypnidium* a distinctive subgenus of *Rhynchostegium* that includes at least two large, aquatic, rheophilous, broad-leaved species: *P. aquaticum* and *P. riparioides*. Therefore I describe these two species under *Rhynchostegium* (below).

The cladistic analyses based on molecular data strongly indicated that *Platyhypnidium fuegianum* is better placed in its present genus than in *Eurhynchium*. However, in the combined analysis of molecular and morphological data, *Rhynchostegium* (including *Platyhypnidium*) was resolved as monophyletic without *P. fuegianum*. The PCAs also grouped *P. fuegianum* with *Eurhynchium*. For these reasons, *P. fuegianum* is discussed here under *Eurhynchium*.

Platyhypnidium pringlei turned out to be closely related to *E. hians*, the type species of *Oxyrrhynchium* (Zijlstra 2005); and therefore it is discussed here under *Oxyrrhynchium*. The *Oxyrrhynchium* lineage seems to be well characterized by loosely-foliate, \pm complanate plants with pointy leaves (never blunt) which are somewhat plicate and twisted medially when dry. Most species are dioicous and have rough setae. *Platyhypnidium*, as represented by the five species included in this study, was rendered polyphyletic by the inclusion of *P. pringlei*.

A GenBank sequence of *P. austrinum*, a rough-setaed Australian species, was included in the analysis of ITS2. In that analysis, *P. austrinum* was resolved within the *Oxyrrhynchium* clade, but in an isolated position. *Platyhypnidium austrinum* is therefore also discussed here under *Oxyrrhynchium*. The rough seta is incongruous in *Platyhypnidium*, so the removal of *P. austrinum* from the genus is desirable.

Undoubtedly there are fewer species of *Platyhypnidium s. str.* than are listed in Table 1. The following key may be used to distinguish between most aquatic specimens that one would be tempted to call *Platyhypnidium*:

Key to *Platyhypnidium*

J. Wynns, IV/2006

1. Plants somewhat to distinctly complanate; leaves distant, often noticeably plicate; seta (when present) rough.....2
1. Plants terete; foliation denser; seta (when present) smooth.....5
2. Leaves normally less than 1.5 mm long; costa thick.....3
2. Some leaves exceeding 1.5 mm; leaves broad; costa slender.....4
3. Plants obligately aquatic; leaves ovate-lanceolate, acute or short-acuminate, frequently homomallous; costa occupying 75–95% of leaf.....*P. pringlei*
3. Plants not obligately aquatic; leaves often ovate or oblong-ovate, heteromallous; costa occupying 65–85% of leaf.....*E. hians*
4. Costa usually occupying 65–75% of leaf; from Australia or nearby.....*P. austrinum*
4. Costa usually occupying 80–90% of leaf; Hawaiian endemic.....*E. selaginellifolium*
5. Leaves less than 1.4 mm long, ovate-acuminate; costa stout; plants bushy; endemic of southern South America.....*P. fuegianum*
5. Plants without the above combination of characters.....6
6. Plants not obligately aquatic, medium-sized, bright green and shiny; leaves oblong-ovate, appressed to erect; costa weak; from Central America.....*P. subruscifforme*
6. Plants without the above combination of characters; subaquatic to aquatic, robust.....7
7. Ultimate branches julaceous, homomallous; leaves secund, broadly decurrent, longly and broadly apiculate.....*Brachythecium rivulare*
7. Ultimate branches loosely foliate, heteromallous; leaves not decurrent or longly apiculate.....8

8. Leaves ovate-lanceolate, acuminate; costa thick, ending near apex.....9
 8. Leaves broadly ovate or oblong-ovate, obtuse or acute; costa slender.....10
9. Plants dark green, terete; leaf lamina with multistratose streaks.....*P. mutatum*
 9. Lamina unistratose.....*P. riparioides*
10. Plants brownish, subjulaceous; leaves narrow, oblong-ovate; median leaf cells narrow, 4–8 µm wide; costa weak; from England and western Europe..*P. lusitanicum*
 10. Leaves large, broad, ovate or ovate-acuminate, not appressed; some cells broader....11
11. Plants usually green; branches not crispate at tips; leaves ovate or broadly ovate, obtuse or acute; median leaf cells long, ca. 13:1; cilia of endostome long, in groups of 3–4.....*P. riparioides*
 11. Plants often golden; branch tips spreading–crispate; leaves broadly ovate to suborbicular, acute or apiculate, narrowed at the insertion, pinched at the apex; median leaf cells shorter and broader, ca. 9:1; cilia of endostome short, paired or in groups of three.....*P. aquaticum* (including *P. muelleri* & *P. mac-owanianum*)

Rhynchostegium

Based on morphology, all the species of *Rhynchostegium* I have seen [*R. alopecuroides* (Brid.) A. J. E. Smith, *R. aquaticum* A. Jaeger, *R. confertum*, *R. megapolitanum* (F. Weber & D. Mohr) Schimp., *R. murale*, *R. planiusculum* (Mitt.) A. Jaeger, *R. riparioides*, *R. serrulatum*, and *R. subruscifforme*] form a natural group characterized by relatively robust, shiny plants with smooth, concave, rather closely-spaced leaves. Many species are yellowish and/or flattened. The leaf cells are long and narrow, the alar differentiation is slight, and the single costa is relatively slender. All species are autoicous and have smooth setae. The homogeneity of *Rhynchostegium* is also supported by cytological studies (McAdam 1982). *Rhynchostegium confertum*, *R. murale*, *R. megapolitanum*, *R. rotundifolium* and *R. riparioides* all possess a chromosome number of 11 (apparently the basal number in the Brachytheciaceae). In contrast, many species of *Eurhynchium* (e.g., *E. hians* and *E. praelongum*), have a lower number, which

seems to have been achieved through fusion of telocentric chromosomes (a derived condition).

Principal Components Analysis did not unite the three terrestrial species of *Rhynchostegium* that were included in the study. *Rhynchostegium confertum* always appeared close to *R. murale*, whereas *R. serrulatum* occupied an isolated position. Analysis of Variance revealed that costa length-to-leaf length ratio could be used to separate terrestrial species of *Rhynchostegium* from *Platyhypnidium s. str.* (much higher in *Platyhypnidium*). On the other hand, ANOVA united *Platyhypnidium* with the terrestrial species of *Rhynchostegium* in terms of basal cell dimensions.

In the phylogenetic analysis based on morphology, the terrestrial species of *Rhynchostegium* occupied a basal position that gave rise to a paraphyletic *Platyhypnidium* clade. *Eurhynchium* was resolved as a monophyletic derivative of *Platyhypnidium*. Therefore, *Rhynchostegium* was rendered paraphyletic in this analysis by the exclusion of *Eurhynchium* and *Platyhypnidium*. This is consistent with the nomenclature used by McFarland (1994), who treated the whole species complex as *Rhynchostegium*. Presumably outgroup selection (= *Scleropodium obtusifolium*) influenced the placement of the terrestrial *Rhynchostegium* clade in Figure 5. In contrast to the tree based on morphology, in all cladistic analyses that included molecular data *Rhynchostegium* appeared to be a natural genus separate from *Eurhynchium*.

Rhynchostegium riparioides. This widespread species is highly variable, with several distinct phenotypes. The leaves of U. S. plants tend to very broadly ovate, with blunt apices and long slender costae (Figure 9.d). From Mexico southward (where this

species is often replaced by *R. aquaticum*), the leaves can be shorter, obtuse, and suborbicular (Figure 9.b,c). In Scandinavia and western Europe, where this species is often represented by the variety *atlanticum* (Brid.), the leaves are long and relatively narrow; their shape is more suggestive of terrestrial species of *Rhynchostegium* (Figure 9.g). In eastern Europe and Asia, a pale and very large-leaved form with pointy apices is found (Figure 9.f). In India a whole range of phenotypes are found; and identification of Indian plants may be further complicated by the sympatric occurrence of several other similar taxa: *R. muelleri* A. Jaeger, *Oxyrrhynchium pringlei* (Cardot) n. comb., and *O. hians*.

Overall, *Rhynchostegium riparioides* is the largest species of the genus. Many of the leaves are blunt-tipped, even when \pm acute. *Rhynchostegium aquaticum* is clearly a sister species; and *R. confertum* is apparently another close relative. The branches of depauperate specimens are more complanate than in well-developed material; the dense foliation and terete branches of well-developed plants will separate them from species of *Oxyrrhynchium*. The leaves of *R. riparioides* are less broadly ovate than those of *R. aquaticum*; they are larger and more broadly ovate than those of *O. pringlei*. The large, inflated, decurrent alars frequently found in *Brachythecium rivulare* are never present.

Rhynchostegium riparioides var. *atlanticum* is a robust form of the species with large, secund leaves and strong costae. I have seen specimens from Germany and Iceland. I have not seen the German collection of this taxon that was included in some of the phylogenetic analyses (leg. *Frahm*, Allerheiligen). However, I have seen a closely-related specimen of *Platyhypnidium mutatum* Ochyra & Vanderpoorten that was collected from the same site (*Frahm* 8593, 24 July 2005; hb. Wynns); and these plants

are a good match for *R. rusciforme* var. *atlanticum* Brid. *Platyhypnidium mutatum* is a mutant strain of *R. riparioides* with multistratose streaks in the costa (Stech & Frahm 1999b). Multistratosity is a well-documented syndrome reported in several unrelated aquatic pleurocarpous lineages (Vanderpoorten et al. 2003).

According to Podpera (1954), *P. riparioides* var. *atlanticum* is a synonym of *R. rusciforme* var. *lutescens*, which I can confirm based on my study of only one specimen so named (*Schleicher s. n.*, DUKE). The phylogenetic analysis based on morphology placed this specimen sister to a collection of *R. aquaticum*. In PCA this specimen was very close to *R. serrulatum*, and far removed from *R. riparioides*. These results seem to suggest that *R. riparioides* is a polyphyletic taxon, and that European forms of the species may be more closely related to terrestrial species of *Rhynchostegium* than they are to New World forms of the species. But since only one locus was analyzed, the implied evolutionary distance may be exaggerated.

One sequence of “*P. riparioides*” (GenBank #AF403594) that was included in the ITS2 analysis (Figure 7) was resolved in a clade with *Bryhnia novae-angliae*, *Eurhynchiadelphus eustegia* (Besch.) Ignatov & Huttunen, and *Brachythecium rivulare*. Probably this specimen was incorrectly identified. It may in fact belong to the last species; some phenotypes of *B. rivulare* are look-alikes for *P. riparioides*.

Rhynchostegium riparioides has an extensive synonymy which includes *Platyhypnidium obtusifolium* (Besch.) Broth., *P. platyphyllum* (Müll. Hal.) M. Fleisch. (*vide* Koponen 1987), *P. schottmuelleri* (Broth.) M. Fleisch. (*vide* Iwatsuki 1991), and *P. tenuinerve* (Cardot) Broth. (*vide* Noguchi 1991).

Rhynchostegium riparioides (Hedw.) Cardot

Plants robust, aquatic, growing attached to rocks, soil and debris in and along streams and reefs. Primary stems rhizomatous, shiny, dark brown or black. Branches terete or somewhat complanate. Pseudoparaphyllia rounded in outline. Leaves usually imbricated, twisted medially dry, very shiny, often with a metallic sheen, pure green to dark green, sometimes streaked with red, or blackish when encrusted with diatoms, spoon-shaped, longly to broadly ovate, somewhat to deeply concave, slightly to noticeably asymmetrical, smooth to striolate, 1.5–2.5 mm long at maturity (rarely less or more); leaf apex obtuse, mucronate, apiculate, or acute, generally blunt, flat or showing a tendency to twist, but usually too abrupt to do so; leaf margins plane, serrulate all round, more pronouncedly so above and on immature leaves. Costa rather slender but quite long, tapered, sometimes spurred, occasionally forking, in some populations ending in a small dorsal prickle. Alar cells poorly differentiated, somewhat incrassate, sometimes \pm porose, enlarged in a small group that is confluent with the basal leaf cells. Median leaf cells (50)70–110(130) μm in length. Apical cells short, not expanded, frequently somewhat incrassate; ultimate cell(s) emarginate.

Autoicous. Perichaetial leaves lanceolate, serrate, weakly costate or ecostate. Seta smooth, orange-red. Capsule rather large, plump, reddish-brown, sometimes with a modest basal apophysis. Exothecial cells wavy-irregular, not collechymatous. Operculum long-rostrate. Annulus well-defined, red. Exostome red, densely cross-striolate below, hyaline and papillose at tips and ends of ventral trabeculae. Endostome segments yellow, coarsely papillose, conspicuously perforate, about equalling the exostome in length; cilia long, strongly nodose, in groups of 3-4, sometimes fused below.

Specimens examined: ALABAMA. *Reese 18543*, Jackson Co. (DUKE); *Zartman 1402*, Jackson Co. (DUKE). CALIFORNIA. *Fosberg 421*, Los Angeles Co. (TENN). CANARY ISLANDS. *Long 7431*, Barranco del Agua, La Palma (NY). GERMANY. *Rabenhorst, Bryotheca europaea 1091*, leg. *Wagner*, Püttlach, near Pottstein, Oberfranken (sub *R. rusciforme* var. *atlanticum* Schp., NY). GEORGIA. *Anderson 22079*, Stephens Co. (TENN). GREECE. *Düll 74*, Samos Id. (DUKE). HONDURAS. *Allen 11156*, Lempira (DUKE). ICELAND. *Frahm s. n.*, Snaefellsness (sub *P. rusciforme* var. *atlanticum*, NY); *Holmen s. n.*, Geysir, 15 July 1950 (NY). INDIA. *Falconer 682*, NW Himalaya, ex hb. Mitten (NY); *Garden s. n.*, Nestorian Hills & Gawar, 1867 (NY). KAZAKHSTAN. *Allen 10653 & 10659*, Alma Ata Oblast (DUKE). MADEIRA. *Johnson s. n.*, 1861, ex hb. Mitten (NY). MEXICO. *Arsène 9492*, Dist. Fed. (sub *P. obtusifolium* Broth., NY); *Cárdenas 3057a & 3063a*, Zacatecas (DUKE); *Hahn s. n.*, near Mexico (Syntype of *R. obtusifolium* Besch. mss., NY); *Matuda s. n.*, Hacienda, Chiapas (DUKE); *Pringle 15205*, Valley of Mexico, Dist. Fed. (Syntype of *R. obtusifolium*, NY). MICHIGAN. *Sharp s. n.*, Bond Falls, Ontonagan Co. (TENN). NETHERLANDS. *Nannenga-Bremekamp 262*, Heelsum (NY). NEW YORK. *Buck 35187*, Putnam Co. (NY). NORTH CAROLINA. *Amtoft s. n.*, Little Buck Ck., Macon Co. (hb. Wynns); *Anderson 26345 & 27137*, Jackson Co. (DUKE); *Anderson 26455*, Macon Co. (DUKE); *Bachmann 690 & 692*, Haywood Co. (DUKE); *Davison s. n.*, Little Buck Ck., Macon Co. (BOON); *Hicks 5125*, Burke Co. (BOON); *Keith 4*, Caldwell Co. (BOON); *McFarland s. n.*, near Whitewater R., Jackson Co. (BOON); *McFarland s. n.*, Frozen Ck., Transylvania Co. (hb. Wynns); *Shaw 9360*, Macon Co. (DUKE); *Small 74*, Stanley Co. (NY); *Wagner 1831 & 1837*, Jackson Co. (TENN); *Wynns 203, 205, 239-241, 243, 389 & 390*, Watauga Co. (BOON); *Wynns 274-276*, Caldwell Co. (BOON); *Wynns 278*, Burke Co. (hb. Wynns); *Wynns 467, 468 & 473-475*, Transylvania Co. (BOON); *Wynns 584*, Avery Co. (hb. Wynns); *Wynns 700*, Polk Co. (hb. Wynns); *Zartman 1319*, Macon Co. (sub *E. hians*, DUKE). ONTARIO. *Ireland 15653*, Algoma Dist. (TENN). PENNSYLVANIA. *Wynns 313 & 360*, Pike Co. (BOON). RUSSIA. *Ignatov, Mosses of USSR 36*, Oka River, Baskachi, Kashira Dist., Moscow Prov. (NY). SOUTH CAROLINA. *Anderson 24061*, Pickens Co. (sub *E. pringlei*, DUKE); *Hermann 15397*, Oconee Co. (NY); *Hill 29148*, Estatoe River, Pickens Co. (sub *P. pringlei*, DUKE); *Keith & Wynns s. n.*, Reedy Cove Ck., Pickens Co. (BOON); *McFarland s. n.*, Rocky Bottom Ck., Pickens Co. (BOON); *Wynns 478, 479, 482, 544, 549, 554, 555, 560 & 562*, Pickens Co. (BOON); *Wynns 485, 487, 519, 523, 524, 526, 527, 533 & 537*, Oconee Co. (BOON); *Wynns 567, 568, 570 & 574*, Greenville Co. (BOON); *Zartman & Pittillo 456 & 516*, Oconee Co. (DUKE). SWITZERLAND. *Schleicher s. n.*, near Saillon, 1912, comm. hb. Boissier (sub *R. rusciforme* var. *lutescens*, DUKE). VIRGINIA. *Small 471*, Carroll Co. (NY); *Small 477*, Lee Co. (NY).

Illustrations: Bruch et al., *Bryologia europaea* 5, pl. 516; Crum & Anderson, *Mosses of Eastern North America*, f. 526, p. 1073; Dixon, *Student's Handbook of British Mosses*, tab. LV.C; Gangulee, *Mosses of Eastern India* 7, f. 871, p. 1734; Jennings, *Mosses of Western Pennsylvania*, pl. LVIII, p. 382; Ignatov, *Arctoa* 7: 149 (1998); Lawton, *Moss Flora of the Pacific Northwest*, pl. 168; McFarland, *in Moss Flora of Mexico*, f. 702, p. 941 (p. 940 in error); Smith, *Moss Flora of Britain and Ireland*, f. 293.1-3, p. 604; Watson, *British Mosses and Liverworts*, f. 174, p. 374; Wynns, this work, Figure 9.

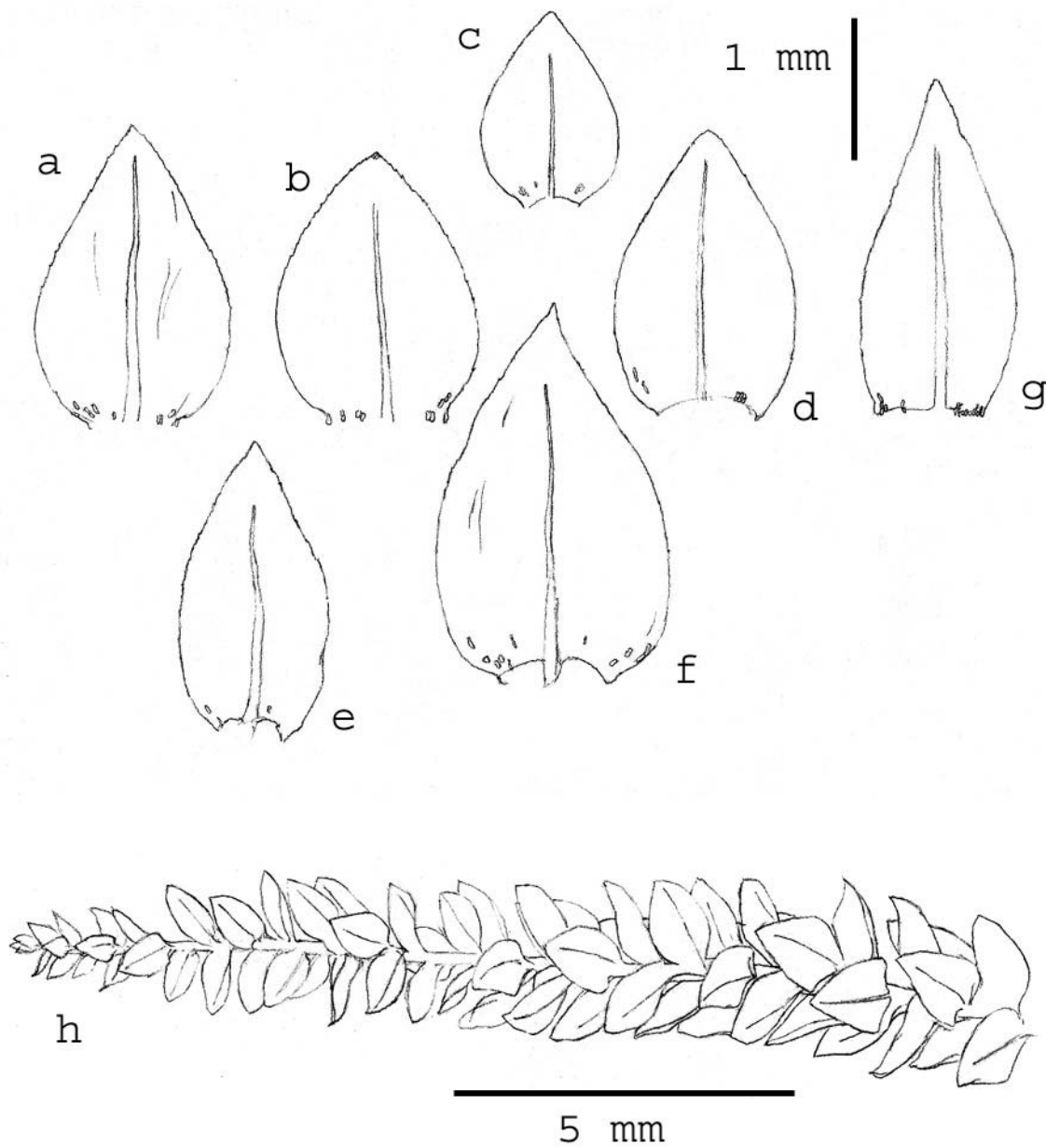


Figure 9. *Rhynchostegium riparioides*: a, h – Buck 35187, New York (NY); b – Pringle 15205, Mexico (Syntype of *R. obtusifolium*, NY); c – Cárdenas 3057a, Mexico (DUKE); d – Keith 4, North Carolina (BOON); e – Falconer 682, Himalayas (NY); f – Allen 10659, Kazakhstan (DUKE); g – Rabenhorst, *Bryotheca europaea* 1091, Germany (*R. rusciforme* var. *atlanticum*, NY).

Rhynchostegium aquaticum. I have reviewed (in Dozy & Molkenboer 1867) the original differentiae that Sande Lacoste gave to separate *Hypnum aquaticum* Hampe (*nom. illeg.*) from *H. muelleri* Sande Lac. (*nom. illeg.*). They are not very satisfactory. Supposedly *H. aquaticum* is more rigid, has straight branches which are blunt and not stoloniferous (the attenuate tips of the branches of *H. muelleri* are prominently figured), leaves which are much narrower at the insertion, and shorter setae. However, seta length is generally too variable among conspecific populations to be taxonomically informative (McFarland, pers. comm.). Also, leaves that are noticeably constricted at the base are actually observed in both species. Third, the production of stoloniferous branches is probably environmentally induced. Fleischer, Möller and Yates all collected specimens of *R. muelleri* from a waterfall in Tjiburrum, Java (presumably representing a single population). Many, but not all, of the stems in these collections are \pm flagelliferous: the leaves are small and closely appressed to the stems. Since appressed leaves would have an adaptive advantage in a (turbulent) waterfall, this phenotype may be environmentally (and not genetically) induced. In fact, every species of Brachytheciaceae included in this study is probably capable of producing flagelliform branches, and in aquatic species the phenomenon is particularly common.

From my own studies of herbarium material, I have come to the conclusion that *R. muelleri* and *R. aquaticum* are one species. There are some minor, inconstant differences between the two taxa: occasional specimens of *R. aquaticum* are quite large (e.g., *Buck* 7962; NY), and in some cases the leaves of *R. aquaticum* are more elongate (less round) than those of *R. muelleri*. The latter taxon exhibits more phenotypic variety than the former; and some of the smaller, rounder-leaved, more denticulate forms of

R. muelleri (e.g., *Musci Japonici* 771, or *Musci Frondosi Archipelagi Indici* 95; NY) might seem distinctive. However, intermediate phenotypes exist; and many correctly-named specimens of *R. muelleri* are indistinguishable from *R. aquaticum*. So defined, the range of *R. aquaticum* is very large, overlapping *R. riparioides* at its northern limit and \pm replacing it in the Southern Hemisphere. There seems to be some argument about whether this species occurs in Australia (Hedenäs 2002). I can say with certainty that the Streimann specimens (listed below) from New South Wales are bona fide *R. aquaticum*.

Several diagnostic features shared by *R. muelleri* and *R. aquaticum* separate these taxa from *R. riparioides*: branches yellowish and crisped at tips; leaves pinched above, sometimes conduplicate, usually acute or apiculate, and finely striolate; cells short, in diagonal files; operculum thick and fleshy; cilia mostly paired, short or rudimentary (but not reduced to the degree shown in Noguchi, 1991). Narrow-leaved specimens of *R. aquaticum* (e.g., *Vital & Buck* 12603, or *Churchill et al.* 19066; NY) can be very difficult to distinguish from *R. riparioides* microscopically; and some robust specimens (e.g., *Churchill et al.* 22535; NY) can be difficult to distinguish macroscopically. However, the species is overall smaller than *R. riparioides*, with a different leaf shape (more broadly ovate, more plicate, and more pinched above and below), and a characteristic golden-coppery sheen. Therefore I disagree with Robinson (1967) in synonymizing the two species. Comparison of Figures 9 & 10 should illuminate their differences.

In the cladistic analyses that included molecular data, three sequences of *R. muelleri* from widely separated localities were never resolved as a monophyletic clade. One Japanese collection (*Musci Japonici Exsic.* 1316) had several molecular synapomorphies with *R. aquaticum*, although in some parts of its ITS sequence it was

intermediate between *R. aquaticum* and the other two sequences of *R. muelleri* included in this study (Appendix 4). Six sequences of *R. aquaticum* from scattered localities in South America were identical, whereas one collection from the Dominican Republic (Buck 7962) showed slight variation. Although I consider *R. aquaticum* and *R. muelleri* to be conspecific, I find it surprising that an obvious derivative of the South American genotype should also occur in Japan. Noguchi (1991) incorrectly referred *Musci Japonici Exsic. 1316* to *R. riparioides*.

The name *Hypnum aquaticum* was published before *H. muelleri*, but both names turned out to be illegal homonyms of earlier names. Jaeger (1878) was the first to correctly apply names to these taxa, and both names appeared in the same publication. They therefore have equal priority. I agree with W. R. Buck (pers. comm.) that the name *Rhynchostegium aquaticum* should be used instead of *R. muelleri* – not only because its basionym was published first, but also because a name that is descriptive is more informative than one that is commemorative.

From only two specimens I have seen (*Vanderpoorten 12 & 114, S Africa; DUKE*); *Platyhypnidium mac-owanianum* (Paris) M. Fleisch. is also conspecific with *R. aquaticum*, but is a larger variety. Leaves of *P. muelleri*, *P. aquaticum* and *P. mac-owanianum* are illustrated together in Figure 10. According to Index Muscorum (Wijk et al. 1964), *Platyhypnidium afrorusiforme* (Müll. Hal.) M. Fleisch. is a synonym of *P. mac-owanianum*.

Rhynchostegium aquaticum A. Jaeger

Plants medium-sized to large, nitid, yellow, green, dark green, or brown, sometimes coppery. Primary stems stoloniferous, blackish, glossy, bearing atypical leaves which are small, wide, acuminate, decurrent, and weakly costate, with flaring hips and excavate corners. Secondary stems sparse, little branched, arching, terete, heteromallous, sometimes spiky below from denuded costae, ultimate branches spreading-crispate and frequently yellow at tips. Rhizoids infrequent, short, smooth, dark wine in color. Axillary hairs 4–5 celled, the lower cells very small, compressed, the terminal cell orange-brown and grainy-papillose. Pseudoparaphyllia rounded or broadly triangular. Leaves imbricate, rather contorted dry, erect– to wide–spreading (or on occasional branches stiffly erect), somewhat concave, often lightly plicate, broadly ovate or orbicular, restricted at the apex and base, often very narrow at the insertion, the leaf bases sometimes sheathing the stem and lending it a fleshy appearance; leaf apex subobtuse, acute, or broadly apiculate due to the restriction; leaf margins serrulate, in some leaves sharply denticulate above. Costa long, slender, tapered, spurred, sometimes forking, smooth, disappearing about $\frac{3}{4}$ of the leaf length or higher. Alar cells few, enlarged, not incrassate, the lowermost row of cells porose and darkly pellucid. Basal cells slightly incrassate, \pm porose, inflated at the stem-junction. Median leaf cells short, (40)45–85(110) μm , vermicular, arranged in diagonal rows, the rows in longitudinal stripes following the plicae: on the whole producing a finely striolate leaf texture. Apical leaf cells abruptly short, not expanded, slightly incrassate.

Autoicous. Seta smooth. Capsules somewhat inclined, rather large, (1.4)1.8–2.6(3.1) mm long, reddish-brown, or blackened with age, plump, with a thick neck, and a

slight but noticeable basal apophysis. Exothecial cells irregularly thickened but not collenchymatous. Operculum with a rather long, thick and fleshy beak, blunt at the tip. Annulus well-defined, composed of two rows of narrowly ovate, thick-walled cells. Exostome teeth strongly curved, striate and dark red below, papillose and hyaline at the tips, bearing stout, hyaline, ventral trabeculae. Endostome yellow, weakly papillose; basal membrane very high; segments long, slightly exceeding the rather short exostome, keeled, narrowly perforate; cilia short, reaching $2/3$ the length of the segments, nodulose to nodose, paired or less frequently in groups of three, sometimes fused above. It seems that the basal cilium number is three, and that there is a tendency for reduction; a vestigial third cilium is sometimes present. Spores rounded-tetrahedral, 12–20 μm in diameter, smooth.

Specimens examined (as *P. aquaticum*): ARGENTINA. *Price et al.* 1673, Tucuman (DUKE). BOLIVIA. *Churchill et al.* 19774, La Paz (NY); *Churchill et al.* 22535, Cochabamba (NY). BRAZIL. *Vital & Buck* 11477 & 12603, São Paulo (NY). COLOMBIA. *Churchill et al.* 15374, Dept. Valle (NY); *Churchill & Luz Arbelaez A.* 15981, Laguna de la Cocha, Pasto, Dept. Nariño (DUKE); *Churchill & Betancur* 16842, Dept. Caquetá (NY); *Churchill et al.* 17169, Dept. Tolima (NY); *Churchill & Betancur* 17999, Dept. Cauca (NY); *Churchill et al.* 19066 & 19069, Dept. Boyacá (NY); *Churchill et al.* 19413, Tausa, Dept. Cudinamarca (DUKE); *Linares C. & Churchill* 3637, Cundinamarca (NY); *Ramírez P.* 2760, Dept. Nariño (NY); *Weir* 292, 363 & 404, New Grenada (NY). COSTA RICA. *Crosby* 3875, near Rio Porrosati, Prov. Heredia (sub *P. riparioides*, DUKE); *Pittier & Tonduz s. n.*, Barba (NY). DOMINICAN REPUBLIC. *Buck* 7962 & 14088, Prov. La Vega (NY). ECUADOR. *Buck* 39450, Prov. Zamora-Chinchipe (NY); *Jameson s. n.*, Pichincha, Quito (Isotype, NY); *Krause s. n.*, det. Hampe (NY). JAMAICA. *Orcutt* 5877, Stony River (DUKE). SOUTH AMERICA. *Spruce, Musci Amazonici et Andini* 1422 (NY). VENEZUELA. *Griffin et al.* 337, Dist. Libertador (sub *R. riparioides*, DUKE).

(as *P. muelleri*): AUSTRALIA. *Streimann* 44736 & 60375, New South Wales (sub *P. austrinum*, NY). CHINA. *Buck* 23832 & 23844, Hangzou Co., Zhejiang Prov. (sub *P. riparioides*, NY); *Chiao s. n.*, Tsinanfu, Shantung Prov., 4 Sep 1930 (sub *E. riparioides*, NY); *Chuang* 2171, Mt. Tai-ping-shan, Ilan Co., Taiwan (sub *E. riparioides*, NY); *Hu* 0076, Mt. Jinfu, Nanchuan Co., Sichuan Prov. (sub *E. riparioides*, NY); *Redfearn et al.* 34866, Xi Cheng River, Sichuan Prov. (sub *E. riparioides*, NY); *Reese* 17710, Hainan Prov. (NY); *Wu* 21163, Sichuan Prov. (sub *E. riparioides*, DUKE). HAWAII. *Bartram*,

Mosses of Hawaii 504, Iao Valley, Maui (NY); *Flynn et al.* 5204, Kauai (NY); *Hoe* 523, Oahu (DUKE, NY, TENN); *Newell s. n.*, 1911, ex hb. Willie (NY); *Welch* 16726, Iao Needle, Iao Valley, Maui (NY). INDIA. *Beddome* 22 & 23, Simla, ex hb. Mitten (NY); *Foreau, Musci Madur. Ind. Merid. Exsic.* 283, Madras State (DUKE, NY); *Gollan s. n.*, 6 Dec 1900 (sub *R. cataractile*, NY); *Griffith* 100, ex hb. Mitten (NY); *Levier, Bryotheca exotica* 71, leg. *Lal*, Mussoorie, NW Himalaya (sub *R. cataractile*, NY); *Thomson* 965, Simla, 10/1849, 8000' (sub *R. rusciforme*, NY). JAPAN. *Glime* 3875, Inohae Valley, Miyazaki (sub *E. riparioides*, DUKE); *Noguchi, Musci Japonici* 771, Kumamoto Pref. (NY, TENN); *Noguchi & Iwatsuki, Musci Japonici Exsic.* 1316, Kagoshima Pref. (TENN); *Sasaoka s. n.*, Mt. Kurobe, Prov. Etchu (NY); *Smith J-951, J-1335 & J-1337*, Kagoshima Pref. (NY). JAVA. *Fleischer, Musci Frondosi Archipelagi Indici* 95, Tjiburrum (NY); *Möller s. n.*, Tjiburrum, 7/2.1897 (DUKE, NY); *Motley* 311, Mt. Panerango (NY); *Yates* 2992, Tjibeurrum (TENN). PAPUA NEW GUINEA. *Balgooy* 814B, Mt. Wilhelm, Eastern Highl. Dist. (NY); *Koponen* 30269, Morobe Prov. (NY); *Koponen* 33269, Morobe Prov. (DUKE); *van Zanten* 331 & 575, Star Mts. (TENN).

(as *P. mac-owanianum*): SOUTH AFRICA. *Vanderpoorten* 12 & 114, East Cape (DUKE).

Illustrations: Bartram, *Manual of Hawaiian Mosses*, f. 159, p. 215; Bartram, *Mosses of the Philippines*, pl. 22; Buck, *Pleurocarpous Mosses of the West Indies*, pl. 97, f. 9–16, p. 249; Dozy & Molkenboer, *Bryologia Javanica* v. 2, tab. CCLXI; Fleischer, *die Musci der Flora von Buitenzorg* 4, p. 1538; Gangulee, *Mosses of Eastern India* 7, f. 872 & 873, pp. 1736 & 1737; Ignatov et al., *Acta Bot. Fenn.* 165: 61 (1999); Noguchi, *Illustrated Moss Flora of Japan* 4, f. 444 & 445.A, pp. 1009 & 1011; Wynns, this work, Figure 10.

***Rhynchostegium confertum*.** This type species of the genus *Rhynchostegium* was not thoroughly investigated in this study. The plants are medium-sized, dark, and inconspicuous. The leaves are concave and frequently homomallous, with denticulate margins. *Rhynchostegium confertum* var. *serrulatum* Brid. (represented in this study by *Bernot s. n.* and *Solms s. n.*) has narrow, subentire leaves, a yellow color, and a complanate habit. Microscopically the leaves are reminiscent of *Brachythecium plumosum*, but the complanate habit and entirely smooth seta separate it from that species.

In the PCAs, *R. confertum* was always united with *R. murale*. In the phylogenetic analysis based on morphology, *R. confertum* was non-monophyletic; one specimen

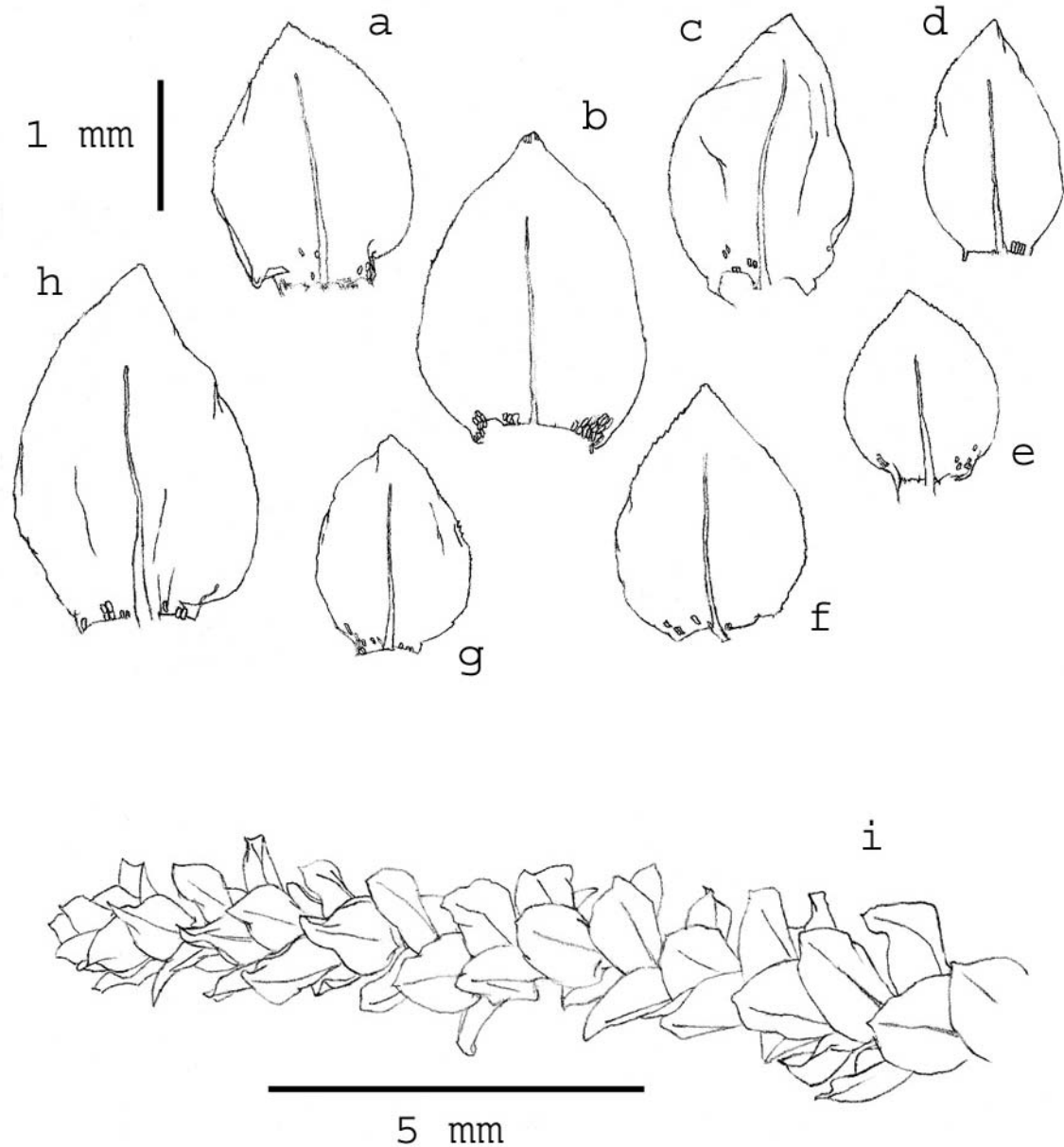


Figure 10. *Rhynchoszegium aquaticum*: a, i – Jameson s. n., Ecuador (Isotype, NY); b – Buck 7962, Dominican Rep. (NY); c – Bartram, *Mosses of Hawaii* 504 (NY); d – Noguchi & Iwatsuki, *Musci Japonici Exsic. 1316* (TENN); e – Noguchi, *Musci Japonici* 771 (NY); f – Fleischer, *Musci Frondosi Archipelagi Indici* 95, Java (NY); g – Koponen 33269, Papua New Guinea (DUKE); h – Vanderpoorten 12, South Africa (DUKE).

clustered with *R. serrulatum*, and another was basal to the aquatic lineages. In the ITS analysis, *R. confertum* had a sister relationship with Old World collections of *R. riparioides*. These results lend support to the inclusion of *Platyhypnidium* in *Rhynchostegium*.

Rhynchostegium confertum (Hedw.) Schimp.

Plants rather small, glossy, yellow-green to green, frequently with a coppery sheen, isophyllous. Stems terete or somewhat complanate. Branches short. Rhizoids smooth. Pseudoparaphyllia acuminate, usually sharply so. Leaves vaguely homomallous, twisted medially, smoothly concave, hardly plicate, denticulate, more noticeably so above; leaf apex flat. Costa rather weak, ending about 2/3 of the way up, smooth to scabrous on abaxial surface and occasionally projecting as a dorsal prickle. Alar region excavate, well defined by quadrate, green, granular, somewhat incrassate cells. Basal cells swollen, slightly incrassate, vaguely to decidedly porose, continuous with alar cells. Median cells vermicular, averaging $80 \times 8 \mu\text{m}$. Apical cells somewhat shorter, not expanded, ca. $35 \times 7 \mu\text{m}$.

Autoicous. Seta smooth. Capsule brown, nearly erect to inclined, plump, short, widest near the base, deeply constricted below the neck when dry. Operculum long-rostrate. Annulus well-defined. Endostome segments yellow, papillose, perforate, with a high basal membrane; cilia long, usually paired, nodose.

Specimens examined: CANARY ISLANDS. *Long 7448*, La Palma (TENN). FRANCE. *Courbiere s. n.*, Cherbourg (NY). GERMANY. *Bruch s. n.*, Oberhausen (TENN). IRELAND. *Wynns 759*, Newgrange, Co. Meath (hb. Wynns). ITALY. *Privitera s. n.*, Etna, Sicily (NY). NETHERLANDS. *Aptroot 2593*, Wieringen, Prov. Noord-Holland (sub *R. murale*, NY); *Gradstein 853*, Middachten (NY). PORTUGAL. *Solms s. n.*,

Algarve, 1866 (sub *E. strigosum*, NY). SCOTLAND. *Chamberlain s. n.*, E Lathian (TENN). SWITZERLAND. *Bernot s. n.*, Aïre, Geneva (NY).

Illustrations: Bruch et al., *Bryologia Europaea* 5, pl. 510; Dixon, *Student's Handbook of British Mosses* (ed. 3), tab. LV.E.; Smith, *Moss Flora of Britain and Ireland*, f. 294.5-8, p. 606; Watson, *British Mosses and Liverworts* (ed. 3), f. 175, p. 375; Wynns, this work, Figure 11.a,b.

***Rhynchostegium murale*.** This is a very distinctive calciphilous species found on walls and stones in Europe and Asia. It is frequently associated with *Ctenidium molluscum* (Hedw.) Mitt. and *Brachythecium populeum* (Hedw.) Schimp. The leaves are deeply concave, oblong-ovate, and have obtuse tips (like in *Platyhypnidium*). The julaceous branches and leaves tinged with red are diagnostic. Herbarium specimens sometimes have a bicolored appearance owing to the tendency of the branches to turn brown with yellow tips; this tendency has also been observed in specimens of *R. confertum* and *Eurhynchium fuegianum*. *Rhynchostegium murale* is usually found fertile. The long beak on the operculum is striking.

Rhynchostegium murale (Hedw.) Schimp.

Plants medium-sized, very glossy, pale green, turning yellow, bronze or reddish-brown, sometimes flattened. Branches short, straight, ± julaceous. Pseudoparaphyllia rounded, erose. Leaves erect or erect-spreading, deeply concave, smooth when wet, dented, striolate and plicate when dry, sometimes scabrous on abaxial surface, 0.8–1.4 × 0.4–0.8 mm, elliptical or oblong-ovate in outline; leaf apex obtuse or apiculate, rarely acute, sometimes cucullate; leaf margins serrulate throughout, weakly so below. Costa weak, varying greatly in length, spurred, tapered, seldom projecting abaxially. Alar region small, often excavate, giving some of the leaves low ‘hips’ at the base; alar cells

usually somewhat enlarged; quadrate or oblong; somewhat incrassate; pellucid; confluent with the basal cells in a broad band. Lower marginal cells somewhat incrassate on well-developed leaves. Median leaf cells slender, vermicular, generally 50–100 μm long.

Autoicous. Calyptra naked. Sporophytes generally present, rather large and conspicuous. Seta smooth. Capsule inclined; usually elongate and curved, less often plump, orange or reddish-brown. Operculum large, with a very long sharp rostrum. Peristome conspicuous, stout, long. Exostome teeth orange-red, cross-striolate below, hyaline and papillose at tips, with rather weak hemidiscoidal ventral trabeculae. Endostome equalling the exostome in length, brownish-yellow, papillose throughout; segments narrowly perforate; cilia coarse, nodose, somewhat reduced, paired or in groups of three. Spores dirty yellowish-green, granular, 10–15 μm in diameter.

Specimens examined: AUSTRIA. *Breidler s. n.*, near Vienna, 11 Nov. 1867 (DUKE). BELGIUM. *Aptroot 2622*, Hamoir, Prov. Luxembourg (NY); *Aptroot 2849 & 9745*, Prov. Liège (NY); *De Sloover 32664*, Faux-les-Tombes, Gesves (DUKE). CHINA. *Tan 93-952*, Huo-cheng Co., Xinjiang Prov. (NY). ENGLAND. *O'Shea s. n.*, near Matlock, Derbyshire (DUKE); *Wilson s. n.*, Cranbeck, 10 Dec. 1856 (DUKE). GERMANY. *Starcs 11093 & 11442*, Kr. Traunstein, Bavaria (NY); *Starcs 11580, 11585 & 14180*, Berchtesgaden, Bavaria (NY); *Vigener 310*, Westfalen, 1858 (DUKE). NETHERLANDS. *Aptroot 3235*, Bloemendaal, Prov. Noord-Holland (NY); *Aptroot 5639*, Scheipersberg, Prov. Zuid-Limburg (NY); *Aptroot 9651*, Utrecht (NY). POLAND. *Ochyra, Musci Poloniae Exsic. 682*, Mt. Luzec, Sudetes Mts. (TENN); *Ochyra 713/82 & 2174/82*, Little Pieniny Mts., W Carpathians (NY); *Stebel, Musci Macroregioni Meridionali Poloniae Exsic. 1091 & 1137*, Krakow-Czeskochowa Upland (NY). PORTUGAL. *Jeanbernat s. n.*, Paderne, Pyrenées, 1878 (DUKE). SLOVAK REPUBLIC. *Franklová, Bryophyta Cechoslovaca Exsic. 298*, Distr. Zilina, W Slovakia (TENN). SWITZERLAND. *Schimper 79*, Mt. Salève, near Geneva, May 1852 (DUKE).

Illustrations: Bruch et al., *Bryologia Europaea* 5, pl. 514; Dixon, *Student's Handbook of British Mosses* (ed. 3), tab. LV.D; Noguchi, *Illustrated Moss Flora of Japan* 4, f. 440.A, p. 1003; Smith, *Moss Flora of Britain and Ireland*, f. 294.1-4, p. 606; Takaki, *J. Hatt. Bot. Lab.* 16: 41 (1956); Wynns, this work, Figure 11.c.

Rhynchostegium serrulatum. A widespread weed in eastern North America, *R. serrulatum* is found growing in lawns, on banks, on damp clayey soil, at the bases of trees, and on rotten wood. Gametophytically the plants are very similar to some species of *Brachythecium* (like *B. rutabulum* (Hedw.) Schimp.). In fruit however, the species is clearly allied with *Rhynchostegium* and other rostrate-operculate Brachytheciaceae. Furthermore, in cell structure, and in the shape and disposition of the leaves, *R. serrulatum* seems well placed in its genus. In leaf size, texture, and areolation, *R. serrulatum* is allied with *R. riparioides*. In the ITS2 analysis, one specimen of *R. muelleri* was resolved in a clade with *R. serrulatum*.

In the phenetic analyses, *R. serrulatum* was resolved in a highly isolated position, mostly due to its long slender leaf acumen with long apical cells. However, in all cladistic analyses, *R. serrulatum* was resolved with other species of *Rhynchostegium*. These results strongly suggest that *R. serrulatum* should be retained in *Rhynchostegium*; I cannot support the transfer of the species to either *Brachythecium* (cf. Robinson 1962) to a segregate genus *Steeeracleus* H. Rob. (cf. Robinson 1987). In gross aspect *R. serrulatum* has all the features of the genus.

Rhynchostegium serrulatum (Hedw.) A. Jaeger

Plants rather robust, deep green, pale green, or stramineous, sometimes with a brassy tinge, usually in soft, flat, glossy mats, or sometimes in loose wefts. Branches frequent, short, and mostly complanate. Rhizoids orange-brown and appearing somewhat granular, smooth externally, in thick fascicles at leaf bases. Pseudoparaphyllia broadly acuminate. Leaves mostly smooth, erect- or wide-spreading, ovate-lanceolate, ± secund,

with long twisted apices, rather concave, older leaves weakly plicate; leaf margins sharply serrulate throughout, recurved at the base, and in young leaves narrowly recurved at the apex. Costa rather weak, ending $\frac{3}{4}$ of the way up the leaf or less, often roughened dorsally and projecting as a modest prickle. Leaf cells 65–150 μm long, flexuose. Basal cells swollen, porose, grading into a poorly differentiated alar region composed of a few somewhat lax, often granular cells. Apical cells a bit shorter, otherwise not differentiated.

Autoicous. Calyptra cucullate, naked. Sporophytes medium-sized. Seta reddish, long, smooth. Capsules brown and slightly bumpy, strongly inclined, plump with a long tapered neck, often strongly curved when dry and constricted below the mouth.

Exothecial cells oblong, unevenly thickened but not collenchymatous. Operculum large, bearing a rather short, sharp beak. Annulus prominent, red. Exostome teeth deep red, cross-striolate and smooth at base, coarsely papillose and hyaline distally. Endostome yellow, of the same stature as the exostome, segments narrowly perforate and densely papillose, surmounting a weakly papillose basal membrane; cilia well-developed, sometimes equalling the segments in length, slender, coarsely papillose, nodose, in groups of 2–3. Spores quite small, 8–12 μm in diameter, oily yellow-green, smooth.

Specimens examined: ARKANSAS. *Buck 40344*, Stone Co. (NY); *Buck 40412*, Sharp Co. (NY); *Buck 43093*, Pope Co. (NY); *Majestyk 1942*, Nevada Co. (hb. Wynns). CONNECTICUT. *Buck 45007*, Litchfield Co. (NY). NORTH CAROLINA. *Amtoft s. n.*, Wake Co. (hb. Wynns); *Wynns 54*, Jackson Co. (NY); *Wynns 175, 188 & 196*, Avery Co. (BOON); *Wynns 428*, Durham Co. (BOON); *Wynns 616*, Watauga Co. (hb. Wynns). PENNSYLVANIA. *Wynns 282, 296 & 302*, Monroe Co., Pa. (BOON); *Wynns 363*, Pike Co. (hb. Wynns). TENNESSEE. *Brown 16*, Carter Co. (TENN); *Clebsch GE109*, Hardeman Co. (TENN); *Sharp 34910*, Meigs Co. (TENN); *Sharp 341010*, Sevier Co. (TENN); *Smith & Davison 110, 182 & 194*, Coffee Co. (TENN). VIRGINIA. *Majestyk 3337*, Chesterfield Co. (BOON).

Illustrations: Breen, Mosses of Florida pl. 79; Brotherus, Die natürlichen Pflanzenfamilien I(3): 1164; Buck, Pleurocarpous Mosses of the West Indies, pl. 98, f. 1–7, p. 252; Crum & Anderson, Mosses of Eastern North America v. 2, f. 522, p. 1064; Hedwig, Species Muscorum, tab. LX; Jennings, Mosses of Western Pennsylvania, pl. LIX, p. 383; Lawton, Moss Flora of the Pacific Northwest, pl. 169; Reese, Mosses of the Gulf South, f. 53.A, p. 213; Sharp et al., Moss Flora of Mexico v. 2, f. 699, p. 937; Sullivant, Icones Muscorum, tab. 107; Wynns, this work, Figure 11.d.

Rhynchostegium alopecuroides [= *Platyhypnidium lusitanicum* (Schimp.) Ochyra & Bednarek-Ochyra] is a narrow-leaved plant with julaceous branches known mainly from the British Isles. It is very similar to *R. riparioides* and probably only distinct from it at the varietal level (to which it was in fact referred by Dixon in 1924, as *E. rusciforme* var. *alopecuroides* Brid.). Most keys use median laminal cell width to segregate *R. alopecuroides* (4–8 µm, vs. 6–10 µm in *R. riparioides*). The somewhat convoluted nomenclatural history of this moss was reviewed in Ochyra & Bednarek-Ochyra (2006).

Specimens examined: ENGLAND. *Townsend 90/55*, Artle Beck, E of Lancaster (DUKE); *s. coll.*, Sussex, ex hb. Mitten (sub *E. rusciforme*, NY). FRANCE. *Frahm s. n.*, Le Saut de Bouchout, Vosges (DUKE). IRELAND. *Wynns 750*, Kinsale, Co. Cork (hb. Wynns).

Illustrations: Smith, Moss Flora of Britain and Ireland, f. 293.4–6, p. 604 (1978); Wynns, this work, Figure 11.h.

Rhynchostegium subrusciforme. Historically *R. subrusciforme* has not been closely studied. Macroscopically this species appears well-placed in *Rhynchostegium*. The slender stems and glossy concave leaves are somewhat suggestive of *R. confertum*; and the plants are autoicous, with smooth setae. Microscopically the leaf shape is strongly reminiscent of some forms of *R. riparioides*. Morphologically, *Rhynchostegium subrusciforme* appears to be transitional between terrestrial and aquatic (= *Platyhypnidium s. str.*) forms of the genus. According to Crum (1951), *R. subrusciforme* is basically aquatic; but according to McFarland (1994) the species grows

in terrestrial habitats and its occurrence is not limited to rocks. The close relationship of *R. subrusciforme* to *R. riparioides* was noted by Bartram (1946, 1949). In the molecular analyses, *R. subrusciforme* was resolved outside of the terrestrial *Rhynchostegium* clade, along with most other specimens of *Platyhypnidium s. str.*

Rhynchostegium subrusciforme is accurately figured in the corrected version of McFarland (1994), but the figures in Bartram (1949) are not helpful, and may actually represent *O. pringlei*. According to McFarland (1994), *Platyhypnidium malacocladum* (Cardot) Broth. may be a synonym of *R. subrusciforme*.

Specimens examined: MEXICO. *Delgadillo 285*, Desierto de Los Leones, Dist. Fed. (NY); *Magill 2326, 2329 & 2335*, Hidalgo (sub *R. pringlei*, TENN).

Illustrations: McFarland in *Moss Flora of Mexico* v. 2, f. 700, p. 938 (corrected); Wynns, this work, Figure 11.g.

Rhynchostegium megapolitanum is a typical species of the genus found on dunes and seashores in the Mediterranean and southern Europe. The plants are generally flattened, creeping, and sparsely branched, with glossy yellow leaves. A large collarlike area of oblong-rectangular pellucid cells at the base of the leaves is diagnostic.

Specimens examined (all at DUKE): AUSTRIA. *Förster s. n.*, Bezirk Mistelbach, Lower Austria, 1 Nov. 1881; *Juratzka s. n.*, Laaerberg, Lower Austria, Oct. 1873. CROATIA. *Weiss s. n.*, near Ragusa, Dalmatia, 28 Dec. 1866. ENGLAND. *Wallace s. n.*, Camber, E Sussex. FRANCE. *Bruch 8810*, western Vogesen. GERMANY. *Hellwig s. n.*, near Grünberg, spring 1869. MALLORCA. *Crundwell 11*, Cala Cap d' Ai o Chada.

Illustrations: Smith, *Moss Flora of Britain and Ireland*, f. 293.7–8, p. 604; Wynns, this work, Figure 11.e.

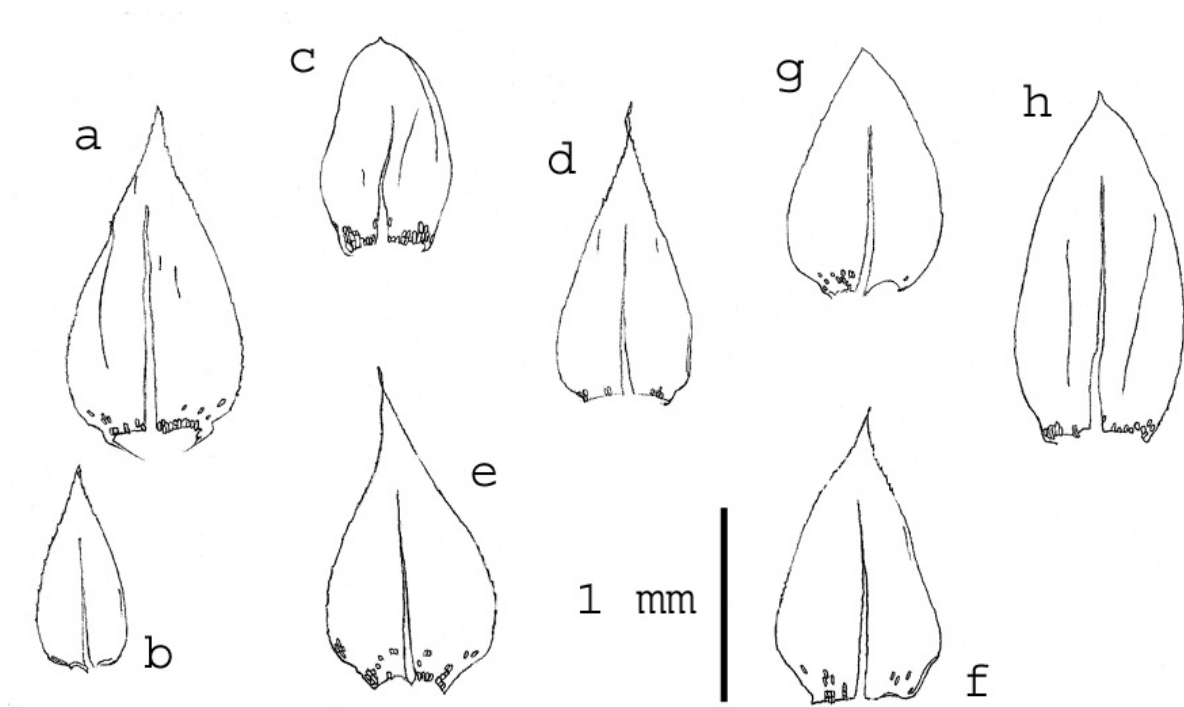


Figure 11. Leaves of some representative species of *Rhynchosstegium*: a, b – Long 7448, Canary Is. (*R. confertum*, TENN); c – Aptroot 2849, Belgium (*R. murale*, NY); d – Wynns 296, Pennsylvania (*R. serrulatum*, BOON); e – Crundwell 11, Mallorca (*R. megapolitanum*, DUKE); f – Gollan 3298, Mussoorie, Indian Himalaya (*R. planiusculum*, NY); g – Delgadillo 285, Mexico (*R. subruscifforme*); h – Townsend 90/55, England (*R. alopecuroides*, DUKE).

Eurhynchium

All molecular data indicated that *Eurhynchium* is heterogenous, as Brotherus (1909) believed it to be. In contrast to the molecular data, in the tree based only on morphology, all species of *Eurhynchium s. l.* (except *E. fuegianum*) were resolved as a monophyletic group, in a derived position. However, extremely high levels of homoplasy were found in that analysis. In the phenetic analyses, *Eurhynchium* also appeared to be fairly homogenous, in some analyses encroaching on *Platyhypnidium aquaticum* and *Rhynchosstegium murale*, but overall forming a distinct cluster of 3–5 of

the species under study. For example, in PCA13, *E. fuegianum*, *E. pulchellum* and *E. hians* formed a close-knit group. Certain features of the genus, such as a strong costa, a serrate margin, and fairly short leaf cells, do provide it with a degree of morphological synapomorphy. However, other characteristics which have traditionally been used to diagnose the genus were not unique to *Eurhynchium* in this study. For example, in some species of *Eurhynchium* (e.g., *E. pulchellum*) the apical leaf cells (especially in branch leaves) are noticeably expanded; but in ANOVA this feature did not prove to be significantly different from *Platyhypnidium*.

Eurhynchium is a model of the problems in generic delimitation which are common in the family. The Brachytheciaceae certainly are “a family of sibling genera,” as stated by Ignatov & Huttunen (2002). Their solution to this problem was evidently to erect segregate genera to accommodate ill-placed species. Although this has a practical advantage, it results in the usage of some genera with a rather nebulous identity. I personally would like to be able to distinguish natural genera in the field. Unfortunately the mosses will not always cooperate!

My study was designed to investigate the phylogenetic position of *Platyhypnidium*, not *Eurhynchium*; and as a consequence, for most species of *Eurhynchium* my data are too scanty to be informative. I have therefore taken a traditional approach to the nomenclature here, retaining *E. pulchellum* and *E. praelongum* in *Eurhynchium*. In contrast, a distinct *Oxyrrhynchium* clade that included *E. hians* and several other (mainly aquatic) taxa was so strongly supported in the ITS analysis that I see no alternative but to recognize *Oxyrrhynchium* as a distinct generic entity. Fortunately, the monophyly of *Oxyrrhynchium* is also supported by several

morphological synapomorphies. Therefore I here discuss *E. hians*, *P. pringlei*, *E. selaginellifolium*, and *P. austrinum* as species of *Oxyrrhynchium*.

***Eurhynchium fuegianum*.** Ignatov & Huttunen (2002) suggested that this aquatic species, an endemic of southern South America, might properly belong to *Platyhypnidium*. Vanderpoorten et al. formally made the transfer in 2005. Trees based on ITS data placed *E. fuegianum* in a nested position within *Rhynchostegium* + *Platyhypnidium*, with moderate bootstrap support (76). In some ways this placement is difficult to accept, because *E. fuegianum* has very much the look of a *Eurhynchium*. Its placement in that genus had never been questioned until Ignatov & Huttunen (2002). The costa of *E. fuegianum* is rather too stout for *Rhynchostegium*, and it protrudes as a prominent dorsal spine, which is a classical feature of *Eurhynchium*. In *E. fuegianum*, the leaves are erect, with acuminate and noticeably serrate tips; and the plants, though aquatic, have the brushy, yellowish aspect of *E. pulchellum* or *E. striatum*.

Based on the phenetic analyses, *E. fuegianum* is well placed in *Eurhynchium s. l.* The species formed regular clusters with *E. pulchellum*, *O. hians*, and *O. pringlei*; and some specimens overlapped with *E. striatum*. In contrast, in the ITS analysis *E. fuegianum* formed a clade with *Rhynchostegium murale*, *R. serrulatum*, *R. confertum*, and European collections of *R. riparioides*, with moderate bootstrap support (72). In the ITS2 analysis, *E. fuegianum* held an unresolved position in a clade that included all species of *Rhynchostegium* and *Platyhypnidium*. *Palamocladium euchloron* (Müll. Hal.) Wijk & Margad. was sister to this clade. In the tree based only on morphology, *E. fuegianum*

appeared in a nested position within *Platyhypnidium s. str.* These data support the transfer of *E. fuegianum* to *Platyhypnidium*.

Some synapomorphies between *E. fuegianum* and *Rhynchostegium* (including *Platyhypnidium*) include: autoicous sexuality (whereas *E. striatum* is dioicous), smooth setae, concave leaves that are twisted medially when dry, and plants forming variegated mats which are brown below but have yellow tips. However, the strong costa of *E. fuegianum* is inconsistent with the reduced costa found in most species of *Rhynchostegium*. Most forms of *Platyhypnidium s. str.* have long but fairly slender costae. Increased costal development is apparently favored in rheophilous, emergent mosses of turbulent aquatic habitats (Vitt & Glime 1984), which may explain the occurrence of so many odd aquatic mosses with exaggerated costae. The strong costa found in *E. fuegianum* is therefore less incongruous than if it were a terrestrial species resolved in the *Rhynchostegium* clade.

In the combined analysis of morphological and molecular data, *E. fuegianum* was resolved sister to *Platyhypnidium + Rhynchostegium*, but with very low bootstrap support (51). Still, based on the combined analysis the retention of *E. fuegianum* in *Eurhynchium* seems reasonable, whereas the other cladistic analyses suggested that the species should be removed to *Rhynchostegium* (or *Platyhypnidium*).

It seems likely that *E. fuegianum* represents an evolutionary intermediate between *Rhynchostegium* and *E. striatum*. Until further studies are conducted, I feel that this species should be retained in *Eurhynchium*. Endemic to a remote part of the world, *E. fuegianum* is apparently somewhat evolutionarily isolated as well. For example, of all the species included in this study, only *E. fuegianum* possesses exothecial cells which are

consistently collenchymatous. Also, the capsules are usually much less inclined than in other species. In contrast to Vanderpoorten et al. (2005), a unique molecular synapomorphy was also found for *E. fuegianum*: a T instead of a C at position 133 of the 5.8S rDNA (Appendix 4). This difference is noteworthy, because the 5.8S region was highly conserved overall: in a matrix of 71 complete 5.8S sequences, only five variable positions were identified out of 159 nucleotides (the standard length of the 5.8S region in mosses, *fide* Capesius 1997).

Eurhynchium fuegianum Cardot

Plants vivid green to yellowish, sometimes ferruginous, often blackish below, medium-sized, in dense mats, growing on rocks in and along streams. Branches rather coarse and brushy, often parallel. Rhizoids smooth, fasciculate at the bases of stem leaves, arising frequently. Pseudoparaphyllia small, foliose, concave, rounded, erose, apiculate, oblong-truncate, or broadly acuminate in outline. Leaves stiffly wide-spreading to erect, twisted medially dry, smooth to distinctly striate, concave, spoon-shaped, ovate, asymmetrical, secund, not decurrent, ovate-lanceolate and cordate at the base when well developed; leaf apex short-acuminate to acute, frequently blunt but never broadly obtuse, generally flat but showing a tendency to twist; leaf margins serrulate, distinctly so above, recurved at base. Costa long and fairly strong, ending near the leaf apex, often toothed dorsally and projecting as a spine. Alar region green, small, weakly defined, composed of somewhat thick-walled, usually porose, rectangular cells, somewhat shorter and broader than median leaf cells but not noticeably enlarged, continuous with basal cells of leaf; those also incrassate and porose in a narrow band.

Supra-alar cells somewhat incrassate and often extending well up the leaf as a distinctive margin. Median cells rather short and narrow, measuring about $70 \times 6 \mu\text{m}$. Apical cells noticeably shortened and somewhat thick-walled, not broadened (or in branch leaves somewhat so), ca. $28 \times 7 \mu\text{m}$, occupying about $\frac{1}{2}$ the region above the tip of the costa.

Autoicous; the perigonia appearing earlier than the perichaetia, usually near the base of stems and branches. Sporophytes medium-sized. Seta smooth, twisted when dry. Capsule dark, reddish-brown, short and plump, erect or somewhat inclined. Exothecial cells bulging, irregularly thickened to distinctly collenchymatous. Operculum long-rostrate and strongly oblique. Annulus well-defined but not strikingly so, composed of two rows of uneven, \pm triangular cells. Exostome teeth orange-brown and striate below, hyaline, papillose, and trabeculate above. Endostome segments pale yellow, surmounting a high basal membrane, keeled, with gaping perforations, papillose above, about as long as the exostome; cilia nodulose, somewhat reduced to rudimentary, paired or in groups of three, sometimes fused above.

Specimens examined (all at NY): ARGENTINA. *Matteri 2442*, Prov. de Tierra del Fuego; *Matteri 2543, 2581, 3729 & 4202* (*Musci Fuegiani Exsic. s. n.*, 27, 63 & 54, respectively), Depto. Ushuaia, Prov. de Tierra del Fuego; *Matteri 4757* (*Musci Patagonici Exsic. 1*), Depto. Lago Argentino, Prov. Santa Cruz; *Schäfer-Verwimp & Verwimp 8004*, Prov. Rio Negro. CHILE. *Buck 41017, 41055, 41073, 41081, 41162, 43395, 43397, 43428, 43432, 45851, 45943 & 46115*, Prov. Antártica Chilena.

Illustrations: Cardot, *Flore Bryologique des Terres Magellaniques* bd. IV(8), f. 38, p. 173; *Matteri & Ochyra*, *J. Hatt. Bot. Lab.* 66: 326 (1989); Wynns, this work, Figure 12.

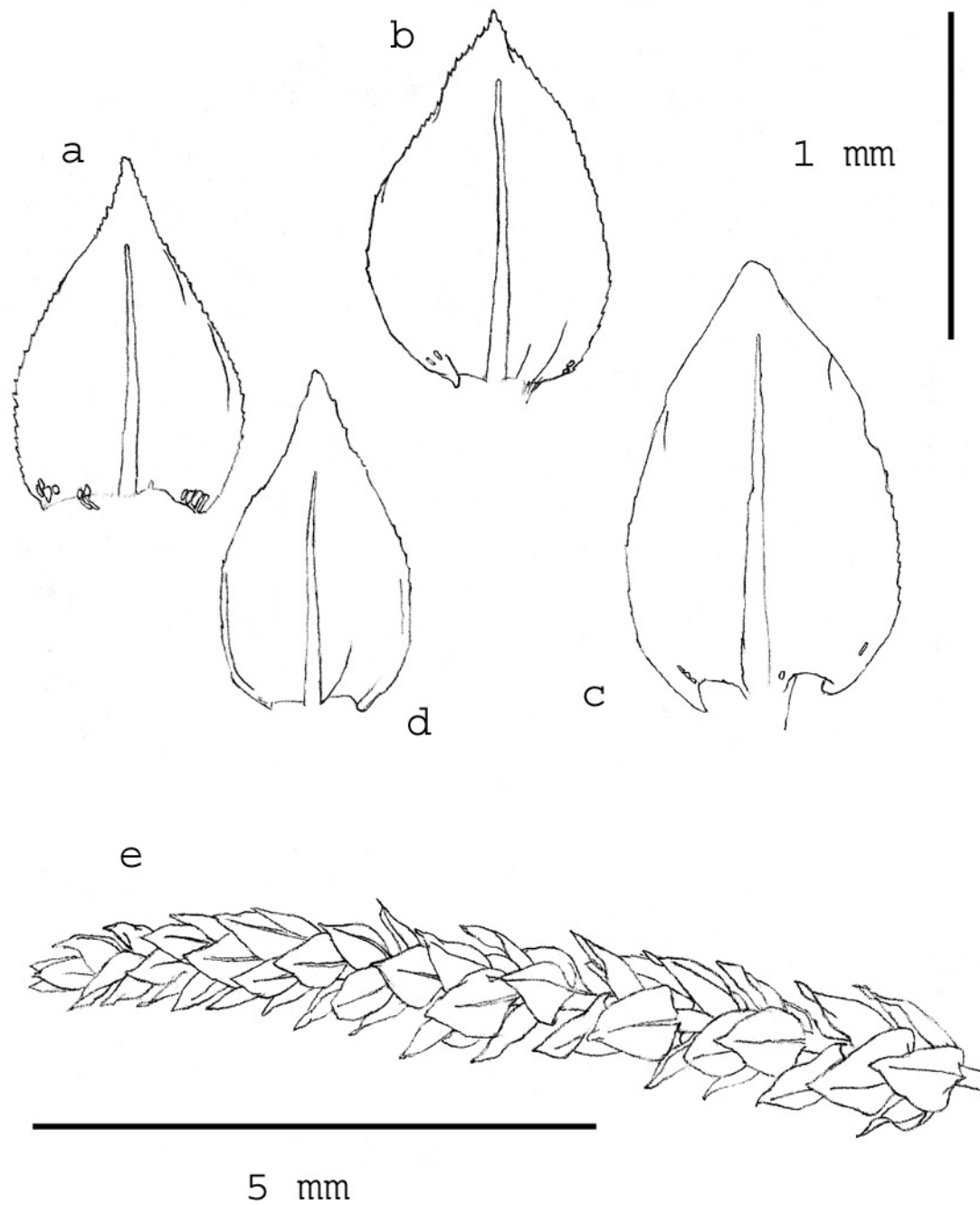


Figure 12. *Eurhynchium fuegianum*. All at NY: a – Schäfer-Verwimp & Verwimp 8004, Argentina; b – Buck 41017, Chile; c – Buck 41162, Chile; d, e – Matteri 4202 [*Musci Fuegiani Exsic.* 54], Argentina.

Eurhynchium striatum. Principal Components Analysis positioned this species somewhere between *Platyhypnidium* and other species of *Eurhynchium*, which actually agreed fairly well with the molecular data. In the analyses that included ITS data, *E. striatum* (including *E. angustirete*) was further removed from the other *Eurhynchia*, being resolved sister to the *Rhynchostegium s. l.* clade (including *E. fuegianum*) with moderate-to-high bootstrap support (76–95). These results suggested that *E. striatum*, the type of *Eurhynchium*, is more closely related to *Rhynchostegium* than it is to other representative species of *Eurhynchium* like *E. pulchellum* and *E. praelongum*. Synapomorphies for *E. striatum* and *Rhynchostegium* + *Platyhypnidium* include large size and a smooth seta. The large stature of *E. striatum* may offer an explanation for its proximity to *R. serrulatum* and *Platyhypnidium s. str.* in the phenetic analyses.

Eurhynchium striatum is an unusually large member of the genus. It is a calciphilous woodland species of western Europe and the Scandinavian peninsula. The only other species of *Eurhynchium* included in this study which really approached it was *E. angustirete* (see below). *Eurhynchium striatum* does bear some resemblance to well-developed forms of *E. pulchellum* (i.e., *E. pulchellum* var. *robustum* (Röll) Jenn.; cf. Jennings 1913); and its leaf shape is like that of *E. praelongum*, but that species is smaller. For comparative purposes, the leaves of all four of these species are presented together in Figure 13.

Eurhynchium striatum (Hedw.) Schimp.

Plants robust, terrestrial, brushy and prostrate, lustrous, yellow, light green or olivaceous. Branches frequent, curved, attenuate or densely tufted at tips. Plants hardly

heterophyllous, but leaf width very plastic. Rhizoids generally smooth, occasionally granular or minutely roughened. Pseudoparaphyllia foliose, concave, rounded-truncate, or broadly acuminate, sometimes minutely apiculate. Leaves imbricate, erect- or wide-spreading, triangular, narrowed at the shoulders from a wide cordate base, distinctly striate, little changed on drying; leaf apex acuminate, usually long; leaf margins serrate, narrowly recurved at the base and frequently throughout, with cell walls thickened in a narrow band above the alar region. Costa stout, long, flexuose, little tapered, toothed dorsally and projecting as a spine. Alar cells inflated in a small area, slightly incrassate. Basal cells strongly porose and distinct from the alar region. Median cells rather short, usually about $45\text{--}70 \times 5\text{--}8 \mu\text{m}$, vaguely porose. Apical cells somewhat shorter than median cells, occasionally also broader.

Dioicous. Sporophytes large, orange-red. Seta smooth. Capsule somewhat inclined, curved, elongate, often exceeding 3 mm in length. Exothecial cells small, thick-walled, only collenchymatous just below the capsule mouth, evenly thickened elsewhere, isodiametric to oblong, longer below. Operculum large, with a long sharp rostrum. Annulus strongly differentiated, red. Exostome teeth rather long, dark red and densely cross-striolate for most of their length, but composed of square, incrassate, hyaline cells at the apex; ventral trabeculae quite modest. Endostome about as long as exostome, golden-yellow, papillose, with a high basal membrane; cilia very long, strongly papillose, appendiculate, mostly in groups of three. Spores golden, not glossy, irregularly dented, $10\text{--}18 \mu\text{m}$ in diameter.

Specimens examined: AUSTRIA. *Juratzka s. n.*, Rekawinkel, near Vienna (DUKE). BELGIUM. *De Sloover 16433 & 23170* (NY). DENMARK. *Holmen 45b*, v. Birkerød (DUKE); *Holmen & Warncke s. n.*, Jylland (DUKE). ENGLAND. *Schofield 104756*, N Cornwall (DUKE). FRANCE. *Eggers et al. 21*, Dep. Haute Saone (NY); *Schleicher*

s. n., Savoie (DUKE). GEORGIAN REPUBLIC. *Vasak s. n.*, Colchis, W Caucasus (NY). GERMANY. *Schumacher s. n.*, Bröltal, Rheinland (DUKE). IRELAND. *Wynns 772*, Burren, Co. Clare (BOON). NORWAY. *Holmen 045*, Bömlo Id. (DUKE). SPAIN. *Buck 15078*, Prov. Asturias (DUKE). SWEDEN. *Seth s. n.*, Huskvarna, May 1873 (DUKE). SWITZERLAND. *Schleicher s. n.*, Onex, near Geneva (DUKE). TURKEY. *Davis & Coode 37473B*, near Akçakoca (DUKE).

Illustrations: Dixon, Student's Handbook of British Mosses (ed. 3), tab. LIV.O; Schimper, Corollarium, pl. 523; Smith, Moss Flora of Britain and Ireland f. 295.1–5, p. 609; Watson, British Mosses and Liverworts (ed. 3), f. 171, p. 369; Wynns, this work, Figure 13.a.

Eurhynchium angustirete is very similar to *E. striatum*. The two species are sympatric, but *E. angustirete* is much more widespread, being the only species found in Asia, and the predominate species in eastern Europe. The two are obviously sister species (if not varieties of the same species), differing primarily in the acute apices of *E. angustirete* and the acuminate apices of *E. striatum* (Figure 13). *Eurhynchium angustirete* is also softer, plumper, more julaceous, less brushy, slightly more robust, and of a paler green color. The leaves of *E. angustirete* are smoother and more concave than those of *E. striatum*. In *E. angustirete*, a plica often forms beside the costa when a leaf is pressed under the coverslip; this makes the costa appear exceptionally stout. Both species are normally dioicous; according to Ignatov (1998), *E. angustirete* can also be phyllodioicous. Both superficially and in cell structure the two species resemble each other very closely, and intermediate phenotypes exist (e.g., *Juratzka s. n.*, Austria; sub *E. striatum*, DUKE). In the molecular analyses *E. angustirete* was always resolved outside, but sister to, *E. striatum*.

I have only seen four specimens of *E. angustirete* (all filed under *E. striatum*).

The Ignatov collection is named “var. *pachycladum* G. Roth [= *E. angustirete* Kop.]”; the

Zetterstedt collection is described as *E. striatum* “forma normalis foliis brevioribus”.

Specimens examined: AUSTRIA. *Klaus s. n.*, St. Pölten, Lower Austria (DUKE). FRANCE. *Zetterstedt, Musc. Pyr. 213*, near Luchon, Pyrénées (DUKE). GERMANY. *Magnus s. n.*, Menz, near Rheinsberg, 18 Aug. 1869 (NY). RUSSIA. *Ignatov, Mosses of USSR 138*, Altai (DUKE).

Illustrations: Ignatov, *Arctoa* 7: 147 (1998); Koponen, *Mem. Soc. Faun. Flor. Fenn.* 43: 54 (1967); Noguchi, *Illustrated Moss Flora of Japan* 4, f. 434.C, p. 989; Takaki, *J. Hatt. Bot. Lab.* 16: 36 (1956; as *E. striatum*); Wynns, this work, Figure 13.b.

Eurhynchiastrum and *Kindbergia*

In the phylogenetic analysis of ITS data, *Eurhynchium pulchellum* and *E. praelongum* were resolved in a big clade that also included *Scleropodium*, *Brachythecium*, and *Bryhnia*. This clade was resolved sister to the *Rhynchostegium* + *Platyhypnidium* + *E. striatum* clade, but without bootstrap support. In this study the sampling of these taxa was too limited to resolve their relationships with confidence. As Huttunen & Ignatov (2004) discovered, ITS data strongly suggested that *Eurhynchium* in its traditional sense is polyphyletic. As a partial solution, Ignatov & Huttunen (2002) moved *E. pulchellum* and *E. praelongum* to the segregate genera *Eurhynchiastrum* Ignatov & Huttunen and *Kindbergia* Ochyra, respectively.

***Eurhynchium pulchellum*.** In the PCAs, *E. pulchellum* formed a cluster with *E. fuegianum*, *O. hians*, and *O. pringlei*. Analysis of Variance only identified one significant dimensional difference between *E. pulchellum* and other species of *Eurhynchium s. l.*: in *E. pulchellum* the leaves are quite slender (narrow in proportion to

their length). The phylogenetic analysis of morphological data resolved *E. pulchellum* in a nested position in a monophyletic *Eurhynchium s. l.* clade, sister to *O. hians* + *E. praelongum*.

In contrast, in the phylogenetic analyses that included molecular data, *E. pulchellum* did not appear to be closely related to other species of *Eurhynchium*. Its nearest (but still distant) congener was *E. praelongum*, which it somewhat resembles in leaf shape. The molecular analyses placed *E. pulchellum* sister to *Brachythecium*, *Bryhnia*, *Eurhynchiadelphus eustegia* [= *Eurhynchium eustegium* (Besch.) Dixon], *Cirriphyllum cirrosum* (Schwägr.) Grout, and *Palamocladium leskeoides* (Hook.) E. Britton. Ignatov & Huttunen (2002) erected the new genus *Eurhynchiastrum* to accommodate *E. pulchellum*, which in their molecular analyses was not resolved very close to *E. striatum* (Huttunen & Ignatov 2004). As far as I can tell, they only found two morphological criteria to separate *Eurhynchiastrum* from *Eurhynchium*: size, and degree of leaf plication. Although I feel that these two characters are more meaningful at the species level, I appreciate their desire to change the classification of *Eurhynchium* to better reflect natural relationships within the Brachytheciaceae. My ITS data also separated *E. pulchellum* from *E. striatum*.

Eurhynchium pulchellum is circumboreal in distribution. In North Carolina this moss is most frequently encountered on moist, shaded banks. Diagnostic features of the species are a small stature, yellowish color, soft brushy aspect, erect branches, and a phyllodioicous sexual condition. In *Anderson 9132* (DUKE), one or two laminal cells near the costa tip are strongly prorate; but this is an aberrant phenotype. Small, julaceous

specimens from eastern Europe (e.g., *Cuba s. n.* & *Wüstnei s. n.*; NY) represent a distinct variety of the species.

The generic identity of an Alaskan collection of *Bryhnia hultenii* (Schofield *et al.* 108026, Pribilof Is.; TENN), originally determined as *E. pulchellum*, was confirmed by the cladistic analyses of DNA sequence data, where it was always resolved sister to species of *Brachythecium*. In PCA11, this specimen was resolved close to *Rhynchostegium*. It was omitted from the cladistic analysis based on morphology to reduce the homoplasy present in the data set.

Eurhynchium pulchellum (Hedw.) Jenn.

Plants rather small, yellow to light green, chartaceous when dry, on mesic to dripping banks. Stems irregularly pinnate, terete, with many erect branches, or smaller branches sometimes complanate. Rhizoids brown, tinted with orange or wine-color, ± smooth, in fascicles along primary stems. Pseudoparaphyllia generally acuminate. Leaves usually close, often imbricate, appressed to erect-spreading, decidedly striate dry, striolate wet, ± asymmetrical, somewhat heterophyllous: stem leaves broadly triangular, long-attenuate, decurrent, and somewhat auriculate; branch leaves narrowly triangular or ovate-lanceolate, acute, and hardly decurrent; leaf apex generally blunt, not twisted but with recurved margins and flaring teeth; leaf margins serrate and noticeably recurved throughout. Degree of variation in the length of the leaf acumen very large, depending on the age of the leaf and its position on the plant. Costa strong, little tapered, ending well below the leaf apex, toothed dorsally, and projecting as a stout spine. Leaf cells narrow and thin-walled, vaguely porose throughout. Alar region concave, ± granular,

well-defined by isodiametric or oblong, sometimes sinuous cells. Inner basal cells longer and narrower than alar cells, somewhat incrassate, porose. Median cells rather long and narrow, ca. $70 \times 5 \mu\text{m}$. Cells at the extreme leaf tip expanded, especially in branch leaves, ca. $35 \times 10 \mu\text{m}$, abruptly grading into median cells below.

Phylloodioicous, having dwarf male plants growing on the stems and leaves of the females. Sporophytes rather large, usually over 2 mm long. Calyptra cucullate, naked. Seta smooth. Capsule short, plump, somewhat inclined. Exothecial cells flat or slightly bulging; the walls irregularly thickened, sometimes nodulose, but not collenchymatous. Operculum with a conspicuous stout beak. Annulus well-defined; composed of 2–3 rows of uneven, rhombic cells. Endostome light yellow, papillose; segments keeled and perforate; cilia nodulose, papillose throughout, somewhat shorter than segments, in groups of 1–3. Spores 10–13 μm in diameter, golden, smooth.

Specimens examined: ALASKA. *Schofield et al.* 99584, Bering Sea (TENN). ARMENIA. *Cuba s. n.*, Caucasus (NY). BRITISH COLUMBIA. *Schofield* 102991, Wells Gray Prov. Pk. (TENN); *Schofield & Godfrey* 98365, Tatshenshini R. (TENN). CALIFORNIA. *Shevock* 17526, Tulare Co. (NY). ECUADOR. *Lewis* 78-2157, Prov. Azuay (NY). GERMANY. *Wüstnei s. n.*, Schwerin, Mecklenburg (NY). MAINE. *Allen* 21390, Franklin Co. (NY). MISSOURI. *Redfearn, Moss. Int. Highl.* 175, Barry Co. (TENN). NORTH CAROLINA. *Anderson* 9132, Macon Co. (sub *E. hians*, DUKE); *Anderson* 20865, Macon Co. (DUKE); *Anderson* 27753, Jackson Co. (DUKE); *Buck* 15378, Graham Co. (DUKE); *Pittillo* 9804, Buncombe Co. (DUKE); *Wynns* 254 & 615, Watauga Co. (BOON); *Zander* 470, Watauga Co. (DUKE); *Zander* 982, Rutherford Co. (DUKE); *Zartman* 1282, Jackson Co. (DUKE). NORTHWEST TERRITORIES. *Talbot* T5034-5, T5034-7 & T5040, Nahanni N. F. (NY). QUEBEC. *Hedderson* 8334, Mingan Archipelago (TENN). RUSSIA. *Ignatov, Mosses of USSR* 83, Kostroma Prov. (NY); *Tan* 97-147 & 97-458, Khabarovsk Terr. (NY). SWEDEN. *Florin s. n.*, Uppland (NY); *Hakelier s. n.*, Rinkaby, Närke, E Gotland (NY); *Tärnlund s. n.*, Uppland (NY); *Tärnlund s. n.*, Västmanland (NY).

Illustrations: Buck, *Pleurocarpous Mosses of the West Indies*, pl. 96, f. 11–18, p. 246; Crum & Anderson, *Mosses of Eastern North America* v. 2, f. 524, p. 1069; Flowers, *Mosses: Utah and the West*, p. 421; Hedwig, *Species Muscorum*, tab. LXVIII; Jennings, *Mosses of Western Pennsylvania*, pl. LVIII, p. 382; Ignatov, *Arctoa* 7: 146 (1998); Lawton, *Moss Flora of the Pacific Northwest*, pl. 169; Reese, *Mosses of the Gulf South*,

pl. 52.E, p. 213; Sharp et al., Moss Flora of Mexico v. 2, f. 696, p. 933; Smith, Moss Flora of Britain and Ireland, f. 296.1–12, p. 611; Wynns, this work, Figure 13.c,d.

Eurhynchium praelongum has long been associated with *O. hians*, partly due to nomenclatural confusion (Grout 1898; Ignatov & Isoviita 2003). The two species are united by a coarsely roughened seta, a strong spinose costa, and rather short leaf cells. *Eurhynchium praelongum* is a rather variable species with at least two well-marked varieties.

In the likelihood analysis *E. praelongum* was resolved sister to *Scleropodium*, in a clade that also included *Brachythecium velutinum* (Hedw.) Schimp. In the PCAs, *E. praelongum* was generally resolved in an isolated position. Based on dimensional differences *Kindbergia* was the most distinct of the segregate genera of *Eurhynchium* proposed by Ignatov & Huttunen (2002). If one wishes to recognize *Kindbergia*, as represented by a few similar species worldwide, it can be distinguished from *Eurhynchium* by plants that are strongly heterophyllous, with decurrent leaves, a subdendroid habit, and smallish, strongly inclined capsules (Robinson 1967).

Eurhynchium praelongum (Hedw.) Schimp.

Plants rather small, fine, deep green, creeping, often appearing sub-dendroid by branching once or twice pinnate. Older stems very thick in proportion to the size of the leaves (as in *Thuidium*). Leaves small, erect-spreading, triangular, cordate at the base, noticeably decurrent; stem and branch leaves strikingly differentiated: branch leaves much narrower; leaf margins coarsely serrate throughout, recurved below, occasionally above. Costa very stout, little tapered, flexuose, coarsely toothed, and abruptly projecting

as a dorsal spine near the leaf apex, on stem leaves often appearing percurrent. Laminal cells usually quite short, 18–64 μm long. Basal and alar cells chlorophyllose, somewhat dilated and incrassate, in older stems the alar cells becoming strongly inflated and hyaline. Median cells 4–7 μm wide. Apical cells somewhat broader than median cells.

Dioicous. Sporophytes rather small and inconspicuous. Seta coarsely roughened. Capsules strongly inclined, tubular, cigar-shaped, or ovoid, sometimes with a distinct apophysis, dark reddish-brown, sometimes with discolored patches. Exothecial cells small, short–oblong or –rectangular, somewhat bulging, not collenchymatous. Annulus differentiated, reddish. Exostome teeth rather thick and blunt, strongly incurved, orangish-red and cross-striolate, hyaline and coarsely papillose at the tips, with well-developed ventral trabeculae. Endostome tawny yellow, with erect keeled segments and a high basal membrane; segments widely perforate, equalling or surpassing the exostome teeth in length; cilia well-developed, stout, coarsely papillose, nodose, in groups of 1–3, sometimes fused above. Spores green with a golden jacket, smooth, 11–17 μm in diameter.

Specimens examined: CALIFORNIA. *Jenkins s. n.*, Monterey Co. (BOON); *Wynns 646*, Marin Co. (BOON). GREECE. *Düll 74*, Samos Id. (sub *R. riparioides*, DUKE). IRELAND. *Wynns 753 & 754*, Slane, Co. Meath (hb. Wynns). POLAND. *Lisowski 96954*, Poznan (sub *E. hians*, DUKE). PORTUGAL. *Solms s. n.*, Algarve, 1866 (sub *E. strigosum*, NY).

Illustrations: Crum & Anderson, *Mosses of Eastern North America* v. 2, f. 528, p. 1076; Dixon, *Student's Handbook of British Mosses* (ed. 3), tab. LIV.D; Gangulee, *Mosses of Eastern India* 7, f. 877, p. 1742; Ignatov & Huttunen, *Arctoa* 11: 261 (2002); Ignatov et al., *Acta Bot. Fenn.* 178: 11 (2005); Koponen, *Mem. New York Bot. Gard.* 45: 510 (1987); Lawton, *Moss Flora of the Pacific Northwest*, pl. 168; Matteri & Ochyra, *J. Hatt. Bot. Lab.* 66: 322 (1989); Schimper, *Corollarium*, pl. 526; Sharp et al., *Moss Flora of Mexico* v. 2, f. 704, p. 944; Smith, *Moss Flora of Britain and Ireland*, f. 297.1–11; p. 613; Watson, *British Mosses and Liverworts* (ed. 3), f. 172, p. 371; Wynns, this work, Figure 13.e–g.

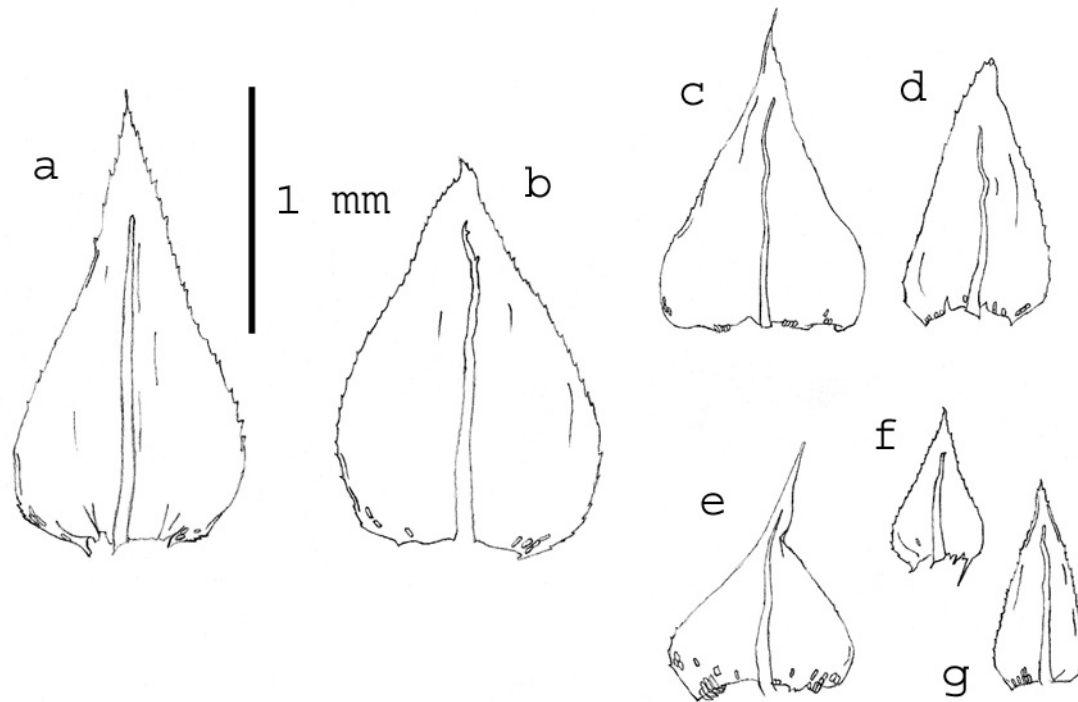


Figure 13. Leaves of four species of *Eurhynchium sensu lato*: a – Buck 15078, Spain (*E. striatum*); b – Ignatov, Mosses of USSR 138, Altai (*E. angustirete*); c, d – Wynns 615, North Carolina (*E. pulchellum*); e–g – Wynns 646, California (*E. praelongum*: e – stem leaf; f, g – branch leaves).

Oxyrrhynchium

Following Brotherus (1909), Ignatov & Huttunen (2002) used the name *Oxyrrhynchium* at the generic level for *Eurhynchium hians* and its allies. The name *Oxyrrhynchium* has a somewhat checkered taxonomic history (cf. Buck 1988), and some species which do not belong to this lineage have passed under *Oxyrrhynchium* in the past (e.g., *R. riparioides* and *E. praelongum*). A proposal submitted by Ignatov & Isoviita (2003) to conserve the genus *Oxyrrhynchium* with *O. hians* (Hedw.) Loeske as the type was recently accepted (Zijlstra 2005).

Morphologically *Oxyrrhynchium* is distinctive. Many specimens show a complanate habit and have pinnate branches of determinate length with sharply serrate, oblong-ovate leaves. The genus is also characterized by plants with a loose foliation and by leaves that are pointy, somewhat plicate, and twisted medially when dry. Many species have very strong costae. Most species have rough setae, and are dioicous. The lineage apparently has a strong tendency to become aquatic; and although *O. hians* is a terrestrial species, it does show a marked preference for permanently moist habitats.

In all analyses that included molecular data, the *Oxyrrhynchium* lineage was clearly discerned, with strong bootstrap support (98–100). In the ITS analysis, the lineage included *O. hians*, *O. pringlei*, *O. selaginellifolium*, *Donrichardsia macroneuron*, and one aquatic collection of uncertain identity, tentatively named *Oxyrrhynchium* sp. 2 (Appendix 2). In the ITS2 analysis another aquatic species, *O. austrinum* (Hook. f. & Wilson) Broth., was also resolved in this clade, along with a clade of terrestrial taxa. In that analysis, *O. vagans* (A. Jaeger) Ignatov & Huttunen occupied a basal position within the *Oxyrrhynchium* lineage. The leaves of several representative species of the genus are illustrated in Figure 15.

The phylogenetic position of the *Oxyrrhynchium* lineage relative to other species of *Eurhynchium* was not well resolved. In the combined analysis, the *Oxyrrhynchium* lineage was resolved sister to the *E. striatum* + *Rhynchostegium* + *Platyhypnidium* clade, with moderate bootstrap support (77); and the same relationship was found in the ITS2 analysis. But in the ITS analysis, the *Oxyrrhynchium* lineage + *Okamuraea hakoniensis* (Mitt.) Broth. was sister to a clade that included all the other ingroup taxa in the study.

Oxyrrhynchium hians exhibits a great deal of phenotypic variation, especially in Europe. The variation and synonymy of this species is discussed in Grout (1898) and Dixon (1924). In the herbarium European collections of this species may be found under *Eurhynchium swartzii* (Turner) Curn. or *E. atrovirens* (Sw.) H. Klinggr. Some populations (more often in Europe) are diminutive, straggling and complanate, with narrow leaves and acuminate leaf apices; other populations have broader, acute leaves and arching, terete branches, forming large loose wefts.

The species was also quite variable genotypically (in terms of ITS; Appendix 4). Of the six sequences I obtained for *O. hians*, only one was redundant. Fortunately, this was one of the species I was able to sample across a broad geographic range, and all molecular analyses found it to be a monophyletic taxon.

In the cladistic analysis based only on morphology, *O. hians* was resolved as paraphyletic. Some collections were resolved sister to *E. praelongum*, some sister to these plus *E. pulchellum*, and some sister to all of these plus *E. striatum*. However, in all other analyses *O. hians* was resolved as a monophyletic taxon, sister to *O. pringlei* and its allies.

It does not appear that this species has been recorded from Mexico and Guatemala until now. However, other Mexican and Central American specimens of *O. hians* misidentified as *Eurhynchium pringlei* or *Rhynchostegium subrusciforme* probably exist.

Oxyrrhynchium hians (Hedw.) Loeske

Plants variable in size, yellow-green, pale green or green, chartaceous when dry, terrestrial or occasionally subaquatic, weedy, usually growing in moist, partially shaded,

disturbed habitats, on soil or humus, in woods, lawns, on banks, and beneath shrubs.

Stems creeping and stoloniferous, or irregularly pinnate, with many parallel, determinate, \pm flattened branches. Rhizoids fasciculate, restricted to leaf bases, usually smooth but with age becoming minutely papillose. Pseudoparaphyllia broadly acuminate in outline. Leaves erect-spreading or widely spreading, somewhat pinched and medially twisted dry, smooth to striate, ovate or ovate-acuminate, asymmetrical, hardly decurrent; leaf apex acuminate or acute, flat but showing a tendency to twist; leaf margins sharply serrulate to serrate, recurved below, sometimes medially, frequently so near the tip. Costa strong, little tapered, ending below the leaf apex, bearing dorsal teeth and projecting as a stout spine. Alar region green or brownish, small but well-defined, composed of decidedly incrassate, vaguely porose cells, with an occasional cell noticeably enlarged. Basal cells continuous with alar region, somewhat incrassate, vaguely to distinctly porose, the lowermost cells frequently enlarged in a collarlike row. Supra-alar and lower marginal cells somewhat incrassate, giving the leaves the suggestion of a border. Median cells rather short, measuring about 50×6 μm . Apical cells short, incrassate, in most leaves noticeably broader than the median cells, ca. 25×9 μm , occupying $\pm \frac{1}{2}$ the region above the tip of the costa, then grading into median cells.

Dioicous. Sporophytes rather large. Calyptra cucullate, naked. Seta coarsely roughened. Capsule orange or reddish-orange, plump, curved, inclined, with stomates at the base. Exothecial cells flat or slightly bulging, the walls irregularly thickened but not collenchymatous. Operculum abruptly long-rostrate. Annulus well defined, composed of 2–3 rows of uneven, rhombic cells. Endostome segments yellow; cilia strongly nodose or

appendiculate, papillose above, somewhat shorter than the segments, paired or in groups of three. Spores smooth, 12–22 µm in diameter.

Specimens examined: ALABAMA. *Wynns 657*, Lauderdale Co. (hb. Wynns). BELGIUM. *Arts 21786*, Prov. Limburg (NY). BRITISH COLUMBIA. *Schofield 109844*, Vancouver (TENN). ENGLAND. *Dixon 275/97*, Northamptonshire (DUKE). GEORGIAN REPUBLIC. *Vasak s. n.*, Distr. Sukhumi, W Caucasus (sub *E. striatum*, NY). GERMANY. *Frahm et al. s. n.*, Wahlheim, Nordrhein (sub *E. pulchellum*, NY). GUATEMALA. *Beer s. n.*, Chichitnango, 8 Apr 1948 (sub *E. subruscifforme*, NY). FINLAND. *Piippo 1543*, Ahvenanmaa, Åland (DUKE). INDIA. *Griffith 160 (677)*, Tongsa, Bhutan (sub *R. herbaceum*, NY); *Wallich s. n.*, ex hb. Mitten (sub *H. cordatum* Harvey, NY). IVORY COAST. *Frahm s. n.*, Mont Toukovi (NY). KANSAS. *Bowers & Timme 22183*, Montgomery Co. (sub *E. pulchellum*, TENN). KENTUCKY. *Risk 11450*, Johnson Co. (TENN). MEXICO. *Sharp et al. 1842c*, Hidalgo (sub *R. pringlei*, TENN). NEBRASKA. *Churchill & Churchill 19723*, Lancaster Co. (sub *E. pulchellum*, NY). NORTH CAROLINA. *Anderson & Jones 9525*, Avery Co. (DUKE); *Grout s. n.*, Pink Beds, Transylvania Co. (DUKE); *Hicks s. n.*, Tater Hill, Watauga Co. (TENN); *Jamieson & Zales 4794*, Swain Co. (DUKE); *Standley 5848*, Haywood Co. (DUKE); *Wynns 621, 622, 744 & 821*, Watauga Co. (BOON); *Zander 470*, Watauga Co. (DUKE). PENNSYLVANIA. *Wynns 326*, Monroe Co. (BOON). POLAND. *Ochyra et al. 169/93*, Western Carpathians, S Poland (NY); *Stebel 576/97*, Lower Silesia (NY). RUSSIA. *Ignatova & Ignatov, Mosses of USSR 70*, Moscow (NY); *Zickendrath s. n.*, Zarizyno, Moscow (DUKE). SCOTLAND. *Chamberlain s. n.*, E Lathian (sub *R. confertum*, TENN). SWEDEN. *Alstlin s. n.*, 10 Nov 1901 (DUKE); *Gram s. n.*, Etelhem, Gotland (DUKE); *Hamnström s. n.*, Charlottenborg, Ostergotland (DUKE); *Medelius s. n.*, Småland (DUKE). SWITZERLAND. *Bernet 28*, near Geneva, Dec. 1869 (sub *E. striatum*, DUKE); *Gay s. n.*, near Lausanne (NY); *Schleicher s. n.*, comm. hb. Boisser, 1912 (DUKE). TENNESSEE. *Amtoft 2005b*, Carter Co. (BOON). TEXAS. *Whitehouse 26870*, Johnson Co. (sub *E. riparioides*, NY).

Illustrations: Breen, *Mosses of Florida*, pl. 78.1–6; Crum & Anderson, *Mosses of Eastern North America* v. 2, f. 525, p. 1071; Dixon, *Student's Handbook of British Mosses* (ed. 3), tab. LIV.E; Gangulee, *Mosses of Eastern India* 7, f. 875 & 876, pp. 1739 & 1741; Hedwig, *Species Muscorum*, tab. LXX; Ignatov, *Arctoa* 7: 145 (1998); Ignatov et al., *Acta Bot. Fenn.* 178: 16 (2005); Jennings, *Mosses of Western Pennsylvania*, pl. LVIII, p. 392; Noguchi, *Illustrated Moss Flora of Japan* 4, f. 437, p. 996; Reese, *Mosses of the Gulf South* f. 53.B–D, p. 213; Smith, *Moss Flora of Britain and Ireland* f. 298.1–7, p. 615; Watson, *British Mosses and Liverworts* (ed. 3), f. 173, p. 372; Wynns, this work, Figure 15.a–d.

Oxyrrhynchium pringlei. Dimensional differences between *O. pringlei* and *O.*

hians were similar enough that they could not be separated by PCA. In the molecular analyses, the two species were always resolved together in the *Oxyrrhynchium* lineage,

along with *Eurhynchium selaginellifolium* and *Donrichardsia macroneuron*. All analyses that included molecular data strongly supported the exclusion of *O. pringlei* from both *Platyhypnidium* and *Rhynchostegium*, and the inclusion of the species in *Oxyrrhynchium*.

In the phylogenetic analysis based on morphology, *O. pringlei* was basal to a clade that included *O. hians*, *E. pulchellum*, *E. praelongum*, and *E. striatum*, but not *E. fuegianum*. In this analysis, the aquatic condition appeared to be basal in *Eurhynchium s. l.*, and *O. pringlei* itself may have arisen from aquatic species of *Platyhypnidium*.

Although *O. pringlei* is primarily a Central American species, it is also disjunct to certain drainages of the southern escarpment of the Blue Ridge Mountains in the southeastern United States. These Appalachian plants represent a homomalous form of the species with more triangular leaves and with longer costae. It is likely that U. S. populations of *O. pringlei* are relicts of a milder-climate flora that once prevailed in the Southern Appalachian region, but moved southward with the advance of glaciers following the Miocene (Crum 1951). Both Mexican and Appalachian collections of *O. pringlei* are sterile. The conspecificity of Mexican and Southern Appalachian populations of *O. pringlei* was supported by PCA11.

On a recent visit to NY, I came across some moss specimens from India which are good matches for *O. pringlei*. Two duplicate specimens of a collection made by J. F. Duthie at a waterfall in Phedi, Tehri-Garhwal, northern India on October 19, 1891 (filed as types of “*R. cataractile* C. M. *in litt.* 1891”) closely resemble Appalachian material, whereas another specimen from the Mitten herbarium collected by Hugh Falconer in “NW Himalaya” represents a slightly larger form of the species (Figure 15). Surprisingly, the specimens were fertile, thus allowing me to describe the sporophytes of *O. pringlei*

for the first time (below). The discovery of Indian material of *O. pringlei* dramatically increases the range of this species.

Two aquatic specimens at NY identified as *Eurhynchium pringlei* (Bryant 1682, Clear Creek, Grand Canyon N. P., Az.; Sharp 5250, Rio San Juan, Huehuetenango, Guatemala) were included in the morphometric analyses, in part to confirm their specific identity. Both specimens are the size of a *Platyhypnidium* (leaves broad, and exceeding 1.5 mm in length), but have strong costae and pointy leaves like in *O. pringlei*. In PCA11, neither specimen appeared particularly close to *O. hians* or *O. pringlei*, but instead clustered with *R. muelleri*. Both specimens appeared basal to the monophyletic *Eurhynchium s. l.* clade identified in the cladistic analysis based on morphology. Bryant 1682 is apparently dioicous (the collection is female) and may represent the first record of fertile *O. pringlei* from the U. S. However, the plants are larger than is typical, and the leaves are unusually broad for *O. pringlei*. I am unsure of the identity of Bryant 1682.

Neither was the specific identity of Sharp 5250 established in this study. The specimen is too large for *O. pringlei*, which it resembles in having pointy leaves and a strong costa projecting as a short dorsal spine. The leaf shape (broadly cordate-triangular) and plication disagree with *R. aquaticum*, which it resembles at the cellular level. The costa is too stout for *Brachythecium rivulare*, another species that has a decurrent alar region composed of enlarged, thin-walled cells (Appendix 3). If setae were present the identity Sharp 5250 would be easier to establish. According to the original description (Herzog 1927), *Platyhypnidium intermedium* Herzog from Brazil is another taxon having characteristics of both *R. aquaticum* and *Oxyrrhynchium*.

Oxyrrhynchium pringlei (Cardot) J. Wynns ined.

Plants aquatic, bright green to dark green, medium-sized, growing on rocks in streams, springs and persistent seeps. In cross-section stems with (1)2-3(5) rows of thick-walled cells surrounding a core of thin-walled cells; a central strand of small thin-walled cells is present. Branches infrequent, long, curved, and oriented in direction of flow, rather loosely foliate, often complanate, sometimes flagelliferous. Rhizoids smooth, burgundy-brown, fasciculate at the bases of stem leaves, occurring frequently.

Pseudoparaphyllia usually (but not invariably) acuminate. Leaves erect or erect-spreading, striolate or weakly plicate and twisted medially dry, often homomallous, ovate or oblong-ovate to lanceolate, secund, decurrent, firmly attached to stem, 0.8-1.5(1.7) mm long; plants hardly heterophyllous, but branch leaves often quite narrow; leaf apex acute or short-acuminate, sometimes \pm subulate; leaf margins weakly to sharply serrulate or denticulate throughout, recurved at base, sometimes narrowly so above. Costa green, subpercurrent, stout and little tapered, suddenly disappearing in the acumen or projecting as a modest dorsal spine. Leaf cells short, mostly 40-70 μm in length. Alar and basal cells continuous, very dark green, slightly enlarged, rectangular, with thick, occasionally orangish walls. Supra-alar cells incrassate, continuous with alar and basal cells; apical cells also incrassate; all together creating a nearly continuous border of reinforced marginal cells.

Apparently dioicous; only perichaetial plants have been found. Sporophyte large in proportion to the gametophyte. Seta orange, reddish below, roughened, more weakly so above, 1.3-2.2 cm long. Capsule rather short and plump, ca. 1.8 \times 1.1 cm. Exothecial cells not collenchymatous. Operculum bearing a rather long, sharp rostrum. Annulus

well-defined, in 3–4 rows. Exostome teeth long, brown-orange and finely cross-striolate below, hyaline and papillose above, with conspicuously secund, lanceolate marginal teeth, and modest hemidiscoidal ventral trabeculae. Endostome shorter than the exostome; basal membrane high, yellow; segments yellow, becoming paler above, finely papillose, keeled, with conspicuous to gaping perforations; cilia hyaline, fairly long, but shorter than the segments, papillose, nodose, in groups of 2–3. Spores rounded-tetrahedral, faintly papillose, 12–16 μm in diameter.

Specimens examined: GEORGIA. *Anderson 27319*, Rabun Co. (DUKE); *Zartman 454*, Rabun Co. (DUKE). GUATEMALA. *Steyermark 35164*, Quezaltenango (sub *R. subrusciforme*, NY). INDIA. *Duthie s. n.*, Phedi, Tehri-Garhwal, NW India, 19 Oct 1891 (Type of *R. cataractile*, NY); *Falconer s. n.*, NW Himalaya, ex hb. Mitten (NY); *Gollan s. n.*, Arnigadh, Mussoorie, NW Himalaya, 1675', 13 Dec. 1895, det. Brotherus #3416 (sub *R. rusciforme*, NY); *Gollan s. n.*, Mussoorie, NW Himalaya, 12 Sept. 1900, comm. Krieger, ex hb. Princeton U. (Type of *R. cataractile*, NY); *Koelz 7414*, Tarand-Sarahan, Punjab, 2–8 Nov 1933, det. Bartram (sub *R. planiusculum*, NY); *Thomson s. n.*, hills above Tingi, 13000' (NY); *Thomson 1158*, "Lachoong" [Sikkim], 15000', ex hb. Mitten (NY). MEXICO. *Arsène 4589*, Morelia, Michoacán (sub *E. subrusciforme*, DUKE); *Arsène 4822 & 4827*, Adameo, Michoacán (NY); *Arsène 5006*, Hacienda Batan, Puebla (NY); *Arsène 7534*, near Campanario, Michoacán (sub *E. subrusciforme*, DUKE); *Delgadillo 6044 & 6045*, Michoacán (MEXU); *Frye & Frye 2762*, Cuernavaca, Morelos (sub *E. riparioides*, DUKE); *McFarland & Sharp 8725b*, Michoacán (TENN); *Pringle 761*, Rio Blanco Falls, near Guadelajara, Jalisco (Syntype of *R. pringlei*, NY); *Pringle 10434 & 10525*, Cuernavaca, Morelos (Isosyntypes of *R. pringlei*, NY); *Pringle s. n.*, Cuernavaca, Morelos, 5 Dec. 1907 (Isosyntype of *R. pringlei*, DUKE). NORTH CAROLINA. *Keith 38–45*, Polk Co. (BOON); *Wynns 696 & 704*, Polk Co. (hb. Wynns). SOUTH CAROLINA. *Anderson 22257*, Pickens Co. (TENN); *Buck 17726*, Pickens Co. (NY); *Correll & Wherry 11007*, Pickens Co. (DUKE); *Crum & Anderson, Mosses of North America 924*, Pickens Co. (TENN); *Hill & Heaton 23469*, Greenville Co. (DUKE); *McFarland s. n.*, Rocky Bottom Ck., Pickens Co. (hb. Wynns); *McFarland s. n.*, Camp Branch, Oconee Co. (BOON); *Wynns 487–489, 519, 520, 536–538, & 540*, Oconee Co. (BOON); *Wynns 544, 546, 550, 552–554, & 563*, Pickens Co. (BOON); *Wynns 568 & 572*, Greenville Co. (BOON); *Zartman & Pittillo 240 & 454*, Oconee Co. (DUKE).

Illustrations: *Crum & Anderson, Mosses of Eastern North America v. 2, f. 527, p. 1075*; *McFarland in Moss Flora of Mexico v. 2, f. 701, p. 940 (p. 938 in error)*; *Wynns, this work, Figures 14, 15.i, j.*

***Oxyrrhynchium* sp. 2.** The identity of one aquatic specimen from China (*Buck* 23824, *Zhejiang Prov.*; NY) known in this study as “*Oxyrrhynchium* sp. 2” (Appendix 2) was not established. In many respects the plants resemble type specimens of *Rhynchostegium pringlei* (Figures 14, 15); but most of the stems are flagelliferous, and the specimen may not be showing the phenotype of well-developed material. In all cladistic analyses, *Buck* 23824 was placed in the *Oxyrrhynchium* lineage. In the morphological analysis, it was sister to Mexican specimens of *O. pringlei* (*Delgadillo* 6044 & 6045; MEXU). In the combined analysis, this collection was sister to *O. pringlei* + *O. selaginellifolium*; but in the ITS analysis, it was basal to the *Oxyrrhynchium* lineage. The inclusion of *Buck* 23824 in *O. pringlei* would increase the range of that species to China. The recent discovery of Indian material of *O. pringlei* makes this scenario more likely; however, ITS data suggest that *Buck* 23824 actually represents another, distinct species. One of the few well-developed leaves of *Buck* 23824 is depicted in Figure 15.h.

Oxyrrhynchium selaginellifolium. Three specimens of this aquatic Hawaiian endemic were found in herbaria misidentified as *Platyhypnidium muelleri*. Although *O. selaginellifolium* is not closely related to *Rhynchostegium muelleri*, both of these large-leaved aquatic species occur in Hawaii, so confusion of the two is possible. *Oxyrrhynchium selaginellifolium* may be distinguished from *R. muelleri* by its acuminate, often plicate leaves and its complanate, straggling habit.

In PCA, two specimens of *O. selaginellifolium* were resolved near other large-leaved taxa (namely, *Platyhypnidium* s. str., *R. serrulatum*, and *Sharp* 5250). In the molecular analysis, *O. selaginellifolium* was resolved sister to *Donrichardsia*

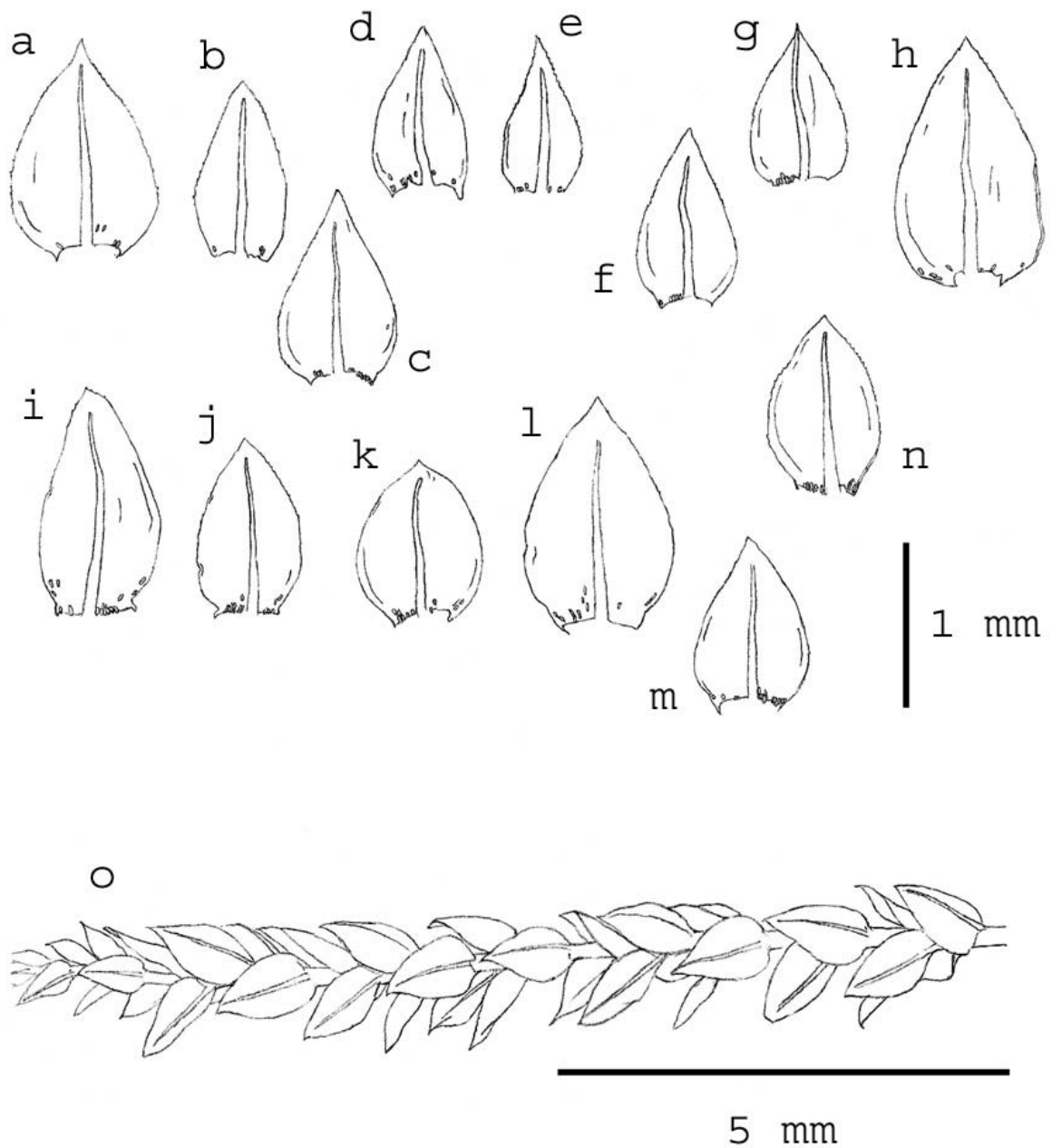


Figure 14. *Oxyrrhynchium pringlei*: a, b – Keith 42, North Carolina; c – Zander 3095, North Carolina; d, e – Wynns 488, South Carolina; f, g – Duthie s. n., India; h – Falconer s. n., Himalayas; i, j – Pringle 761, Mexico; k, l – Pringle 10454, Mexico; m – Delgadillo 6045, Mexico; n – Steyermark 35164, Guatemala; o – Keith 44, North Carolina.

macroneuron. These two formed a clade that was sister to *O. pringlei* (but without bootstrap support).

Oxyrrhynchium selaginellifolium represents the largest aquatic species of the *Oxyrrhynchium* lineage identified thus far, surpassing even *O. austrinum*. The leaves are long (frequently exceeding 2 mm in length), distant, oblong-ovate (cordate in stem leaves), short-acuminate or apiculate, and often have distinct plicae. The plants are stoloniferous and sparingly branched, exactly in the manner of *O. pringlei*, *Platylomella lescurii* (Sull.) A. L. Andrews, and other mosses found in flowing water. They are sterile. Macroscopically, the straggling, complanate, and \pm homomallous habit of *O. selaginellifolium* is very reminiscent of a large *O. pringlei*. Under the microscope the similarity is less apparent, because the unusually strong costa found in *O. pringlei* is not present in *O. selaginellifolium*.

Specimens examined: HAWAII. *Baldwin s. n.*, “Vallies”, W Maui, Dec. 1875 (NY); *Baldwin s. n.*, in valleys, W Maui, 800’, 1875, det. Brotherus #521 (sub var. *recurvirameum* Müll. Hal., DUKE); *Flynn et al. 5359*, Hanalei Valley, Kauai (sub *P. muelleri*, NY); *Hoe 3385*, Waianae Mts., Oahu (sub *P. muelleri*, TENN); *Hoe 4292 & 4296* (*Bryophyta Hawaiica Exsic. 90 & 109* respectively), Iao Valley, Maui (#4296 sub *P. muelleri*, NY); *Newell s. n.*, 1913 (NY).

Illustrations: Bartram, *Manual of Hawaiian Mosses*, f. 160, p. 216; Wynns, this work, Figure 15.f.

Oxyrrhynchium austrinum. Fleischer (1923) included two rough-setaed species in his original diagnosis of *Platyhypnidium*: *Hypnum austrinum* Hook. f. & Wilson, and *H. moorei* Broth. & Geh. According to Hedenäs (1996), *P. moorei* is a synonym of *P. austrinum*. *Oxyrrhynchium austrinum* is evidently not related to *Platyhypnidium s. str.* It is similar to *O. selaginellifolium*, except the costa is weaker, like in *Brachythecium rivulare*. The plants are robust, somewhat complanate, and somewhat homomallous,

with ovate-acuminate, weakly denticulate leaves. The sporophytes are large and inclined, with sharply-rostrate opercula. They are more reminiscent of *O. hians* than are the gametophytes, which seem reasonably placed in *Platyhypnidium*.

In the ITS2 analysis a GenBank sequence of *O. austrinum* appeared in an isolated position, outside of one clade that included *O. hians*, *O. pringlei*, *Donrichardsia macroneuron*, and *O. selaginellifolium*, and another clade that included *Cirriphyllum*, *Okamuraea* Broth., *Rhynchostegiella*, *Aerolindigia* M. Menzel, *Clasmatodon* Hook. & Wilson, and *Homalotheciella* (Cardot) Broth. All these sequences formed a clade sister to *O. vagans*, a smooth-setaed dioicous species. The exclusion of *O. austrinum* from *Rhynchostegium* (including *Platyhypnidium*) has the desirable effect of making a smooth seta a strict synapomorphy for the latter genus.

Specimens examined: AUSTRALIA. *McCann 27*, Oven's River, Victoria (NY); *Weymouth s. n.*, Deep Creek, Mt. Wellington, Tasmania (sub *H. moorei*; NY). NEW ZEALAND. *Berggren s. n.*, Lyttleton, South Id. (DUKE); *Fife 6663*, Lower Basin of the Porarari River, South Id. (NY).

Illustrations: Hedenäs, J. Hatt. Bot. Lab. 92: 51-90 (2002); Wynns, this work, Figure 15.g.

Conclusions

In all analyses, *Platyhypnidium pringlei* appeared to be more closely related to *Oxyrrhynchium hians* than to terrestrial species of *Rhynchostegium*. In contrast, *P. riparioides*, *P. muelleri* and *P. aquaticum* ("*Platyhypnidium s. str.*") appeared to be much more closely related to *Rhynchostegium* than to *Eurhynchium*. Therefore *Platyhypnidium* as circumscribed by Brotherus (1925) is polyphyletic. Morphological similarity between species of the *Oxyrrhynchium* lineage and *Platyhypnidium s. str.* may be attributed to phenotypic convergence due to similar environmental pressures.

Based on herbarium studies, *P. aquaticum* and *P. muelleri* are not distinct. The geographic range of *P. aquaticum* is therefore very large, and a good deal of morphological variation may be expected among different populations of this species.

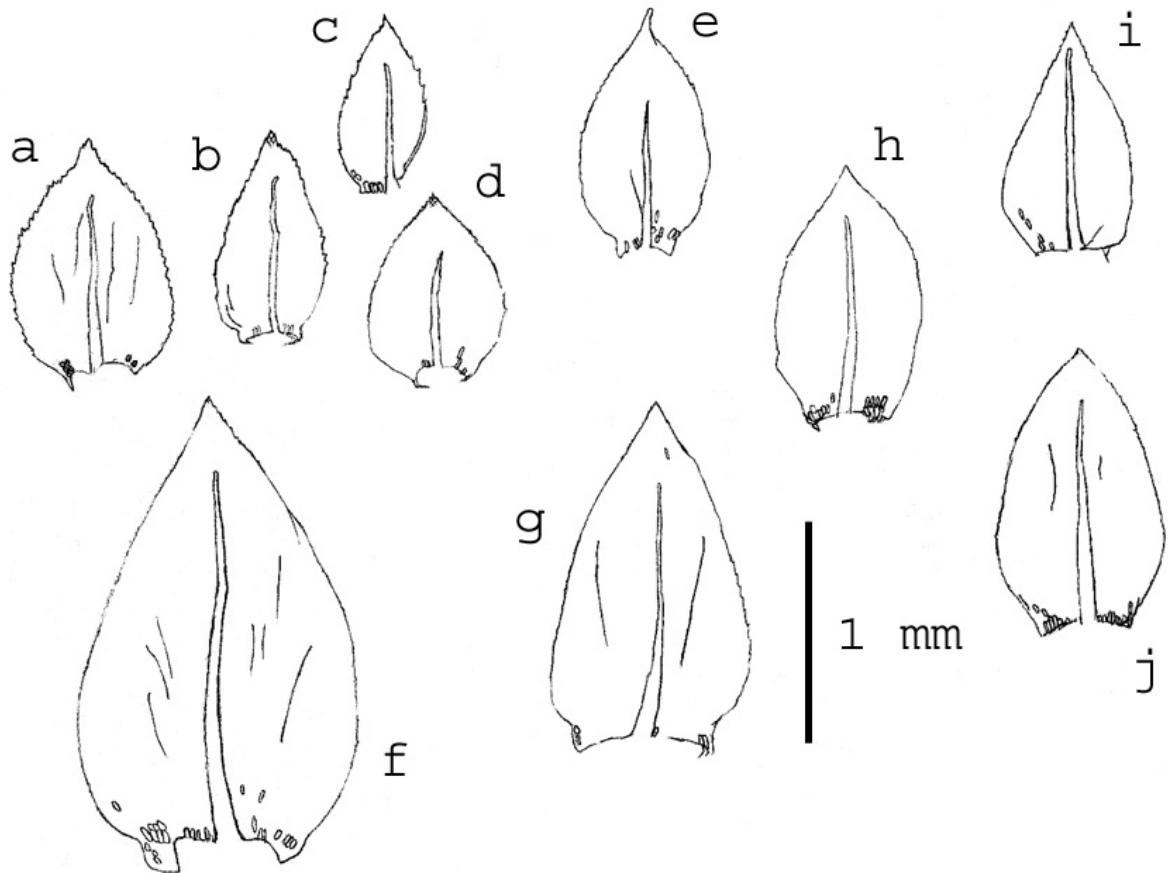


Figure 15. Leaves of several species of *Oxyrrhynchium*: a, b – Wynns 326, Pennsylvania (*O. hians*, BOON); c – Ignatov, *Mosses of USSR 70*, Moscow (*O. hians*, NY); d – Whitehouse 26870, Texas (*O. hians*, NY); e – Fleischer, *Musci Frondosi Archipelagi Indici 338* (*O. vagans*, NY); f – Hoe 4296 [*Bryophyta Hawaiiica Exsic. 109*], Hawaii (*O. selaginellifolium*, NY); g – Fife 6663, New Zealand (*O. austrinum*, NY); h – Buck 23824, China (“*Oxyrrhynchium* sp. 2”, NY); i – Wynns 546, South Carolina (*O. pringlei*, BOON); j – Pringle 10525, Mexico (*O. pringlei*, NY).

A large amount of infraspecific molecular variation was found among geographically-separated populations of both *P. muelleri* and *P. riparioides*. More studies of *Platyhypnidium s. str.*, including *P. subruscifforme* (Müll. Hal.) M. Fleisch., are needed to support the monophyly of the lineage and its evolutionary position relative to terrestrial species of *Rhynchostegium*. In these studies a generic split between *Platyhypnidium* and *Rhynchostegium* was not clearly identified. Costa length-to-leaf length ratio did provide one consistent differentia between the taxa (significantly higher in *Platyhypnidium*), but since increased costal development is adaptive in rheophilous aquatic pleurocarps (Vitt & Glime 1984), this distinction seems less significant in a phylogenetic sense. Therefore *P. aquaticum*, *P. riparioides*, *P. subruscifforme*, and *P. lusitanicum* are here treated as species of *Rhynchostegium*.

The proper generic placement of *P. fuegianum* was not resolved. Based on the cladistic analysis of morphometric data, Vanderpoorten et al. (2005) were correct in transferring this species to *Platyhypnidium*. Although the distinction between *Rhynchostegium* and *Platyhypnidium* was vague in the molecular analyses, the placement of *P. fuegianum* in the lineage was well supported. However, the type species of *Eurhynchium* (*E. striatum*) appeared to be more closely related to *Rhynchostegium* and *Platyhypnidium* than to other species of *Eurhynchium*. Since *P. fuegianum* could represent an evolutionary intermediate between *E. striatum* and *Platyhypnidium/Rhynchostegium*, it is here returned to *Eurhynchium*. *Rhynchostegium* (including *Platyhypnidium s. str.*), *E. fuegianum* and *E. striatum* are all smooth-setaed; and all except the last species are autoicous.

Eurhynchium in its traditional sense is polyphyletic. Based on several morphological and molecular synapomorphies, the genus *Oxyrrhynchium* is well founded and should be recognized. Several species clearly belong to the genus, including *O. hians*, *O. pringlei* and *O. selaginellifolium*. Based on ITS2 data, *O. vagans*, *O. austrinum*, *Platyhypnidium patulifolium*, and *Donrichardsia macroneuron* are also probable congeners (see Appendix 3). More studies are needed to elucidate the evolutionary relationships of *E. pulchellum* and *E. praelongum*; but since molecular data indicate that they are not closely related to *E. striatum*, the transfers made by Ignatov & Huttunen (2002) of *E. pulchellum* to *Eurhynchiastrum* and *E. praelongum* to *Kindbergia* seem to be justified. Based on this study, *Eurhynchium s. str.* only contains *E. striatum*, *E. angustirete*, and perhaps *E. fuegianum*.

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APPENDIX 1.
Specimens Included in the Morphometric Study.

List of specimens included in the morphometric study. See plant descriptions for herbaria where specimens are deposited. Specimens marked with an asterisk were excluded from the phenetic analyses. Specimens marked with ** were excluded from the phylogenetic analysis. Fertile collections are in boldface.

<i>Eurhynchium angustirete</i>	Klaus s. n.	St. Pölten, Austria
<i>Eurhynchium fuegianum</i>	Buck 41017	Isla Navarino, Chile
	Buck 41055	Isla Navarino, Chile
	Buck 41073	Isla Navarino, Chile
	Buck 41081	Isla Navarino, Chile
	Buck 41162	Isla Navarino, Chile
	Matteri 4202	Prov. Tierra del Fuego, Argentina
	Schäfer-Verwimp 8004	Prov. Rio Negro, Argentina
<i>Eurhynchium hians</i>	Standley 5848	Haywood Co., NC
	Wynns 622	Watauga Co., NC
	*Zander 470	Watauga Co., NC
	Wynns 326	Monroe Co., PA
	Amtoft 2005b	Carter Co., TN
	Whitehouse 26870	Johnson Co., TX
	Gay s. n.	near Lausanne, Switzerland
	Stebel 576/97	Lower Silesia, Poland
	Ignatov, Mosses of USSR 70	Moscow
<i>Eurhynchium praelongum</i>	Jenkins s. n.	Monterey Co., CA
	Wynns 646	Marin Co., CA
<i>Eurhynchium pulchellum</i>	Shevock 17526	Tulare Co., CA
	*Pittillo 9804	Buncombe Co., NC
	Buck 15378	Graham Co., NC
	Anderson 27753	Jackson Co., NC
	*Zartman 1282	Jackson Co., NC
	*Anderson 20865	Macon Co., NC
	Wynns 615	Watauga Co., NC
	*Zander 470	Watauga Co., NC
	Hakelner s. n.	E Gotland, Sweden
<i>Eurhynchium selaginellifolium</i>	Hoe 3385	Oahu, HI
	Hoe 4296	Maui, HI
<i>Eurhynchium striatum</i>	Schofield 104756	N Cornwall, England
	Buck 10578	Prov. Asturias, Spain
	Eggers et al. 21	Dep. Haute Saone, France
	Schleicher s. n.	Savoie, France
	Holmen 045	Bömlo Id., Norway
	Seth s. n.	Huskvarna, Sweden
<i>Platyhypnidium aquaticum</i>	Buck 7296	Prov. La Vega, Dominican Rep.
	Buck 39450	Zamora-Chinchiipe, Ecuador
	Ramírez 2670	Dpto. de Nariño, Colombia
	Price et al. 1673	Tucuman, Argentina
	Spruce, Musci Amaz. And. 1422	South America
<i>Platyhypnidium muelleri</i>	Fleischer, Musci Frond. Ind. 95	Tjibirrum, Java
	Yates 2992	Tjibirrum, Java
	Motley 311	Mt. Panerango, Java
	Noguchi, Musci Jap. 771	Kumamoto Pref., Japan
	Noguchi, Musc. Jap. Ex. 1316	Kagoshima Pref., Japan
	G. L. Smith J-951	Kagoshima Pref., Japan
	Wu 21163	Sichuan Prov., China

<i>Platyhypnidium pringlei</i>	Pringle 10454 Delgadillo 6044 Delgadillo 6045 Hill 23469 Wynns 568 Wynns 488 Zartman & Pittillo 240 Zartman & Pittillo 454 Wynns 546	Morelos, Mexico Michoacan, Mexico Michoacan, Mexico Greenville Co., SC Greenville Co., SC Oconee Co., SC Oconee Co., SC Oconee Co., SC Pickens Co., SC
<i>Platyhypnidium riparioides</i>	Keith 4 Wynns 274 Wynns 240 Wynns 241 Buck 35187 Wynns 574 Anderson 24061 Small 74 Matuda s. n. Allen 10659 *Schleicher s. n.	Caldwell Co., NC Caldwell Co., NC Watauga Co., NC Watauga Co., NC Putnam Co., NY Greenville Co., SC Pickens Co., SC Lee Co., VA Chiapas, Mexico Alma Ata Oblast, Kazakhstan near Saillon, Switzerland, 1912
<i>R. rusciforme</i> var. <i>lutescens</i>		
<i>Rhynchostegium confertum</i>	Gradstein 853 Long 7448	Middachten, Netherlands La Palma, Canary Is.
<i>Rhynchostegium murale</i>	Aptroot 2849 Aptroot 9745 Ochyra 713/82 Ochyra, Musc. Polon. Ex. 1091 Ochyra, Musc. Polon. Ex. 1137	Prov. Liège, Belgium Prov. Liège, Belgium W Carpathians, Poland Kraków-Czask. Upland, Poland Kraków-Czask. Upland, Poland
<i>Rhynchostegium serrulatum</i>	Buck 45007 Wynns 175 Wynns 428 Wynns 296 D. K. Smith & Davison 194	Litchfield Co., CT Avery Co., NC Durham Co., NC Monroe Co., PA Coffee Co., TN
COLLECTIONS OF DOUBTFUL IDENTITY		
<i>Platyhypnidium pringlei</i>	Bryant 1682 Sharp 5250	Grand Canyon, AZ Huehuetenango, Guatemala
<i>Rhynchostegium murale</i>	Buck 23824	Zhejiang Prov., China
OUTGROUP TAXA - Brachytheciaceae		
<i>Brachythecium rivulare</i>	**Buck 14068	Prov. La Vega, Dominican Rep.
<i>Bryhnia hultenii</i>	**Schofield 108026	Pribilof Is., AK
<i>Scleropodium obtusifolium</i>	Buck 30299	Grays Harbor Co., WA
OUTGROUP TAXON - Amblystegiaceae		
<i>Hygrohypnum eugyrium</i>	**Wynns 392	Watauga Co., NC

APPENDIX 2.
Specimens Included in the Molecular Study and
Subsequent History of Extracted DNAs.

Taxon	Coll. No.	year	locality	dry wt. used	BMBC-R/LS4-R product?	ITS1/ITS4 product?	# of replicate sequences
<i>Brachythecium rivulare</i>	Buck 14068	1987	DR	39.8 mg	30 & 60 cycles		4
<i>Bryhnia hultenii</i>	Schofield et al. 108026	1997	Alaska	40.1 mg	30 cycles		4
<i>Eurhynchium angustirete</i>	Mosses of USSR 138	1991	Altai	39.5 mg	30 & 60 cycles		4
<i>E. fuegianum</i>	Buck 41017	2001	Chile	20+ mg	30 cycles		4
<i>E. fuegianum</i>	Buck 41055	2001	Chile	40.3 mg	30 cycles		4
<i>E. fuegianum</i>	Buck 41081	2001	Chile	40.9 mg	30 cycles		4
<i>E. fuegianum</i>	Buck 45851	2004	Chile	39.8 mg	30 cycles		4
<i>E. fuegianum</i>	Buck 46115	2004	Chile	40.8 mg	30 cycles		4
<i>E. hians</i>	Amtoft 2005b	2004	Tenn.	41.1 mg	30 cycles		4
<i>E. hians</i>	Frahm et al. s.n.	1995	Germany	40.1 mg	30 & 60 cycles		4
<i>E. hians</i>	Mosses of USSR 70	1990	Moscow	39.6 mg	30 & 60 cycles		4
<i>E. hians</i>	Stebel 576/97	1997	Poland	40.1 mg	30 cycles		4
<i>E. hians</i>	Wynns 326	2004	Pa.	40.3 mg	30 cycles		4
<i>E. hians</i>	Wynns 622	2004	NC	39.5 mg	30 cycles		4
<i>E. praelongum</i>	Jenkins s.n.	2003	Calif.	39.9 mg	30 cycles		4
<i>E. praelongum</i>	Wynns 646	2005	Calif.	32.2 mg	30 cycles		4
<i>E. pulchellum</i>	Allen 21390	1999	Maine	40.3 mg	30 cycles		4
<i>E. pulchellum</i>	Anderson 27753	1999	NC	40.5 mg	30 cycles		4
<i>E. pulchellum</i>	Buck 15378	1987	NC	40.4 mg	30 cycles		3
<i>E. pulchellum</i>	Shevock 17526	1998	Calif.	40.8 mg	30 cycles		4
<i>E. pulchellum</i>	Wynns 615	2004	NC	39.9 mg	30 cycles		3
<i>E. selaginellifolium</i>	Hoe 4296	1976	Hi.	39.1 mg	30 & 60 cycles		4
<i>E. striatum</i>	Buck 15078	1987	Spain	40.4 mg	30, 60 & 90 cycles	30 cycles from PCR product	9
<i>E. striatum</i>	Eggers et al. 21	1981	Germany	39.8 mg	30 cycles		6
<i>E. striatum</i>	Schofield 104756	1995	England	39.6 mg	30 & 60 cycles		4
<i>E. striatum</i>	Vasak s.n.	1986	Rep. of Georgia	40.8 mg	30 & 60 cycles		4
<i>Oxyrrhynchium</i> sp. 2	Buck 23824	1993	China	40.5 mg	30 cycles		4
<i>Platyhypnidium aquaticum</i>	Buck 7962	1982	DR	40.6 mg		30 cycles	4
<i>P. aquaticum</i>	Buck 39450	2001	Ecuador	39.4 mg	30 cycles		4
<i>P. aquaticum</i>	Churchill et al. 19069	1995	Colombia	39.2 mg	30 cycles		4
<i>P. aquaticum</i>	Churchill et al. 19974	1999	Bolivia	41.0 mg	30 cycles		2
<i>P. aquaticum</i>	Churchill et al. 22535	2003	Bolivia	39.6 mg	30 cycles		4
<i>P. aquaticum</i>	Price et al. 1673	1999	Argentina	40.4 mg	30 cycles		4
<i>P. aquaticum</i>	Vital & Buck 12603	1984	Brazil	40.9 mg	30 & 60 cycles		4
<i>P. muelleri</i>	Koponen 30269	1981	Papua NG	40.6 mg	30 & 60 cycles		4
<i>P. muelleri</i>	Musci Japonici Ex. 1316	1975	Japan	33.0 mg		30 cycles	4
<i>P. muelleri</i>	Reese 17710	1990	China	40.1 mg	30 cycles		4
<i>P. pringlei</i>	Hill & Heaton 23469	1992	SC	40.5 mg	30 cycles		2
<i>P. pringlei</i>	Keith 42	2005	NC	32.0 mg	30 cycles		4
<i>P. pringlei</i>	Wynns 488	2004	SC	39.5 mg	30 cycles		4

Taxon	Coll. No.	year	locality	dry wt. used	BMBC-R/LS4-R product?	ITS1/ITS4 product?	# of replicate sequences
<i>P. pringlei</i>	Wynns 540	2004	SC	40.0 mg	30 cycles		4
<i>P. pringlei</i>	Wynns 546	2004	SC	40.2 mg	30 cycles		4
<i>P. pringlei</i>	Wynns 568	2004	SC	28.3 mg	30 cycles		2
<i>P. pringlei</i>	Zartman & Pittillo 240	1995	SC	41.0 mg	30 cycles		5
<i>P. riparioides</i>	Allen 10659	1991	Kazakhstan	40.4 mg	30 & 60 cycles		4
<i>P. riparioides</i>	Buck 35187	1998	NY	40.3 mg	30 cycles		3
<i>P. riparioides</i>	Keith 4	2004	NC	40.4 mg	30 cycles		4
<i>P. riparioides</i>	Wynns 240	2004	NC	20+ mg.	30 cycles		3
<i>P. riparioides</i>	Wynns 241	2004	NC	20+ mg.	30 cycles		3
<i>P. riparioides</i>	Wynns 574	2004	SC	39.8 mg	30 cycles		3
<i>Rhynchosstegium confertum</i>	Long 7448	1978	Canary Is.	40.2 mg		30 cycles	4
<i>R. murale</i>	Aptroot 2849	1977	Belgium	40.3 mg		30 cycles	4
<i>R. murale</i>	Musc. Macr. Pol. Ex. 1091	1997	Poland	39.6 mg	30 cycles		4
<i>R. murale</i>	Musc. Macr. Pol. Ex. 1137	1997	Poland	41.1 mg	30 & 60 cycles		4
<i>R. murale</i>	Ochrya 713/82	1982	Poland	40.7 mg	30 cycles		2
<i>R. serrulatum</i>	Buck 40412	2001	Ark.	40.2 mg	30 cycles		2
<i>R. serrulatum</i>	Smith & Davison 194	1998	Tenn.	40.6 mg	30 cycles		4
<i>R. serrulatum</i>	Wynns 175	2003	NC	40.0 mg	30 cycles		3
<i>R. serrulatum</i>	Wynns 296	2004	Pa.	40.9 mg	30 cycles		3
<i>R. subruscifforme</i>	Delgadillo 285	1966	Mexico	37.3 mg		30 cycles	4

DNA was extracted from the following specimens which did not contribute to the molecular analysis

<i>E. selaginellifolium</i>	Hoe 3385	1975	Hi.	39.8 mg	PCR reactions unsuccessful		
<i>E. selaginellifolium</i>	Flynn et al. 5204	1993	Hi.	41.1 mg	60 cycles	30 cycles	
<i>E. striatum</i>	Holmen 045	1967	Norway	39.7 mg		60 cycles	
<i>P. muelleri</i>	Koponen 33269	1981	Papua NG	22.3 mg	60 cycles	30 cycles	2
<i>P. muelleri</i>	Musci Japonici 771	1959	Japan	40.9 mg	60 cycles	30 cycles	
<i>P. muelleri</i>	Wu 21163	1986	China	42.0 mg	60 cycles		2
<i>P. pringlei</i>	Delgadillo 6044	1996	Mexico	7.0 mg	60 cycles		
<i>P. pringlei</i>	Delgadillo 6045	1996	Mexico	7.7 mg	60 cycles		
<i>P. pringlei</i>	Keith 38	2005	NC	31.1 mg	30 cycles		
<i>R. serrulatum</i>	Buck 45007	2003	Conn.	40.5 mg	30 cycles		
<i>R. serrulatum</i>	Wynns 428	2004	NC	40.6 mg	30 cycles		
<i>R. subruscifforme</i>	Magill 2335	1974	Mexico	40.2 mg	PCR reactions unsuccessful		
<i>Scleropodium obtusifolium</i>	Buck 30299	1996	Wash. St.	40.8 mg	30 cycles		
<i>S. obtusifolium</i>	Wynns 647	2005	Calif.	32.7 mg	30 cycles		

APPENDIX 3.
Notes on Other Taxa

Donrichardsia

Donrichardsia macroneuron is an unusual aquatic moss known from a single calcareous spring in Texas (Wyatt & Stoneburner 1980). The weird morphology of *D. macroneuron*, which has multistratose laminae and unusually broad percurrent costae, has made its systematic placement difficult. But since segregation of *D. macroneuron* into its own monotypic family does not seem to be justified (Stech & Frahm 1999b, 2000; Vanderpoorten et al. 2003), the placement of this species in the Brachytheciaceae by Ignatov & Huttunen (2002) is reasonable. In this study *D. macroneuron* was resolved as a close relative of *Oxyrrhynchium pringlei* and *O. selaginellifolium*. Huttunen & Ignatov (2004) also resolved *D. macroneuron* in the *Oxyrrhynchium* lineage, sister to *Platyhypnidium patulifolium*. Their ITS data indicate that a transfer of *D. macroneuron* to *Oxyrrhynchium* may be warranted.

Platyhypnidium patulifolium (Cardot & Thér.) Broth.

Based on the molecular data of Huttunen & Ignatov (2004), *P. patulifolium* belongs to the *Oxyrrhynchium* lineage. Thériot (1911) compared this species with *R. rusciforme* [= *R. riparioides*], but the differences he gave are more suggestive of *O. hians*. The representative collection of *P. patulifolium* from Hunan Province, China (Koponen et al. 53920; H) that is included Huttunen & Ignatov's (2004) phylogeny apparently disagrees with the isotype and protologue of *R. patulifolium* Cardot & Thér. in a few particulars. But, based on the descriptions and illustrations in Ignatov et al. (2005), Koponen et al. 53920 seems to be comfortably placed in the *Oxyrrhynchium* lineage. I have seen no material of *P. patulifolium*.

Platyhypnidium intermedium Herzog

According to the original description (Herzog 1927), *P. intermedium* has some of the features that characterize *Oxyrrhynchium*: plants complanate; leaves ovate, acute; leaf margins spinose-serrulate all round; costa projecting as a spine. However, the seta was described as smooth, whereas *O. hians* and its allies have roughened setae. Herzog compared *P. intermedium* with both *P. aquaticum* and *P. regnellii* (nom. hb.). According to Index Muscorum (Wijk et al. 1962), *Hypnum regnellii* Hampe is a synonym of *Eurhynchium clinocarpum* (Taylor) Paris [= *O. clinocarpum* (Taylor) Broth.], a relative of *O. hians* from Central and South America that has ovate leaves with long, broad apiculae (see Buck 1998). I have seen no material of *P. intermedium*.

Platyhypnidium longirameum (Müll. Hal.) M. Fleisch.

This species was recognized in Wang et. al (2003) as *Eurhynchium longirameum* (Müll. Hal.) Y. F. Wang & R. L. Hu. Their illustrations suggest a relationship with *Oxyrrhynchium*. I have seen no material.

Platyhypnidium patentifolium (Müll. Hal.) M. Fleisch.

According to Ignatov et al. (2005), *R. patentifolium* Müll. Hal. is a synonym of *Oxyrrhynchium vagans*. I have seen no material.

Platyhypnidium wildei Zanten

Ignatov et al. (1999) synonymized this taxon with *O. vagans* var. *bergmaniae* (E. B. Bartram) Ignatov. From my study of the type of *P. wildei* (*de Wilde* 854, Sangjar, West Papua; NY), this plant does appear to be a broad-leaved version of the plants

distributed by Fleischer as *Rhynchostegium vagans* A. Jaeger (*Musci Frondosi Archipelagi Indici* 338; NY). The constricted, elongate leaf apex and sharply serrate leaf margins of *P. wildei* are incongruous in *Platyhypnidium*. The squarrose-recurved leaf tips are striking.

Okamuraea

Okamuraea is a mainly corticolous genus endemic to Japan and China (Noguchi 1953; Cao et al. 2002). Species of this genus have erect capsules with reduced peristomes and hairy calyptrae, syndromes consistent with epiphytism. They also have short, thick-walled, fusiform leaf cells, which makes the plants seem awkwardly placed in the Brachytheciaceae. Brotherus compared the plants with *Forsstroemia* Lindb., in the Leucodontaceae, a family with many corticolous members (*vide* Cao et al. 2002).

Okamuraea was placed in the Rhytidiaceae by Fleischer in 1923, whereas Andrews (1954) thought it was allied with the Meteoriaceae, Wu (1992) placed it in the Hypnaceae, and Noguchi (1991) and Cao et al. (2002) placed it in the Leskeaceae. Tsubota et al. (2002) transferred the genus to the Brachytheciaceae based on nucleotide data. The phylogeny of Huttunen & Ignatov (2004) also supported the inclusion of *Okamuraea* in the Brachytheciaceae; they resolved the genus in their subfamily Rhynchostegielloideae (which includes the *Oxyrrhynchium* lineage), sister to a *Cirriphyllum* clade [interestingly, most of the species originally placed in *Eurhynchium* subgenus *Oxyrrhynchium* in the “*Bryologia europaea*” are now placed in *Cirriphyllum* (*vide* Buck 1988)]. Illustrations of both *Okamuraea hakoniensis* and *O. brachydictyon* (Cardot) Noguchi may be found in Noguchi (1953; 1991), Cao et al. (2002) and Ignatov et al. (2005).

Clasmatodon parvulus (Hampe) Sull., included in the Brachytheciaceae by Ignatov & Huttunen (2002), is another mainly corticolous species with short rhombic cells, erect capsules, and a reduced peristome. *Homalotheciella subcapillata* (Hedw.) Broth. also reflects some of these characteristics; and like in *Okamuraea*, the calyptra is sparsely hairy. Both *H. subcapillata* and *C. parvulus* were resolved close to *O. hakoniensis* in the ITS2 analysis.

Brachythecium

In the ITS analysis, *Brachythecium rivulare*, *B. salebrosum* (F. Weber & D. Mohr) Schimp., and *Bryhnia hultenii* formed a clade with low bootstrap support (67). In the ITS2 analysis, the clade was expanded to include *Brachythecium geheebii* Milde, *B. laetum* [syn. *B. oxycladon* (Brid.) Jaeg.], *B. acuminatum* (Hedw.) Aust., *Bryhnia novae-angliae*, *Eurhynchiadelphus eustegia*, and *Palamocladium leskeoides*. The close relationship of *Brachythecium* to *Bryhnia* was confirmed by these results.

Brachythecium appleyardiae McAdam & A. J. E. Smith, an endemic of England and western Europe, was until recently considered a rather rare species with conservation status. However, it has just been synonymized with *Scleropodium cespitans* (Müll. Hal.) L. F. Koch based on molecular data (Blockeel et al. 2005). The close relationship of *B. appleyardiae* to *S. cespitans* was confirmed in this study; and in general *Scleropodium* appeared to be a very homogenous genus in terms of ITS.

Brachythecium velutinum was resolved in the ITS2 analysis sister to a clade composed of *Scleropodium* and *E. praelongum*. Ignatov & Huttunen transferred *B. velutinum* to the segregate genus *Brachytheciastrum* Ignatov & Huttunen in 2002.

Platyhypnidium microrusciforme (Müll. Hal.) M. Fleisch

According to Redfearn et al. (1996), this is a synonym of the common Chinese species *Brachythecium buchananii* (Hook.) A. Jaeger. I have seen no material.

Platyhypnidium validum (Herzog) Ochyra

I have seen only one specimen named *P. validum* (*Frahm et al. 2310*, Prov. Chachapoyas, Dep. Amazonas, Peru; det. Ochyra; NY); it apparently belongs to *Brachythecium rivulare*. Many of the leaves are decidedly *Platyhypnidium*-like under the microscope; but the basal decurrencies, mostly subentire margins, regular plicae, and elongate acumina unite them with *B. rivulare* and separate them from *P. aquaticum*. Also, the ultimate branches are plump, homomallous, and secund, in too regular a fashion for *Platyhypnidium*. The sometimes forked costa of varying strength also agrees better with *B. rivulare*.

The disjunctive occurrence of north-temperate species at the higher elevations of Hispaniola and in the northern Andes was noted by Buck (1998). The leaves of *Frahm et al. 2310* have a sizeable area of squarish alar cells and a basal band of large, thick-walled, porose cells; whereas North American collections of *B. rivulare* have a large area of inflated thin-walled basal cells. Apparently this is a population-level difference. Two Dominican specimens of *B. rivulare* that I have seen (*Buck 14068* and *Jones & Norris 1325E*, Prov. La Vega; NY) agree more closely with the Peruvian material than North American collections do. Hedenäs confirmed the generic identity of *P. validum* in 2003; but further studies may be warranted.

Platyhypnidium peruvienne (R. S. Williams) Ochyra

Based on the original description and illustrations (Williams 1916), this species may have been correctly placed in *Hygrohypnum*. It shares several features with the specimen named *P. validum* discussed above: ultimate branches much stouter than the stems, leaves subentire and broadly apiculate, basal cells dilated, costa thick and frequently divided. I have seen no material named *P. peruvienne*.

Platyhypnidium obscurum (Besch.) M. Fleisch.

From the illustrations and description in Whittier (1976), it appears that this endemic of Tahiti belongs to *Hygrohypnum*. Based on the short leaf cells, forking costa and broadly apiculate leaf tip, it can probably be excluded from *Platyhypnidium*. However, I have seen no material.

Platyhypnidium hedbergii (P. de la Varde) Ochyra & Sharp

This is another plant with forked costae that was described (sterile) as a *Hygrohypnum* (Potier de la Varde 1954). From both the description and the original illustration it seems to belong to *Platyhypnidium s. str.*; it is very close to *P. riparioides* according to Ochyra & Sharp (1988). Again, I have seen no material.

Platyhypnidium esquirolii (Cardot & Thér.) Broth.

According to Ignatov et al. (2005), *P. esquirolii* is a synonym of *R. inclinatum* (Mitt.) A. Jaeger. *Rhynchostegium inclinatum* is not obligately aquatic. Its acuminate

leaf shape, long cells, weak costa, smooth seta and autoicous sexuality indicate that it is well placed in its genus. The isotype of *R. esquirolii* Cardot & Thér. is figured in Ignatov et al. (2005). I have seen no material.

Platyhypnidium fontinaliopsis M. Fleisch

Fleischer (1923) attributed the species to Mongolia and the name to Brothaus; according to Index Muscorm (Wijk et al. 1964), *P. fontinaliopsis* is a *nomen nudum*.

Platyhypnidium brotheri (Paris) Wijk & Margad. [syn. *P. julaceum* (Broth.) M. Fleisch., *nom. illeg.*]

This species is reported from Brazil (Yano 1981), but is otherwise unknown to me.

APPENDIX 4.
Data Matrix of 107 Partial and Complete ITS Sequences.

Key to Data Matrix

seq1	<i>Platyhypnidium muelleri</i> . Koponen 30269, Papua New Guinea
seq2	<i>P. muelleri</i> . Reese 17710, China
seq3	<i>P. aquaticum</i> . Churchill 19774, Bolivia
seq4	<i>P. aquaticum</i> . Churchill 19069, Colombia
seq5	<i>P. aquaticum</i> . Buck 39450, Ecuador
seq6	<i>P. aquaticum</i> . Buck 7962, Dominican Republic
seq7	<i>P. aquaticum</i> . Churchill 12535, Argentina
seq8	<i>P. aquaticum</i> . Vital & Buck 12603, Brazil
seq9	<i>P. muelleri</i> . Musci Japonici Exsic. 1316
seq10	<i>P. aquaticum</i> . Price et al. 1673, Argentina
seq11	<i>Rhynchostegium subrusciforme</i> . Delgadillo 285, Mexico
seq12	<i>P. riparioides</i> . Wynns 240, NC
seq13	<i>P. riparioides</i> . Buck 35187, NY
seq14	<i>P. riparioides</i> . Wynns 241, NC
seq15	<i>P. riparioides</i> . Wynns 574, SC
seq16	<i>P. riparioides</i> . Keith 4, NC
seq17	<i>R. serrulatum</i> . D. K. Smith & Davison 194, Tenn.
seq18	<i>R. serrulatum</i> . Buck 40412, Ark.
seq19	<i>R. serrulatum</i> . Wynns 296, Pa.
seq20	<i>R. serrulatum</i> . Wynns 175, NC
seq21	<i>P. fuegianum</i> . Buck 46115, Chile
seq22	<i>P. fuegianum</i> . Buck 41017, Chile
seq23	<i>P. fuegianum</i> . Buck 41055, Chile
seq24	<i>P. fuegianum</i> . Buck 41081, Chile
seq25	<i>P. fuegianum</i> . Buck 45851, Chile
seq26	<i>P. riparioides</i> . Allen 10659, Kazakhstan
seq27	<i>P. riparioides</i> var. <i>atlanticum</i> . Frahm s. n., Germany
seq28	<i>R. confertum</i> . Long 7448, Canary Is.
seq29	<i>R. murale</i> . Ochyra 713/82, Poland
seq30	<i>R. murale</i> . Musci Poloniae Exsic. 1091
seq31	<i>R. murale</i> . Musci Poloniae Exsic. 1137
seq32	<i>R. murale</i> . Aptroot 2849, Belgium
seq33	<i>R. rotundifolium</i> . AF230984/AF230999
seq34	<i>Eurhynchium angustirete</i> . Mosses of USSR 138, Altai
seq35	<i>E. striatum</i> . AF230985/AF231000
seq36	<i>E. striatum</i> . Eggers et al. 21, Germany
seq37	<i>E. striatum</i> . Buck 15078, Spain
seq38	<i>E. striatum</i> . Schofield 104756, England
seq39	<i>E. striatum</i> . Vasak s. n., Russia
seq40	<i>E. striatum</i> . AY166450
seq41	<i>Palamocladium euchloron</i> . AF403623
seq42	<i>Myuroclada maximowiczii</i> . AF403625
seq43	<i>Bryoandersonia illecebra</i> . AF403626
seq44	<i>Platyhypnidium austrinum</i> . AY166449
seq45	<i>Aerobryum speciosum</i> . AF403619
seq46	<i>Hygrohypnum luridum</i> . AF168137
seq47	<i>Pseudoscleropodium purum</i> . AF403663
seq48	<i>E. angustirete</i> . AF403621
seq49	<i>Scorpiurium deflexifolium</i> . AF403599
seq50	<i>Eurhynchiopsis eustegium</i> . AF403602
seq51	<i>Bryhnia novae-angliae</i> . AF403665
seq52	<i>Platyhypnidium riparioides</i> . AF403594
seq53	<i>Eurhynchium praelongum</i> . Wynns 646, Calif.

seq54 *E. praelongum*. Jenkins s. n., Calif.
 seq55 *Kindbergia praelonga*. AY654610
 seq56 *Brachythecium appleyardiae*. AY654619
 seq57 *Scleropodium obtusifolium*. AY173520
 seq58 *S. touretii*. AY173519
 seq59 *S. touretii*. AY654611
 seq60 *S. cespitans*. AY654614
 seq61 *Brachytheciastrum olympicum*. AY952446
 seq62 *Homalothecium sericeum*. AF403587
 seq63 *H. lutescens*. AF403642
 seq64 *H. aureum*. AF403650
 seq65 *Brachythecium velutinum*. AF403667
 seq66 *Eurhynchium pulchellum*. AF395635
 seq67 *E. pulchellum*. Anderson 27753, NC
 seq68 *E. pulchellum*. Buck 15378, NC
 seq69 *E. pulchellum*. Wynns 615, NC
 seq70 *E. pulchellum*. Allen 21390, Maine
 seq71 *E. pulchellum*. Shevock 17526, Calif.
 seq72 *Bryhnia hultenii*. Schofield 108026, Alaska
 seq73 *Brachythecium rivulare*. Buck 14068, Dominican Republic
 seq74 *B. salebrosum*. AY654609
 seq75 *B. acuminatum*. AF403654
 seq76 *B. geheebii*. AF403660
 seq77 *B. laetum*. AY166445
 seq78 *Bryhnia novae-angliae*. AF403588
 seq79 *Palamocladium leskeoides*. AF403596
 seq80 *Cirriphyllum cirrosum*. AF403641
 seq81 *Rhynchostegiella jacquinii*. AF230987/AF231002
 seq82 *E. pumilum*. AF230986/AF231001
 seq83 *R. jacquinii*. AF403569
 seq84 *Aerolindigia capillacea*. AF395634
 seq85 *Okamuraea hakoniensis*. AY568552
 seq86 *Clasmatodon parvulus*. AF403614
 seq87 *Cirriphyllum piliferum*. AF403608
 seq88 *E. crassinervium*. AF403668
 seq89 *Homalotheciella subcapillata*. AF403658
 seq90 *Rhynchostegium psilopodium*. AF403643
 seq91 *Oxyrrhynchium vagans*. AF403652
 seq92 *Platyhypnidium pringlei*. Keith 42, NC
 seq93 *P. pringlei*. Wynns 488, SC
 seq94 *P. pringlei*. Wynns 540, SC
 seq95 *P. pringlei*. Wynns 546, SC
 seq96 *P. pringlei*. Zartman & Pittillo 240, SC
 seq97 *P. pringlei*. Hill & Heaton 23469, SC
 seq98 *P. pringlei*. Wynns 568, SC
 seq99 *Donrichardsia macroneuron*. AF167350
 seq100 *E. selaginellifolium*. Hoe 4296, Hawaii
 seq101 *Oxyrrhynchium* sp. 2. Buck 23824, China
 seq102 *E. hians*. Frahm et al. s. n., Germany
 seq103 *E. hians*. Wynns 326, Pa.
 seq104 *E. hians*. Wynns 622, NC
 seq105 *E. hians*. Amtoft 2005b, Tenn.
 seq106 *E. hians*. Mosses of USSR 70, Moscow
 seq107 *E. hians*. Stebel 576/97, Poland

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seq18   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq19   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
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seq23   -----TGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq24   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCA-C
seq25   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq26   -----TGCACACACGAGTTGCAGCCAAC
seq27   -----AGTTGCAGCCAAC
seq28   -----TCCTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq29   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq30   -----GTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq31   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq32   -----AGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC
seq33   -----AGTTGCAGCCAAC
seq34   -----TGCACACACAAGTTGCAGCCAAC
seq35   -----AGTTGCAGCCAAC
seq36   GTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC

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	100	110	120	130	140	150	160	170	180	190
seq37
seq38	-----CACACACAAGTTGCAGCCAAC									
seq39	-----TGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq40	-----CGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq41	-----									
seq42	-----									
seq43	-----									
seq44	-----									
seq45	-----									
seq46	-----CCTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC									
seq47	-----									
seq48	-----									
seq49	-----									
seq50	-----									
seq51	-----									
seq52	-----									
seq53	GTTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq54	GTTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq55	-----C									
seq56	-----									
seq57	-----CCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq58	-----CCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq59	-----									
seq60	-----									
seq61	-----									
seq62	-----									
seq63	-----									
seq64	-----									
seq65	-----									
seq66	-----									
seq67	-----AAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq68	-----AACAAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq69	-----CCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq70	-----CACAAGTTGCAGCCAAC									
seq71	-----TTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									
seq72	GTTTCATTAACCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC									

	100	110	120	130	140	150	160	170	180	190							
seq73	-----	TTATC	ATTTAG	AGGAAG	GAGAAC	TCGTA	ACAAGG	TTTCCG	TAGGTG	AACCTG	CGGAAG	GATCATT	GCACAC	ACGAG	TTGCAG	CCAAC	
seq74	-----																
seq75	-----																
seq76	-----																
seq77	-----																
seq78	-----																
seq79	-----																
seq80	-----																
seq81	-----															AGTTGCAGCCAAC	
seq82	-----															AGTTGCAGTAAAC	
seq83	-----																
seq84	-----																
seq85	-----															TGCGGAAGGATCATTGCACACACGAGTTGCAGCCAAC	
seq86	-----																
seq87	-----																
seq88	-----																
seq89	-----																
seq90	-----																
seq91	-----																
seq92	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq93	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq94	-----																TGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq95	-----																ACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq96	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq97	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq98	-----																TGCACACACAAGTTGCAGCCAAC
seq99	-----																CGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq100	-----																AAGTTGCAGCCA-C
seq101	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq102	-----																ACAAGTTGCAGCCA-C
seq103	-----																GAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq104	-----																GTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC
seq105	GTT	CATTAA	ACCTT	ATCATT	TAGAGG	AAGGAG	AAGTCG	TAAACA	AGGTTT	CCGTAG	GTGAAC	CTGCGG	AAGGAT	CATTGC	CACACA	CAAGTT	GCAGCCAAC
seq106	-----																AAGTTGCAGCCA-C
seq107	-----																CCTTATCATTTAGAGGAAGGAGAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCACACACAAGTTGCAGCCAAC

	200	210	220	230	240	250	260	270	280	290
seq37	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	--CGG-CGCC-TCGCGGCGTT	---	GCGGCCGGCCGTCTCCC	--TTCGTCAC	----		
seq38	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	--CGG-CGCC-TCGCGGCGTT	---	GCGGCCGGCCGTCTCCC	--TTCGTCAC	----		
seq39	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	--CGG-CGCC-TCGCGGCGTT	---	GCGGCCGGCCGTCTCCC	--TTCGTCAC	----		
seq40	-----									
seq41	-----									
seq42	-----									
seq43	-----									
seq44	-----									
seq45	-----									
seq46	CCGCGGCGAACGAACACATTGTCCCC	-----	TCGGCGGGTCG	-TTGG-CGCC-TCGCGGCGTT	---	GCGGCCGGCCGGCTCCC	--TTCGCCACGCGC	----		
seq47	-----									
seq48	-----									
seq49	-----									
seq50	-----									
seq51	-----									
seq52	-----									
seq53	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCCCTCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTACGC	----		
seq54	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCCCTCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTACGC	----		
seq55	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCCCTCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTACGC	----		
seq56	-CGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq57	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq58	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq59	-CGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq60	-CGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCATT	---	CGCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq61	-----	TCCCC	--NNTTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTACGC	----		
seq62	-----									
seq63	-----									
seq64	-----									
seq65	-----									
seq66	-----									
seq67	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq68	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq69	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq70	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq71	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TA--CGCC-TCGCGGCGTT	---	GCGGCCGGCCGTCTCCC	--TCGTAC	----		
seq72	CCGCGGCGAACGAACACATTGTCCCC	-----	TTCGGCGGGTCG	-TGG-CGCC-TCGCGGCGTC	---	GCGGCCGGCCGTCTCCC	--TCGTACGC	----		

	200	210	220	230	240	250	260	270	280	290
seq73	CCGCGGCGAACGAACACATTGTCCCCCCCCCTTCGGCGGGTTCG--TGG-CGCCCTCGCGGCGTC---GCGGCCGGCCGTCACCCC--TCGTCAC----									
seq74	-CGCGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCG--TGG-CGCC-TCGCGGCGTC---GCGGCCGGCCGTCACCCC--TCGTCAC----									
seq75	-----									
seq76	-----									
seq77	-----									
seq78	-----									
seq79	-----									
seq80	-----									
seq81	CCGCGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCG--TGG-CGCCCTCGCGGCGTC---ACGGCCGGCCGTCACCCCCTTCGTCAC----									
seq82	CCGCGGCGAACGAACACACTGTCCCCC-----TTCGGCGGGTTCG--TGG-CGCCCTCGCGGCGTC---GCGGCCGGCCGTCACCCCCTTCGTCAC----									
seq83	-----									
seq84	-----									
seq85	CCGCGGCGAACGAACACATTGTCCCCCCCCGTTTCGGCGGGTTCG--TGG-CGCCCTCGCGGCGTC---GCGGCCGGCCGTCACCCCCTTCGTCAC----									
seq86	-----									
seq87	-----									
seq88	-----									
seq89	-----									
seq90	-----									
seq91	-----									
seq92	-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----G									
seq93	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq94	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq95	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq96	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq97	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq98	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq99	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq100	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq101	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq102	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGAGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq103	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq104	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq105	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq106	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									
seq107	C-TTGGCGAACGAACACATTGTCCCCC-----TTCGGCGGGTTCGCGTGG-CGCC-TCCCGGCGTCGTCGCGGCCGGTTCGTCACCCC--TCGTCAC----									

	300	310	320	330	340	350	360	370	380	390
seq37	-----	GAGCTTCGT	-----	GGCGTCGGG	TTTCCAC	--GATGCC	CACCTTGACCGAATGACTGAGTCCC	GAAT	-----	
seq38	-----	GAGCTTCGT	-----	GGCGTCGGG	TTTCCAC	--GATGCC	CACCTTGACCGAATGACTGAGTCCC	GAAT	-----	
seq39	-----	GAGCTTCGT	-----	GGCGTCGGG	TTTCCAC	--GATGCC	CACCTTGACCGAATGACTGAGTCCC	GAAT	-----	
seq40	-----		-----						-----	
seq41	-----		-----						-----	
seq42	-----		-----						-----	
seq43	-----		-----						-----	
seq44	-----		-----						-----	
seq45	-----		-----						-----	
seq46	GAGC-GGGTTCTCGTGAGCTCCCTCGCGACGCGGCGTCGGG				TTTCCACACGATGTATT	CACCTTGACCGAATGACTGAGTCCC			GAAAACACTTTTT	
seq47	-----		-----						-----	
seq48	-----		-----						-----	
seq49	-----		-----						-----	
seq50	-----		-----						-----	
seq51	-----		-----						-----	
seq52	-----		-----						-----	
seq53	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCAAACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq54	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCAAACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq55	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCAAACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq56	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq57	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGGG	TTTCCACACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq58	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq59	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq60	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACC	-----CGAATGACTGAGTCCC	GAAT	-----	
seq61	AAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACC	-----CGAACGACTGAGTCCC	GAAT	-----	
seq62	-----		-----						-----	
seq63	-----		-----						-----	
seq64	-----		-----						-----	
seq65	-----		-----						-----	
seq66	-----		-----						-----	
seq67	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAC	CACC	-----TGAATGACTGAGTCCC	GAAT	-----	
seq68	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAC	CACC	-----TGAATGACTGAGTCCC	GAAT	-----	
seq69	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAC	CACC	-----TGAATGACTGAGTCCC	GAAT	-----	
seq70	GAGCCG	-----CGAGCTCCKT	-----	GGCGTCGTG	TTTCCACACGATGCWC	CACC	-----KGAAGGACTGAKTCTCGAAT		-----	
seq71	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGA	TTTCCACACGATGCAC	CACC	-----TGAATGACTGAGTCCC	GAAT	-----	
seq72	GAGC-G	-----CGAGCTTCGT	-----	GGCGTCGGG	TTTCCACACGATGCAT	CACCT	-----GAATGACTGAGTCCC	GAAT	-----	

	400	410	420	430	440	450	460	470	480	490	
seq37	-----	ACTTGGAT	--ACAGGA	---TTGG	-TGAG	--TTCCGTCCCC	-T----	TGAG	-----	CTT-GCGAA	----GGGGGT-C
seq38	-----	ACTTGGAT	--ACAGGA	---GTGG	-TGAG	--TTCCGTCCCC	-T----	TGAG	-----	CTT-GCGAA	----GGGGGT-C
seq39	-----	ACTTGGAT	--ACAGGA	---GTGG	-TGAG	--TTCCGTCCCC	-T----	TGAG	-----	CTT-GCGAA	----GGGGGT-C
seq40	-----								-----		
seq41	-----								-----		
seq42	-----								-----		
seq43	-----								-----		
seq44	-----								-----		
seq45	-----								-----		
seq46	ACTTAAAACTT	GGA	--GAGGA	---GTGGGTGCG	AACTCGCTCCCTCTT	---	CGAG	-----	TTGAGT	--TGAGTT	-----GTG
seq47	-----								-----		
seq48	-----								-----		
seq49	-----								-----		
seq50	-----								-----		
seq51	-----								-----		
seq52	-----								-----		
seq53	-----	ACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	CGAGCGAGCGGGCTT	-----	GCTT-GCGAACTCGAGGTGTGC		
seq54	-----	ACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	CGAGCGAGCGGGCTT	-----	GCTT-GCGAACTCGAGGTGTGC		
seq55	-----	ACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	CGAGCGAGCGGGCTT	-----	GCTT-GCGAACTCGAGGTGTGC		
seq56	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	GGAGCGAGCGGGCTT	-----	TGCCTT-GCGAGCTCGAGGGGTGC		
seq57	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCCCT	----	GGAGCGAGTGGGCTT	-----	TGCCTT-GCGAGCTCGAGGGGTGC		
seq58	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	GGAGCGAGTGGGCTT	-----	TGCCTTAGCGAGCTCGAGGGGTGC		
seq59	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	GGAGCGAGTGGGCTT	-----	TGCCTTAGCGAGCTCGAGGGGTGC		
seq60	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	GGAGCGAGCGGGCTT	-----	TGCCTT-GCGAGCTCGAGGGGTGC		
seq61	-----	ACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----	CGAGCGAGCGGGCTT	-----	GCTT-GCGAACTCGAGGGGCGC		
seq62	-----								-----		
seq63	-----								-----		
seq64	-----								-----		
seq65	-----								-----		
seq66	-----								-----		
seq67	-----	ACTTGGTT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----				TCGGTGGAGGA	
seq68	-----	ACTTGGTT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----				TCGGTGGAGGA	
seq69	-----	ACTTGGTT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----				TCGGTGGAGGA	
seq70	-----	ACTTGGTT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----				TCGKKGAGGA	
seq71	-----	ACTTGGTT	--GGAGGA	---GTGGGTGCG	--TTCCGTCCCC	-T----				TCGGTGGAGGA	
seq72	-----	AGACTTGGAT	--GGAGGA	---GTGGGTGCG	--TTTCGTGCCC	-T----	CGAGCGA	-----		GCTCGGGGTGCGC	

	400	410	420	430	440	450	460	470	480	490
seq73	-----	ACTTGGAT--GGGGGA---	GTGGGTGCGCGTTCCGTCCCC-T---	CGA-----	-----	-----	-----	-----	GCGAGCTCGGGGCGTGC	
seq74	-----	ACTTGGAT--GGAGGA---	GTGGGCGCG--TCGCGTCTCC-T---	GGAGCGAGCGGGCTT-----	TGGCTT--GCGAACTCGAGGTGCGC					
seq75	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq76	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq77	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq78	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq79	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq80	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq81	-----	GCTTGGAT--GGA--AGGAGCGG-TGCGTTTCGCGTCCCC-T---	GGAGCGACCGGGCTGGCTTGCTGGCTC--GCGAACTCGAGCGG--GC							
seq82	-----	GCTTGGAT--GGA--AGGAGTGG-TGCG--TTCCGTCCCC-TTGGGCGAGTGAGCGGGCTTGC-TGCTGGCTT--GCGAACTCGAGGGGCGC								
seq83	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq84	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq85	-----	GCTTGGAT--GGA--AGGAGTGGGTGCG--TTCCGTCCCC-TTGGG-----	CTC--GCGAGCTCGAGGGGCGC							
seq86	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq87	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq88	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq89	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq90	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq91	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq92	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq93	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq94	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq95	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq96	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq97	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq98	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGAGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq99	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq100	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGTGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq101	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGCGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq102	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq103	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq104	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq105	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq106	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						
seq107	-----	ACTTGGAT--GGAGGA---	GTGG-TGCG--TTCCGTCCCC-TTGGGCGAGCGAGTGAGCT----	TGCTGGCTT--GCGAACTCGAGGGGCGC						

	500	510	520	530	540	550	560	570	580	590	
seq37	GGCGCTCGCC	-GTTTACCTTG	--TGA--	CGAGTT--	GGAACAT--	AACTTTGAAAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA		
seq38	GGCGCTCGCC	-GTTTACCTTG	--TGA--	CGAGTT--	GGAACAT--	AACTTTGAAAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA		
seq39	GGCGCTCGCC	-GTTTACCTTG	--TGA--	CGAGTT--	GGAACAT--	AACTTTGAAAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA		
seq40	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq41	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq42	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq43	-----	-----	-----	-----	-----	-----	-----	-----	-----	ATGAA	
seq44	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq45	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq46	-----	-----	-----	GTGTGGAACAT	--AACC---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	TGCAACGATGAA		
seq47	-----	-----	-----	-----	-----	-----	-----	-----	-----	CGATGAA	
seq48	-----	-----	-----	-----	-----	-----	-----	-----	-----	ATGAA	
seq49	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq50	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq51	-----	-----	-----	-----	-----	-----	-----	-----	-----	ATGAA	
seq52	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq53	GGCGCGCGCC	-AGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq54	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq55	GGCGCGCGCC	-AGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq56	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAWCA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq57	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq58	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq59	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq60	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq61	GGCGCGCGCC	-NGGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq62	-----	-----	-----	-----	-----	-----	-----	-----	-----	AA	
seq63	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq64	-----	-----	-----	-----	-----	-----	-----	-----	T-GCATCGATGAA		
seq65	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq66	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq67	GGCACGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAATCT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq68	GGCACGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAATCT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq69	GGCACGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAATCT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq70	GGCACGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	
seq71	G---	CGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACGT--	AATCA--	AAAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA
seq72	GGCGCGCGCC	-GGTTACCTTA	--CGA--	CGAGTT--	GAAACTT--	AACAA--	AGAACA	ACTCTCAGCAAC	GGATATCTTGGCTCTT	-GCAACGATGAA	

	500	510	520	530	540	550	560	570	580	590
seq73	GGCGCGCGCC	-GGTTACCTCA	--CGA--	CGAGTT--	GAAACAT--	AACCA---	AAAACA	ACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA	
seq74	GCGGCGCGCC	-GGTTACCTTACACGA	--CGA--	CGAGTT--	GAAACAT--	AACTA---	AAAACA	ACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA	
seq75	-----	-----	-----	-----	-----	-----	-----	-----	-T-GCATCGATGAA	
seq76	-----	-----	-----	-----	-----	-----	-----	-----	-TCGATGAA	
seq77	-----	-----	-----	-----	-----	-----	-----	-----	-----	
seq78	-----	-----	-----	-----	-----	-----	-----	-----	-----	-TCGATGAA
seq79	-----	-----	-----	-----	-----	-----	-----	-----	-----	-CATCGATGAA
seq80	-----	-----	-----	-----	-----	-----	-----	-----	-----	-T-GCATCGATGAA
seq81	G-CGTGCGCC	-GCCTACCTTA	--CGG--	CGAGTT--	GAAACAT--	AAATCA	-----	-----	-----	-----
seq82	GGCGCGCGCC	-GGCTACCTTA	--CGA--	CGAGTT--	GAAACAT--	AATCA	-----	-----	-----	-----
seq83	-----	-----	-----	-----	-----	-----	-----	-----	-----	-TCGATGAA
seq84	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq85	GGCGCGCGCC	-GGTTACCTGC	--CGA--	CGAGTTGTGAAACGT	--AATCC-G-	AAAACA	ACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA		
seq86	-----	-----	-----	-----	-----	-----	-----	-----	-----	-ATGAA
seq87	-----	-----	-----	-----	-----	-----	-----	-----	-----	-AA
seq88	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq89	-----	-----	-----	-----	-----	-----	-----	-----	-----	-T-GCATCGATGAA
seq90	-----	-----	-----	-----	-----	-----	-----	-----	-----	-T-GCATCGATGAA
seq91	-----	-----	-----	-----	-----	-----	-----	-----	-----	-T-GCATCGATGAA
seq92	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq93	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq94	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq95	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq96	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq97	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq98	GGCGTGCGCC	-GGCTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq99	GGCGCGCGCC	-GGTTGCCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq100	GGCGCGCGCC	-GGTTGCCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq101	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq102	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq103	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq104	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq105	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq106	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					
seq107	GGCGCGCGCC	-GGTTACCTTGATCGAAACGAGTTGTGAAACGT	--AATCA---	AAA-CAACTCTCAGCAACGGATATCTTGGCTCTT	-GCAACGATGAA					

	700	710	720	730	740	750	760	770	780	790
seq73	CCGCTAGAGCGTCACCGC-GCCCCCCCACCGATCCAC--TCTCGCCGC---GAGGCGCCAGTC-----GGGT-CGAGTGCAAGTGGCCGTCCCCGT---									
seq74	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCCAGTC-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq75	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCCAGTC-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq76	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCCAGTC-----GGTT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq77	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCCAGTC-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq78	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCGTGTGTC-----GTGT-CGAGTGGAAGTGGCCGTCCCTG---									
seq79	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCGTGTGTC-----GTGT-CGAGTGGAAGTGGCCGTCCCTG---									
seq80	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAC--TCTCGCCGC---GAGGCGCAAGTC-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq81	-----GC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGCTAGTCG-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq82	-----GC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGC-CTAGTTGGCTAAGGGT-CGAGTGGATGTGGCCGTCCCCGG---									
seq83	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGCCAGTCG-----GGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq84	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGCTAGTCGGCCAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq85	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGCTAGTTGGCCGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq86	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGCTAGTTGGCCGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq87	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCCGCGCCGC---GAGGCGC-----TGAGGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq88	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCAAACTCTCGCCGC---GAGGCGC-----TGAGGGT-CGAGTGCAAGTGGCCGTCCCCGG---									
seq89	CCGCTAGAGCGTCACCGC-GCCCCCCCACCGATCCAAACTCCGCGCCGC---RAGGCGYTAGTTGGCTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq90	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCGC--TCCCGCCGC---GAGGCGCCAGTC-----GGCT-CGAGTGGAAGTGGCCGTCCCCGT---									
seq91	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTGTTTTGCTCAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq92	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq93	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq94	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq95	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq96	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq97	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq98	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq99	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq100	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq101	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq102	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq103	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq104	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq105	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGCTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq106	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGGTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									
seq107	CCGCTAGAGCGTCACCGC-GCCCCCC-ACCGATCCACACTCCGCGCCGC---GAGGCGGTAGTTTGTGTAAGGGT-CGAGTGGAAGTGGCCGTCCCCGG---									

	800	810	820	830	840	850	860	870	880	890
seq37	-----CGCGGCCTT-CGCAAGAAGGC-----	-----CTTGAGCG--AGT----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq38	-----CGCGGCCTT-CGCAAGAAGGC-----	-----CTTGAGCG--AGT----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq39	-----CGCGGCCTT-CGCAAGAAGGC-----	-----CTTGAGCG--AGT----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq40	-----CGCGGCCTT-CGCGAGAAGGC-----	-----CTTGAGCG--AGTTT--	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq41	-----CGCGGCCTT-CGCGAGAAGGC-----	-----CTTGAGCG--AGT----	GAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq42	-----CGCGGCCTT-CGCGAGAAGGC-----	-----CTCGAGCG--AGT----	CAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq43	-----TGGGC-----GAAGGC-----	-----CTTAAGGGTTGGCCGAAATGGACGGAATCGGGCCGCCGTGGTG--A								
seq44	-----TGGCCTT-CGCGAGAGGGC-----	-----TAAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq45	-----CGCGCGCGGCCTT-CGCAAGAAGGC-----	-----CTCGGG--TAAGTGAC--GAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq46	-----AGCGTCGGGCTT-CGC-----GGC-----	-----CTGACGGAGGGTCGGCTGAAATGGAAGGAATCGGGCCGCCGTGGTG--A								
seq47	-----CGCGCGGCCTT-CGCAAGAAGGC-----	-----CTTGAGCGCAAGT----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq48	-----CGCGGCCTT-CGCAAGAAGGC-----	-----CTTGAGAGCGAGC----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A							
seq49	-----CGCGGCCTTCTT--CGAGAAGGC-----	-----CCAAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq50	---GGTGAAGTGGCCTTCTTTACGAGGAGGC-----	---TAAGTT---ACGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq51	---GGTGAAGTGGCCTCCTTTACGAGGAGGC-----	---TAAGTT---ACGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq52	---GGTGAAGTGGCCTCCTTTACGAGGAGGC-----	---TAAGTT---ACGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq53	---GGTGAAGTGGCCTTCT--CACGA--AGGC-----	---CAAGTTTCTAAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq54	---GGTGAAGTGGCCTTCT--CACGA--AGGC-----	---CAAGTTTCTAAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq55	---GGTGAAGTGGCCTTCT--CACGA--AGGC-----	---CAAGTTTCTAAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq56	-TCGGTGACTTGGCCTTCT--CGCGA--AGGC-----	-CAAGTTCTTGAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq57	-TCGGTGACTTGGCCTTCT--CGCGA--AGGC-----	-CAAGTTCTTGAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq58	-TCGGTGACTTGGCCTTCT--CGCGA--AGGC-----	-CAAGTTCTTGAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq59	-TCGGTGACTTGGCCTTCT--CGCGA--AGGC-----	-CAAGTTCTTGAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq60	-TCGGTGACTTGGCCTTCT--CGCGA--AGGC-----	-CAAGTTCTTGAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq61	TTACNNTAAGTGGTGGTCTT-CTCGCAAGGC--CACCCTT-AGAANNNG----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq62	TTTTCTAAGTGTGGTCTT-CGCGAGAAGGC--CCTCCTT-AGTAGAAG----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq63	TTTTCTAAGTGGTGGTCTT-CGCGAGAAGGC--CATCCTT-CGAAGAAG----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq64	GCTGAGT-GGTGG--TCTT-CTCGAGAAGGCCGCCATCCTT-GG-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq65	---ACGA-GGTGG--TCTT-CTCGCAAGGC--CATCCTT-AG-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq66	---KACGGAGTGG--TCTT-CGCGAGAAGGC--CACCCTT-AG-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq67	---GACGGAGTGG--CCTT-CGCGAGAAGGC--CATACTGTC-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq68	---GACGGAGTGG--CCTT-CGCGAGAAGGC--CATACTGTC-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq69	---GACGGAGTGG--TCTT-CGCGAGAAGGC--CATACTGTC-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq70	---GACGGAGTGG--YCTT-CGCGAGAAGGC--CATACTGTT-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq71	----ACGGAGTGG--CCTT-CGCGAGAAGGC--CATGCTGTT-----	AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--A								
seq72	-----CGAAGCGGCCTTCTTTACGAGGAGTC--CGCACTTGG-----	CTAAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--A								

	800	810	820	830	840	850	860	870	880	890
seq73	-----GGAGCGGGCCTCCTTTTCGCGAGGAGGC---	CCGACTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq74	-----CGAAGTGGCCTTCTTTTCACGAGGAGGC---	CGTCCTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq75	-----CGAAGTGGCCTTCTTTTCACGAGGAGGC---	CGTCCTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTGTGA							
seq76	-----CGAAGCGGCCTTCTTTTCACGAGGAGGC---	CGTCCTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGTGCCGCCGTGGTG--	A						
seq77	-----CGAAGTGGCCTTCTTTTCACGAGGAGGC---	CGTCCTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq78	-----CGAAGCGGCCTTCTTTTCACGAGGAGGC---	CGCCCTTGT-----	CCAAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq79	-----CGAAGCGGCCTTCTTTTCACGAGGAGGC---	CGCCCTTGT-----	CCAAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq80	-----CGAAGTGGCCTTCTTTTCACGAGAAGGC---	CGTTCCTTGG-----	AAGGGTCGGCTGAAATGGATGGAATCGAGCCGCCGTGGTG--	A						
seq81	-----CGC-CAGTT-CGC-----		GAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq82	-----CGC-TAGTT-CGC-----		GAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq83	-----CGC-CAGTT-CGC-----		GAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq84	-----CGCCTGGTT-CGC-----		GAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq85	-----CGC-TGGTT-CGC-----		CGAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq86	-----CGC-TAGTG-GGC-----		GAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq87	-----CGCGC-TAGTT-CGC-----		AAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq88	-----CGCGC-TAGTT-CGC-----		AAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq89	-----CGC-TAGTT-GGC-----		AAGGGTCGGCTGAAATGGACGGAATCGGGCCGCCGTGGTG--	A						
seq90	-----CGCGATCTT-CGCGAG-----		GAGGGTCGGCTGAAATGGATGGAATCGGGCCGCCGTGGTG--	A						
seq91	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq92	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq93	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq94	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq95	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq96	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq97	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq98	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq99	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq100	-----CGCGAGAAGGC-----		TCAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq101	-----CGCGAGAAGGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq102	-----CGCGAGAACGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq103	-----CGCGAGAACGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq104	-----CGCGAGAACGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq105	-----CGCGAGAACGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq106	-----CGCGAGAATGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						
seq107	-----CGCGAGAATGC-----		AAGGGTCGGCTGAAATGGATGGAATTGGGCCGCCGTGGTG--	A						

	900	910	920	930	940	950	960	970	980	990
seq37	CACAGTCCGCGATCGGGTG-ATTTT-ATGGCGAGCC--TCCCC-----GGGAGGGCCGACCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq38	CACAGTCCGCGATCGGGTG-ATTTT-ATGGCGAGCC--TCCCC-----GGGAGGGCCG-CCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq39	CACAGTCCGCGATCGGGTG-ATTTT-ATGGCGAGCC--TCCCC-----GGGAGGGCCG-CCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq40	CACAGTCCGCGATCGGGTG-ATTTT--TCGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq41	CACAGTCCGCGATCGGGTG-ATTTT--TCGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT--CTAAGTGCCTGG--CTGCGT									
seq42	CACAGTCCGCGATCGGGTG-ATTTT--TCGCGAGCC--TCCTC-----GGGAGGGTCGCCCTGGA-TTTTT-CTAAGTGCCTGG--CTGCGT									
seq43	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCTGC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGTGTGG--CTGCGT									
seq44	CACAGTCCGCGATCGGGTG-ATTTT--ACGCGAGCC--TCCCGC-CTGC-----GGGAGGGTCG-CCGTGGATCTTT-CTAAGTGCCTGG--CTGCGT									
seq45	CACAGTCCGCGATCGGGTG-ATTTT--CCGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGT--CTGCGT									
seq46	CACAGTCCGCGATCGGGTG-AT----CCGCG-----CTCCCGAATTTTTTC---GGGAG-----CCTGGAATTTTT-CTAAGTGCCTGT--GCTGCGT									
seq47	CACAGTCCGCGATCGGGTG-ATTTT--ACGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq48	CACAGTCCGCGATCGGGTG-ATTTT--TCGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGG--CTGCGT									
seq49	CACAGTCCGCGATCGGGTG-ATTTT-G-CGCGGGCC--TCCTC-----GGGAGGTTTCG-CCGTGGATTTTT-CTAAGTGCCTGG--CTGCGT									
seq50	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCT-----GAGGTTCT-TGGTGAATTTTT-CTAAGTGCTTGG--CTGCGT									
seq51	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTGCGGTGC-----GGGAGGTTCT-TGGTGAATTTTT-CTAAGTG-TTGG--CTGCGT									
seq52	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTGCGGTGC-----GGGAGGTTCT-TGGTGAATTTTT-CTAAGTGTTGG--CTGCGT									
seq53	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGCGGTTTCG-CCGTGAATTTTT-CTAAGTGCAGG--CTGCGT									
seq54	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGCGGTTTCG-CCGTGAATTTTT-CTAAGTGCAGG--CTGCGT									
seq55	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGCGGTTTCG-CCGTGAATTTTT-CTAAGTGCAGG--CTGCGT									
seq56	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGT--CTGCGT									
seq57	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGGATTTTT-CTAAGTGCCTGT--CTGCGT									
seq58	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGT--CTGCGT									
seq59	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGT--CTGCGT									
seq60	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCCTGT-GCTGCGT									
seq61	CACAGTCCGCGATCGGGTGNATTTT-GYCGCGAGCC--TCCTCT-----GGGAGGGTCG-CCGTGAATTTTTNCTAAGTGCAGAG--CTGCGT									
seq62	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGGTCG-CGGTGAATTTTT-CTAAGTGCAGT--CTGCGT									
seq63	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGGTCG-CGGTGAATTTTT-CTAAGTGCAGT--CTGCGT									
seq64	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCAGT--CTGCGT									
seq65	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCAGT--CTGCGT									
seq66	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq67	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq68	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq69	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq70	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq71	TTCAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GGGAGGTTCA-TGGTGAATTTTT-CTAAGTGTGCGAGGCTGCGT									
seq72	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTC-----GTGAGGCTCT-CGTTGAATTTTT-CTAAGTGCTTGG--GCTGCGT									

	900	910	920	930	940	950	960	970	980	990
seq73	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGGC--TCCTTC-----GGGAGATTCT-CGGCGAATTTTTTCTAAGTGCTTG--GCTGCGT									
seq74	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq75	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTGCGCTGC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq76	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCCG-CTGC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq77	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTGCGATGC-----GGGAGGCTCT-TGGTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq78	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTCC-----GTGAGGCTCT-CGTTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq79	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTCC-----GTGAGGCTCT-CGTTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq80	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCTCCGG-----GAGGCTCT-TGGTGAATTTTT-CTAAGTGCTTG--GCTGCGT									
seq81	CACAGTCCGCGATCGGGTG-ATTTT-GTTGCGAGCC--TCCCC-----GGCTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq82	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TC-----AGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq83	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCC-----GGCTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq84	CACAGTCCGCGATCGGGTG-ATTTT-GTGGCGAGCC--TCCTGC-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGAGG--CTGCGT									
seq85	CACAGCCC GCGATCGGGTG-ATTTT--ACGCGAGCCTCTCCCCG-CTGCGGGGAGGGAGGGTCG-CCGTGAATCTTT-CTAAGTGCGTGG--CTGCGT									
seq86	CACAGTCCGCGATCGGGTG-ATTTTTCGTCGCGAGCC--TCCTGC-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq87	CACAGTCCGCGATCGGGTG-ATTTT--ACGCGGTCC--TCCCCG-CTGC-----GGGAGGGTCG-CCGTGAATCTTT-CTAAGTGCGTGG--CTGCGT									
seq88	CACAGTCCGCGATCGGGTG-ACTTC--ACGCGGTCC--TCCCCG-CTGC-----GGGAGGGTCG-CCGTGAATCTTT-CTAAGTGCGTGG--CTGCGT									
seq89	CACAGTCCGCGATCGGGTG-ATTTTTGTCGCGAGCC--TCCTGC-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGA--CTGCGT									
seq90	CACAGTCCGCGATCGGGTG-ATTTT--CCGCGAGCC--TCCCC-----GGGAGGGTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq91	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCC-----GAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGT--CTGCGT									
seq92	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq93	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq94	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq95	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq96	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq97	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq98	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGTGT									
seq99	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTTCGT									
seq100	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-CTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq101	CACAGTCCGCGATCGGGTG-ATTTT-TTCGCGAGCC--TCCCCG-TTGC-----GGGAGGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq102	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq103	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq104	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq105	CACAGTCCGCGATCGGGTG-ATTTT-GTCGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq106	CACAGTCCGCGATCGGGTG-ATTTT-GTTGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									
seq107	CACAGTCCGCGATCGGGTG-ATTTT-GTTGCGAGCC--TCCCCG-CTGC-----GGGAGTTTCG-CCGTGAATTTTT-CTAAGTGCGTGG--CTGCGT									

	1000	1010	1020	1030	1040	1050	1060	1070	1080
seq37	-CCCCCAGT	CGGTTTCGG	-TTACCT-	CGTGCAGGT	ACGTGCGCGCCCC	-GCGGCGCGCGTCA	----	TCGCATCAGACCT	CTAATCGGAAAAGACTACC
seq38	-CCCCCAGT	CGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq39	-CCCCCAGT	CGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq40	-CCCCCAGT	TGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCT-----
seq41	-CCCCCAGT	TGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq42	-CCCCCAGT	TGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC	
seq43	-CCCCCAGT	TGGTTTCGGGTTACCT	-CGTGCAGGT	-CGCGCGCGCCCCA	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq44	-CCCC	-AGTTGGCCTTGG	-TTACCT-	CGAGCAGGT	-CGAGCGCGCCCC	-GTGGCGCGCGTCA	-----	CGCATCAGACCTCT-----	
seq45	-CCCCCAGT	TGGTTTCGGGTTACCT	-CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC	
seq46	-CCCC	-AGTTGGCTCCGG	-TTACCC-	CTTGCAGGT	-CGAGCGCGCC	----	-GCGGCGCGCGTCA	CAGTACGCATCAGACCTCTAATCGGAAAAGACTACC	
seq47	-CCCCCAGT	TGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq48	-CCCCCAGT	TGGTTTCGG	-TTACCT-	CGTGCAGGT	-CGTGC	GCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC	
seq49	-CCCCCAGT	TGGCTTCGG	-TTCCCT-	CGTGCAGGT	-CGTGC	GCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC	
seq50	-CCCCCAGT	TGGCTMGGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq51	-CCCCCAGT	TGGCTCGGG	-TTACCT-	CATGCAGGT	-CTTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq52	-CCCCCAGT	TGGCTCGGG	-TTACCT-	CATGCAGGT	-CTTGC	GCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC
seq53	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq54	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq55	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAA-----		
seq56	-CCCCCAGT	TGGCTTCGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAA-----		
seq57	-CCCCCAGT	TGGCTTCGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq58	-CCCCCAGT	TGGCTTCGG	-TTCCCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq59	-CCCCCAGT	TGGCTTCGG	-TTCCCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAA-----		
seq60	-CCCCCAGT	TGGCTTCGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAA-----		
seq61	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGC-----				
seq62	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq63	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq64	-CCCCCAGT	TGGCTTTTTGGTTCCCT	-CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC			
seq65	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq66	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTC-----		
seq67	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq68	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq69	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq70	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq71	-CCCCCAGT	TGGCTTTGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCCCGCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC		
seq72	-CCCCCAGT	TGGCTCGGG	-TTACCT-	CATGCAGGT	-CGAGCGCGCCCC	-GCGGCGCGCGTCA	-----	CGCATCAGACCTCTAATCGGAAAAGACTACC	

	1090	1100	1110	1120	1130	1140	1150	1160	1170	1180	
seq1	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq2	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCG-
seq3	CGCTGA-----										
seq4	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq5	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCG-
seq6	CGCTGAGTTTAA	G	CATATCACT	-----							
seq7	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq8	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAA-----							
seq9	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	AAA-----						
seq10	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGGA-----							
seq11	CGCTGA-----										
seq12	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq13	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq14	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq15	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq16	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGGA-----							
seq17	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq18	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq19	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq20	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq21	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq22	CGCTGAGTTTAA	G	CATATCACT	-----							
seq23	C-----										
seq24	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq25	CGCTGAGTTTAA	G	CATATCACTA	AAGC-----							
seq26	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT
seq27	-----										
seq28	CGCTGAGTTTAA	G	CATATCACT	-----							
seq29	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGGA-----							
seq30	CGCTGAGTTTAA	G	CATATCACTAA-----								
seq31	CGCTGAGTTTAA-----										
seq32	-GCTGAGTTTAA	G	CATATCA-----								
seq33	-----										
seq34	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGGA-----							
seq35	-----										
seq36	CGCTGAGTTTAA	G	CATATCACTA	AAGCGGAGG	GAGAAGAACT	AACCAGGATTT	CCCTAGTAAC	GGCGAGCGA	ACCGGAAAG	AGCCCAGCTT	GAAAATCGT

	1090	1100	1110	1120	1130	1140	1150	1160	1170	1180
seq37	CGCTGAG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq38	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq39	CGCTGAGTTTAAGCATATCACTAAGCGGAGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq40	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq41	CGCTGAGTTTAAGCATATCAATAAGCGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq42	CGCTGAGTTTAAGCATATCAATAAGCG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq43	CGCTGAGTTTAAGCATATCAATAAGC	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq44	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq45	CGCTGAGTTTAAGCATATCAATAAGCGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq46	CGCTGAGTTTAAGCATATCAATAAGCGGAGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq47	CGCTGAGTTTAAGCATATCAATAAGCG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq48	CGCTGAGTTTAAGCATATCAATAAGCG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq49	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq50	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq51	CGCTGAGTTTAAGCATATCAATAAGC	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq52	CGCTGAGTTTAAGCATATCAATAAGCGGAGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq53	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGGAAAGAGCCCAGCTTGAAA	-----	-----	-----	-----	-----	-----	-----	-----
seq54	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----	-----	-----
seq55	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq56	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq57	CGCTGAGTTTAAGCATATCA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq58	CGCTGAGTTTAAGCATATCA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq59	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq60	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq61	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq62	CGCTGAGTTTAAGCATATCAATAA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq63	CGCTGAGTTTAAGCATATCAATAAGCGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq64	CGCTGAGTTTAAGCATATCAATAAGCGGAG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq65	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq66	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq67	CGCTGAGTTTAAGCATATCACTAAGCGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq68	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----	-----	-----
seq69	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----	-----	-----
seq70	CG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq71	CGCTGAGTTTAAGCATATCACTAA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq72	CGCTGAGTTTAAGCATATCACTAAGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----	-----	-----

	1090	1100	1110	1120	1130	1140	1150	1160	1170	1180
seq73	CGCTGAGTTTAA	GCATATCACTAA	-----	-----	-----	-----	-----	-----	-----	-----
seq74	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq75	CGCTGAGTTTAA	GCATATCAATAA	AGCGGAGGA	-----	-----	-----	-----	-----	-----	-----
seq76	CGCTGAGTTTAA	GCATATCAATAA	AGCG	-----	-----	-----	-----	-----	-----	-----
seq77	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq78	CGCTGAGTT	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq79	CGCTGAGTTTAA	GCATATCAATAA	AGCG	-----	-----	-----	-----	-----	-----	-----
seq80	CGCTGAGTTTAA	GCATATCAATAA	AGCGGAG	-----	-----	-----	-----	-----	-----	-----
seq81	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq82	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq83	CGCTGAGTTTAA	GCATATCAATAA	AGCGGAGGA	-----	-----	-----	-----	-----	-----	-----
seq84	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq85	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq86	CGCTGAGTTTAA	GCATATCAATAA	AGC	-----	-----	-----	-----	-----	-----	-----
seq87	CGCTGAGTTTAA	GCATATCAATAA	AGC	-----	-----	-----	-----	-----	-----	-----
seq88	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGA	-----	-----	-----	-----	-----	-----	-----
seq89	CGCTGAGTTTAA	GCATATCAATAA	AGCGGAGGA	-----	-----	-----	-----	-----	-----	-----
seq90	CGCTGAGTTTAA	GCATATCAATAA	AGCGG	-----	-----	-----	-----	-----	-----	-----
seq91	CGCTGAGTTTAA	GCATATCAATAA	AGCGGAGGA	-----	-----	-----	-----	-----	-----	-----
seq92	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----
seq93	CGCTGAGTTTAA	GCATATCACTAA	AGCGG	-----	-----	-----	-----	-----	-----	-----
seq94	CGCTGAGTTTAA	GCATATCACTAA	AGC	-----	-----	-----	-----	-----	-----	-----
seq95	CGCTGAGTTTAA	GCATATCACTA	-----	-----	-----	-----	-----	-----	-----	-----
seq96	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----
seq97	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAA	-----	-----	-----	-----	-----	-----	-----
seq98	CGCTGAGTTTAA	GCATATCACTAA	AGCGGA	-----	-----	-----	-----	-----	-----	-----
seq99	CGCTGAGTTTAA	NCATATCAATAA	AGCGGAG	-----	-----	-----	-----	-----	-----	-----
seq100	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGC	-----	-----	-----	-----	-----	-----	-----
seq101	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----
seq102	CGCTGAGTT	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq103	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGAAAGAGCCCAGCTTGAA	-----	-----	-----	-----	-----	-----
seq104	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGG	-----	-----	-----	-----	-----	-----	-----
seq105	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGATTTCCCTAGTAACGGCGAGCGAACC	CGAAAGAGCCCAGCTTGAAAATCGT	-----	-----	-----	-----	-----	-----
seq106	CGCT	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq107	CGCTGAGTTTAA	GCATATCACTAA	AGCGGAGGAGAAGAACTAACCAGGA	-----	-----	-----	-----	-----	-----	-----

	1190	1200	1210	1220	1230	1240	1250	1260	1270	1280
seq1	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq2	-----									
seq3	-----									
seq4	-----									
seq5	-----									
seq6	-----									
seq7	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGA-----									
seq8	-----									
seq9	-----									
seq10	-----									
seq11	-----									
seq12	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq13	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq14	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq15	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq16	-----									
seq17	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGAACCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACA-----									
seq18	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq19	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq20	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq21	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGCCGCGCCGGACCCA-----									
seq22	-----									
seq23	-----									
seq24	GGTGCCTCGTAMCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCG-----									
seq25	-----									
seq26	GGTGCCTCGCACCTC-----									
seq27	-----									
seq28	-----									
seq29	-----									
seq30	-----									
seq31	-----									
seq32	-----									
seq33	-----									
seq34	-----									
seq35	-----									
seq36	GGTGCCTCGTACCTCGAATTGTAGTCTGGAGAAGGTCC-TCTGCGCCGCGCCGGAC-----									

	1190	1200	1210	1220	1230	1240	1250	1260	1270	1280

seq37	-----									
seq38	-----									
seq39	-----									
seq40	-----									
seq41	-----									
seq42	-----									
seq43	-----									
seq44	-----									
seq45	-----									
seq46	-----									
seq47	-----									
seq48	-----									
seq49	-----									
seq50	-----									
seq51	-----									
seq52	-----									
seq53	-----									
seq54	GGCGCCTCGCGCCTCGAATTGTAGTCTGGA-----									
seq55	-----									
seq56	-----									
seq57	-----									
seq58	-----									
seq59	-----									
seq60	-----									
seq61	-----									
seq62	-----									
seq63	-----									
seq64	-----									
seq65	-----									
seq66	-----									
seq67	-----									
seq68	GGCGCCTCGCGCCTCGAATTGTAGTCTGGA-----									
seq69	GGCGCCTCGCGCCTCGAATTGTAGTCTGGAGAAGGTCCCTCTGCGGCGCGCCGGACCCAAGTTCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG									
seq70	-----									
seq71	-----									
seq72	GGCGCCTCGCGCCTCGAATTGTAGTCTGGAGAARGTCCCTCTGCGGCGCGCCGGA-----									

	1190	1200	1210	1220	1230	1240	1250	1260	1270	1280
seq73
seq74	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq75	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq76	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq77	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq78	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq79	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq80	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq81	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq82	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq83	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq84	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq85	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq86	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq87	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq88	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq89	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq90	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq91	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq92	GGCGCCTCCCGCCTCGAGTTGTAGTCTGG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq93	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq94	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq95	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq96	GGCGCCTCGCGCCTCGAGTTGTAGTCTGGAGAAGGTCCCTCTGCGGCGCGCCGGACCCAAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq97	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq98	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq99	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq100	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq101	GGCGCCTCGCGCCTCGAGTTGTAGTCTGGAGAAGGTCCCTCTGCGGCGCGCCGGA	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq102	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq103	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq104	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq105	GGCGCCTCGCGCCTCGAGTTGTAGTCTGGAGAANGTCCCTCTGCGGCGCGCCGGACC-AAGTTCCCTGGAAAGGGACGTCATCGAGGGTGACAACCCCG	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq106	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq107	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

	1290	1300	1310	1320	1330	1340	1350	1360	1370	1380
seq1	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGC									
seq2	-----									
seq3	-----									
seq4	-----									
seq5	-----									
seq6	-----									
seq7	-----									
seq8	-----									
seq9	-----									
seq10	-----									
seq11	-----									
seq12	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq13	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq14	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq15	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq16	-----									
seq17	-----									
seq18	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq19	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq20	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq21	-----									
seq22	-----									
seq23	-----									
seq24	-----									
seq25	-----									
seq26	-----									
seq27	-----									
seq28	-----									
seq29	-----									
seq30	-----									
seq31	-----									
seq32	-----									
seq33	-----									
seq34	-----									
seq35	-----									
seq36	-----									

	1290	1300	1310	1320	1330	1340	1350	1360	1370	1380
seq37
seq38	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq39	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq40	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq41	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq42	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq43	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq44	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq45	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq46	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq47	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq48	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq49	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq50	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq51	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq52	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq53	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq54	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq55	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq56	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq57	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq58	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq59	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq60	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq61	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq62	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq63	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq64	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq65	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq66	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq67	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq68	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq69	TCCGTGCCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAGGCTAAA									
seq70	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq71	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq72	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

	1290	1300	1310	1320	1330	1340	1350	1360	1370	1380
seq73
seq74	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq75	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq76	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq77	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq78	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq79	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq80	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq81	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq82	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq83	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq84	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq85	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq86	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq87	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq88	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq89	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq90	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq91	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq92	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq93	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq94	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq95	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq96	TCCGCGCCCGGAACGCGTCGCTCCACGAGGACCTGTCTGCGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCTTCTAAGGCTAAA									
seq97	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq98	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq99	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq100	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq101	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq102	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq103	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq104	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq105	TCCGCGCCCGGAACGCGTCGCTCCACGAGGAC-----									
seq106	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
seq107	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

	1390	1400	1410	1420
seq1
seq2	-----	-----	-----	-----
seq3	-----	-----	-----	-----
seq4	-----	-----	-----	-----
seq5	-----	-----	-----	-----
seq6	-----	-----	-----	-----
seq7	-----	-----	-----	-----
seq8	-----	-----	-----	-----
seq9	-----	-----	-----	-----
seq10	-----	-----	-----	-----
seq11	-----	-----	-----	-----
seq12	TATGGGCAAGAGACCGATAGCGAACAAGTACCGCG-			
seq13	TATGGGCAAGAGACCGATAGCGAACAAGTACCGC--			
seq14	TATGGGCAAGAGACCGATAGCGAACAAGTACCG---			
seq15	TATGGGCAAGAGACCGATAGCGAACAAGTACCGC--			
seq16	-----	-----	-----	-----
seq17	-----	-----	-----	-----
seq18	TATGGGCAAGAGACCGATAGCGAACAAG-----			
seq19	TATGGGCAAGAGACCGATAGCGAACAAGTACCG---			
seq20	TATGGGCAAGAGACCGATAGCGAACAAGTACCG---			
seq21	-----	-----	-----	-----
seq22	-----	-----	-----	-----
seq23	-----	-----	-----	-----
seq24	-----	-----	-----	-----
seq25	-----	-----	-----	-----
seq26	-----	-----	-----	-----
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seq31	-----	-----	-----	-----
seq32	-----	-----	-----	-----
seq33	-----	-----	-----	-----
seq34	-----	-----	-----	-----
seq35	-----	-----	-----	-----
seq36	-----	-----	-----	-----

	1390	1400	1410	1420
seq37
seq38	-----	-----	-----	-----
seq39	-----	-----	-----	-----
seq40	-----	-----	-----	-----
seq41	-----	-----	-----	-----
seq42	-----	-----	-----	-----
seq43	-----	-----	-----	-----
seq44	-----	-----	-----	-----
seq45	-----	-----	-----	-----
seq46	-----	-----	-----	-----
seq47	-----	-----	-----	-----
seq48	-----	-----	-----	-----
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VITA

Justin Wynns was born in San Francisco, California, on June 17, 1974. He grew up in that city, and completed his secondary education in June 1992 at the Urban School of San Francisco. In September 1992 he enrolled at the University of California – Santa Cruz. In June 1996 he was awarded his Bachelor of Arts degree in Art, with an emphasis in Printmaking. In September 1997, he moved to Asheville, North Carolina, where his interest in plants and plant science began. In August 1999 he enrolled at the University of North Carolina at Asheville, where he pursued further undergraduate coursework in the natural sciences. In May 2000, he moved to New York City to work at the New York Botanical Garden in the Bronx; first as a herbarium intern, and later as a curatorial assistant in the Cryptogamic Herbarium. In August 2002, he returned to North Carolina to pursue a Master of Science degree in the Department of Biology at Appalachian State University. The M.S. was awarded in May 2006.

Mr. Wynns is a member the American Bryological and Lichenological Society and the Southern Appalachian Botanical Society. He lives with his grandmother, Nora Percival, and his girlfriend, Anja Amtoft, at 478 Greer Lane, in Vilas, North Carolina. His parents are George and Jill Wynns of San Francisco.