

Originally published in Bulletin of the Buffalo Society of Natural Sciences 36: 81–115. 1998
Repaginated here. Reissued online September 11, 2012.

A PHYLOGRAMMATIC EVOLUTIONARY ANALYSIS OF THE MOSS GENUS *DIDYMODON* IN NORTH AMERICA NORTH OF MEXICO

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Abstract: A key is presented for the 22 known species of *Didymodon* (Musci) in North America north of Mexico, with taxonomic commentaries for each. A phylogram combining PCA ordination and a cladogram shows evident morphological convergence between five pairs of species. Six species are interpreted as surviving ancestors. Phylogenetic analysis is an assumption-laden and belief-oriented attempt at reconstructing a past unique conditional chain of events. Through misapplication of the theory of statistical relevance, the fine structure of trees of maximum synapomorphy is generally artificial and antiparsimonious; also, trees of maximum likelihood are often not probabilistic estimations. Cladistic analysis, however, may be useful under certain conditions in devising general classifications and in phylogrammatic analysis.

The moss genus *Didymodon* as expanded by Saito (1975) has proven large and complex in North America (e.g., studies by Zander 1978a, 1981, 1994). Work on the genus *Didymodon* for the bryophyte volume of the Flora of North America (FNA Editorial Committee 1993) is sufficiently advanced that an annotated key to the 22 known species might be profitably presented in advance of FNA final publication four or five years from now. A phyletic evolutionary study addresses apparent morphological convergence, while the statistical assumptions and methods used for obtaining modern detailed classifications are reviewed.

Many species of the genus are common and often difficult to distinguish. The present study updates the above-cited previous work. The key below should aid considerably the floristic and ecological studies by other botanists that have been given impetus by the FNA project. Descriptions and details of geographic ranges, habitats and sporophyte maturation dates will be given in that work.

TAXONOMY

DIDYMODON Hedw., Sp. Musc. 104, 1801.

Sections of the genus previously recognized for North America north of Mexico are: *Didymodon* Hedw. sect. *Didymodon*, type: *Didymodon rigidulus* Hedw.; *Didymodon* sect. *Asteriscium* (C. Müll.) Zand., type: *Didymodon umbrosus* (C. Müll.) Zand.; *Didymodon* sect. *Fallaces* (De Not.) Zand., type: *Didymodon fallax* (Hedw.) Zand.; and *Didymodon* sect. *Vineales* (Steere) Zand., type: *Didymodon vinealis* (Brid.) Zand. Sectional synonyms and descriptions were given and species were assigned to the sections by Zander (1978a, 1993). Many species, however, remain problematic in assignment to sections.

There are about 122 species of *Didymodon* worldwide (Zander 1993), growing on a variety of substrates, mostly soil and rock. It is a large genus widely diversified in temperate and montane areas worldwide.

The genus *Didymodon* is distinguished from a similarly widely distributed relative *Barbula* Hedw., with which it is often confused, by its usually lanceolate to long-lanceolate leaves, axillary hairs with one or more brown basal cells, basal laminal cells less strongly differentiated from the upper, ventral costal cells usually quadrate (six species have elongate ventral costal cells), laminal papillae absent or simple or only occasionally multiplex, gemmae composed of only 1–10 cells, and peristome teeth seldom long and twisted (see also Saito 1975).

KEY TO *DIDYMODON* IN NORTH AMERICA NORTH OF MEXICO

1. Leaf apices caducous or very fragile.
 2. Leaf apices not swollen, usually evenly narrowing.
 3. Cells of leaf apex smooth..... 1. *Didymodon rigidulus* (var. *icmadophilus*)
 3. Cells of leaf apex weakly conic-mamillose..... 14. *Didymodon sinuosus*
 2. Leaf apices apically swollen as a propagulum.
 4. Upper laminal cells 13–15 mm wide..... 3. *Didymodon johansenii*
 4. Upper laminal cells 8–10 mm wide..... 2. *Didymodon anserinocapitatus*
1. Leaf apices intact or only occasionally broken.
 5. Plants in nature red- to black-brown, leaves not keeled, not highly recurved, margins finely crenulate by bulging cell walls, usually plane above midleaf, costa thin, 2–3 cells wide above midleaf, laminal papillae absent or low, massive and lens-shaped.
 6. Leaves dimorphic: cochleariform, epapillose leaves present on fragile branchlets or portions of some stems..... 9. *Didymodon subandreaeoides*
 6. Leaves monomorphic.
 7. Plants often fruiting, leaf apices acute, propagula absent 7. *Didymodon nigrescens*
 7. Plants sterile, leaf apices obtuse, clusters of unicellular propagula in the leaf axils..... 8. *Didymodon perobtusius*
 5. Plants without the above exact combination of characters, usually green, orange or red, sometimes keeled or highly recurved, margins usually entire or dentate, often recurved above midleaf, costa usually broad, of 2–4 or more cells wide above midleaf, laminal papillae seldom absent or massive and lens-shape.
 8. Costa with elongate superficial ventral cells.
 9. Leaf base auriculate or weakly winged at insertion, apex often whip-like, very long-acuminate..... 18. *Didymodon leskeoides*
 9. Leaf base gradually or quickly narrowed to the insertion, not flaring, apex obtuse to acuminate.
 10. Leaves ovate to long-elliptical, apex often obtuse, costa often ending before the apex..... 21. *Didymodon tophaceus*
 10. Leaves short- to long-lanceolate, apex always acute, costa subpercurrent to short-excurrent.
 11. Plants with axillary gemmae, leaves mostly 0.9–1.1 mm long, catenulate when dry..... 17. *Didymodon michiganensis*
 11. Plants lacking gemmae in leaf axils, leaves usually 1.2–5.0 mm long, appressed-incurved to weakly spreading when dry.
 12. Leaves when moist spreading to weakly recurved, usually lying flat, costa usually distinctly widened at base.
 13. Leaves 0.8–1.7(–2.5) mm, acuminate, upper cell walls little thickened or irregularly thickened and lumens angular, trigones absent or weakly developed..... 15. *Didymodon fallax*
 13. Leaves usually 2.0(–3.5) mm, upper cell walls irregularly thickened and trigonous, trigones as large as

- the lumens or nearly so..... 20.
Didymodon giganteus
12. Leaves when moist strongly recurved and keeled, lying on their sides, costa little widened at base.
 14. Stems to 2.5 cm, leaves usually 0.8–2.0 mm long 16.
Didymodon ferrugineus
14. Stems usually more than 3 cm, leaves mostly 2.0–2.5 mm long 19. *Didymodon maximus*
8. Costa with quadrate or occasionally short-rectangular superficial ventral cells, or, if elongate, then upper laminal cells bistratose.
15. Leaves ventrally with a narrow medial channel about the width of the costa at least at leaf apex, apex mostly apiculate by one or more conical cells, costa usually percurrent, margins usually recurved, often to near the apex, laminal color reaction to KOH usually brick-red, occasionally orange.
16. Entire leaf strongly both reflexed backwards and strongly keeled when moist, papillae when present simple, stem central strand usually absent 22. *Didymodon asperifolius*
16. Entire leaf spreading to weakly reflexed backwards and weakly keeled when moist, papillae when present bifid to multiplex, stem central strand present.
17. Leaves deltoid to short-lanceolate, to 1.5 or rarely to 2.0 mm long, margins recurved or revolute to near apex, propagula sometimes present.
 18. Costa often with an apical conical cell, costa gradually narrowing distally, ventral surface nearly flat and not forming a wide pad of cells (but costa occasionally thickened and bulging ventrally), guide cells in 1 layer, leaf margins recurved to tightly revolute, gemmae often present in leaf axils
 12. *Didymodon brachyphyllus*
18. Costa usually lacking an apical conical cell, costa wider at midleaf than below, with bulging ventral surface forming a long-elliptical unistratose pad of cells, guide cells in 2(–3) layers, leaf margins loosely revolute, tubers occasional on basal rhizoids
 13. *Didymodon nevadensis*
17. Leaves short- to long-lanceolate or long-triangular, to 4.0 mm long, margins recurved near base or up to lower 2/3 of leaf, propagula rare.
 19. Leaves long-ovate to broadly lanceolate, apex blunt to broadly acute, upper marginal cells bistratose marginally, throughout or or occasionally in patches, laminal color reaction to KOH deep yellow or orange-brown to red-brown 11. *Didymodon nicholsonii*
19. Leaves triangular to narrowly lanceolate, apex narrowly acute, upper marginal cells unistratose or occasionally bistratose in patches, laminal color reaction to KOH deep red to red-brown
 10. *Didymodon vinealis*
15. Leaves ventrally very widely channeled medially or merely slightly concave across leaf, apex seldom apiculate by a conical cell, costa percurrent or excurrent as a multicellular, stout mucro, margins plane to recurved below midleaf, laminal color reaction to KOH usually negative, yellow or orange, seldom brick-red.
20. Axillary gemmae present.
 21. Propagula all multicellular, leaf apex acute 1. *Didymodon rigidulus* (var. *rigidulus*)
 21. Propagula mostly unicellular, leaf apex broadly obtuse.
 22. Costa narrow, usually 2 cells wide at midleaf, not strongly spurred 8. *Didymodon perobtusius*
22. Costa broad, 4–6 cells wide at midleaf and often strongly spurred by rows of lateral cells ending abruptly in the lamina 6.
Didymodon revolutus
20. Axillary gemmae absent.
 23. Upper lamina unistratose or occasionally bistratose in small patches.

24. Plants flagellate, leaves strongly appressed when dry, linear-lanceolate, costa long-excurrent
 1. *Didymodon rigidulus* (var. *ditrichoides*)
24. Plants not flagellate, leaves appressed-incurved to weakly twisted and weakly spreading when dry, short- to long-lanceolate, costa short- to long-excurrent.
25. Leaf base rectangular and gradually widened, costa short-excurrent, unbroken, basal leaf cells short-rectangular 1. *Didymodon rigidulus* (var. *gracilis*)
25. Leaf base ovate and often abruptly widened, costa long-excurrent, often fragile, basal leaf cells quadrate 1. *Didymodon rigidulus* (var. *icmadophilus*)
23. Upper lamina bistratose totally or just along margins.
25. Upper lamina entirely bistratose 1. *Didymodon rigidulus* (var. *subulatus*)
25. Upper lamina bistratose along margins.
26. Basal laminal cells with firm, weakly to strongly thickened walls, differentiated usually only medially.
27. Leaves long-ligulate to lanceolate 1. *D. rigidulus* (var. *rigidulus*)
27. Leaves short-ovate..... 6. *D. revolutus*
26. Basal laminal cells thin-walled and usually somewhat inflated, often bulging-rectangular, differentiated across leaf base.
28. Leaves long-lanceolate, usually smooth or weakly papillose, marginal basal cells narrowly rectangular in 2–4 rows, ventral superficial cells of costa usually elongate, stem with hyalodermis..... 5. *Didymodon umbrosus*
28. Leaves short-lanceolate, smooth to strongly papillose, marginal basal cells not or weakly differentiated from the medial, ventral superficial cells of costa quadrate, stem lacking hyalodermis or this weakly differentiated.. 4. *D. australasiae*

1. *Didymodon rigidulus* Hedw., Sp. Musc. 104. 1801.

Barbula acuta var. *bescherellei* (Sauerb. ex Jaeg. & Sauerb.) Crum; *Barbula bescherellei* Sauerb. in Jaeg.; *Barbula rigidula* (Hedw.) Mild.; *Barbula valida* (Limpr.) Möll.; *Barbula waghornei* Kindb.; *Didymodon fuscoviridis* Card.; *Didymodon mexicanus* Besch.; *Didymodon rigidulus* subsp. *validus* (Limpr.) Loeske; *Didymodon rigidulus* var. *validus* (Limpr.) R. Düll; *Tortula rigidula* (Hedw.) Lindb.; *Trichostomum rigidulum* (Hedw.) Turn.

The species s. lat., as emended by Zander (1981) is polymorphic, with several varieties distinguished by fairly good correlations of combinations of characters. Specimens of intermediate morphology that are not clearly assignable to any one variety may be identified as *D. rigidulus* s. lat. Although some authors use the presence of axillary gemmae as diagnostic of the typical variety, the other varieties, notably var. *gracilis*, may occasionally have such. These gemmae are also found in other species, especially those of the *D. vinealis* complex, which may likewise have a bistratose upper lamina, e.g., *D. vinealis* itself may have bistratose upper laminal

cells, and should be carefully distinguished. From *D. vinealis*, this species may be distinguished by the combination of long-triangular or oblong-lanceolate leaf shape, usual presence of many gemmae in the leaf axils and the commonly yellow-green color in nature (sometimes blackish green, rarely reddish below) and yellow or yellow-orange color in KOH.

KEY TO VARIETIES OF *DIDYMODON RIGIDULUS*

1. Upper lamina entirely bistratose...1b. *Didymodon rigidulus* var. *subulatus*
1. Upper lamina unistratose or bistratose only at the extreme leaf apex or on the margins.
 2. Leaves oblong-lanceolate to long-triangular; costa usually short-excurrent and blunt; apex and upper margins generally bistratose; gemmae often present
 - 1a. *Didymodon rigidulus* var. *rigidulus*
 2. Leaves lanceolate; costa percurrent to long-excurrent, usually sharp; upper margins unistratose or less commonly bistratose in patches; gemmae usually absent.
 3. Plants flagellate, leaves strongly appressed when dry, linear-lanceolate, costa long-excurrent..... 1c. *Didymodon rigidulus* var. *ditrichoides*
 3. Plants thickly leaves, leaves appressed to spreading when dry, short-lanceolate to long-lanceolate; costa percurrent to long-excurrent.
 4. Leaves short- to long-lanceolate; base evenly broadened, square or rectangular; costa percurrent to long-excurrent as a rigid subula; upper cells generally papillose, oval or rounded-quadrate; basal cells short-rectangular; gemmae occasionally present..... 1d. *Didymodon rigidulus* var. *gracilis*
 4. Leaves long-lanceolate; base abruptly broadened, ovate; costa long-excurrent as a straight or flexuose, often fragile subula; upper cells usually smooth, lumens usually angular, basal cells usually quadrate; gemmae very rare 1e. *Didymodon rigidulus* var. *icmadophilus*

1a. *Didymodon rigidulus* Hedw. var. *rigidulus*

Didymodon rigidulus var. *rigidulus* is relatively uniform in eastern North America, with slightly spreading, oblong-lanceolate to long-triangular leaves with thickened upper margins, percurrent or short-excurrent costa, thick-walled cells, gemmae usually present, and the peristome straight or only weakly twisted (var. *gracilis* and var. *icmadophilus* sometimes have long peristomes which are somewhat twisted). When the upper margins are not bistratose or are only slightly so, it can be difficult to identify, especially as it may occasionally have the costal groove of *D. vinealis*. It intergrades in the West with the other varieties, and propagula are less common. The typical variety, with distinctive oblong-lanceolate leaf shape and propagula, is rare in the Arctic.

1b. *Didymodon rigidulus* var. *subulatus* (Thér. & Bartr.) Zand., Cryptogamie, Bryol. Lichénol. 2: 395. 1981.

Didymodon mexicanus var. *subulatus* Thér. & Bartr. ex Bartr., Bryologist 29: 1. 1926.

This variety is similar to var. *icmadophilus* in leaf shape and most other characters, and intergrades occur. It may be regarded as a somewhat distinctive geographical variant.

1c. *Didymodon rigidulus* var. *ditrichoides* (Broth.) Zand., Phytologia 41: 20. 1978.

Barbula ditrichoides Broth., Sitzungsab. Akad. Wiss. Wien Math. Nat. Kl. 133: 566. 1924;
Didymodon acutus var. *ditrichoides* (Broth.) Zand.

The var. *ditrichoides* is a highly reduced, flagellate form of the var. *icmadophilus* but has a distinctive appearance. It is disjunct from montane China (Chen 1941). The olive coloration and general appearance is similar to that of *D. leskeoides* but the plant is somewhat smaller and the alar auricles are lacking.

1d. *Didymodon rigidulus* var. *gracilis* (Hook. & Grev.) Zand., Cryptogamie, Bryol. Lichénol. 2: 393. 1981.

Tortula gracilis Hook. & Grev., Edinburgh J. Sci. 1:300. 1824; *Barbula acuta* (Brid.) Brid.;
Didymodon acutus (Brid.) Saito; *Tortula acuta* Brid.

The var. *gracilis* may sometimes have gemmae and the upper lamina is sometimes bistratose in patches, but it differs from var. *rigidulus* most clearly in its short- to long-lanceolate leaves. The upper laminal cells are commonly papillose, and their lumens are oval or rounded-quadrate. Because of intergradation, some collections must be assigned to this variety only on the basis of a majority of the characters given in the key. Problems involving synonymy of heterotypic type specimens that cannot be confidently assigned to any infraspecific taxon are discussed by Zander (1981). Although leaves in this variety are short in dry habitats—in the lower range for the species, which commonly causes the stems to appear filiform—leaf length in collections from moist environments may be in the upper range.

1e. *Didymodon rigidulus* var. *icmadophilus* (C. Müll.) Zand., Cryptogamie, Bryol. Lichénol. 2: 394. 1981.

Barbula icmadophila C. Müll., Syn. Musc. 1: 614. 1849; *Barbula acuta* subsp. *icmadophila* (C. Müll.) Amann; *Barbula acuta* var. *icmadophila* (C. Müll.) Crum; *Barbula acuta* ssp. *icmadophila* (C. Müll.) Podp.; *Barbula gracilis* ssp. *icmadophila* (C. Müll.) Amann; *Barbula gracilis* var. *icmadophila* (C. Müll.) Moenk.; *Didymodon acutus* var. *icmadophilus* (C. Müll.) Zand.; *Didymodon icmadophilus* C. Müll.) Saito as “*icmadophyllus*”; *Tortula icmadophila* (C. Müll.) Lindb.

This taxon is similar to var. *gracilis* in general aspect but the leaf apices are usually hairlike, the upper laminal cells are usually smooth and their lumens usually angular. Var. *icmadophilus* is common on the North American Plains, where it may occur in association with *D. fallax*. The var. *icmadophilus* is dark green, sometimes with a blue-black cast, and has boat-shaped, elongate, erect leaves that are only slightly incurved when dry, laminal cells smooth and costa excurrent and often flexuose. *Didymodon fallax* has light green to reddish green color and triangular leaves that are often incurved or even catenulate when dry, costa percurrent and leaves papillose.

2. *Didymodon anserinocapitatus* (X.-j. Li) Zand., Bull. Buffalo Soc. Nat. Sci. 32: 162. 1993.

Barbula anserinocapitata X.-j. Li, Acta Bot. Yunnan. 3: 103, 1981.

This rare Asian species is known from only two sites in the New World: Colorado (Freemont Co., 4.5 km up lower portion of Phantom Canyon, 1500–2200 m elev., red-sandstone cliff, Weber, Herman & Feddema, 1 June 1971, herb. no. B-37528, COLO), and New Mexico (San Miguel Co., Pecos, along Pecos River, 2100 m elev., Richards & Drouet 456, 21 Oct. 1939, DUKE). It differs from *D. johanssenii* mainly by the smaller upper laminal cells and the double layer of guide cells, with the appearance of a robust *D. rigidulus* var. *icmadophilus*, which differs, however, by leaf apices never swollen though sometimes fragile. Details were reported by Zander and Weber (1997).

3. *Didymodon johanssenii* (Williams) Crum, Canad. Field-Nat. 83: 157. 1969.

Barbula johanssenii Williams, Rep. Canad. Arctic Exped. 1913–18, Bot. 4E: 4. 1921.

Distinctive characters of this Arctic species are the striate peristome teeth, deciduous, clavate leaf apex and large, trigonous laminal cells. Most collections of *D. johanssenii* have truncate leaves, with the propaguliform apex fallen in all but the most immature leaves; the leaves are oblong-lanceolate. Some specimens (e.g., Northwest Territories, Scotter 22404, MICH) of this species, however, approach *D. rigidulus* var. *icmadophilus* in the green color, ovate leaf base, not much widened or tapering and apparently non-deciduous leaf apices. These collections can be rightly placed by the presence of claviform apices in at least some leaves (especially those near an inflorescence) and the large upper laminal cells, which often have trigones. *Didymodon nigrescens* has fragile, clavate tips to its perichaetial leaves, but the crenulate upper leaf margins and very thin costa will distinguish it.

4. *Didymodon australasiae* (Hook. & Grev.) Zand., Phytologia 41: 21. 1978.

Tortula australasiae Hook. & Grev., Edinburgh J. Sci. 1: 301. 1824; *Didymodon diaphanobasis* Card.; *Didymodon diaphanobasis* var. *angustifolius* Thér. in Bartr.; *Didymodon torquescens* Card.; *Husnotiella torquescens* (Card.) Bartr.; *Trichostomopsis australasiae* (Hook & Grev.) Robins.; *Trichostomopsis brevifolia* Bartr.; *Trichostomopsis crispifolia* Card.; *Trichostomopsis diaphanobasis* (Card.) Grout; *Trichostomopsis fayae* Grout

In *Didymodon*, hydroids are found only in the costae of *D. australasiae*, *D. umbrosus*, *D. revolutus* and *D. vinealis*. The ventral stereid band usually absent in well developed specimens of the first three species, and is often absent in the fourth. Intergrades exist between *D. australasiae* and *D. umbrosus*, but the extreme forms are common and quite distinctive.

5. *Didymodon umbrosus* (C. Müll.) Zand., Phytologia 41: 22. 1978.

Barbula umbrosa C. Müll., Linnaea 42: 340. 1879; *Didymodon australasiae* var. *umbrosus* (C. Müll.) Zand.; *Trichostomopsis crispifolia* Card.; *Trichostomopsis umbrosa* (C. Müll.) Robins.

This species is one of a number of mundivagant taxa the distribution of which is associated with

human activities (e.g., Eckel 1986). The transversely slit basal cells are distinctive in many specimens though also found in taxa of the Dicranaceae (Zander & Cleef 1982).

6. *Didymodon revolutus* (Card.) Williams, Bryologist 16: 25. 1922.

Husnotiella revoluta Card., Rev. Bryol. 36:71. 1909; *Husnotiella revoluta* var. *palmeri* (Card.) Thér.

Distinctive characters in combination are: arid habitat, ovate leaves with often revolute margins, subpercurrent, strongly spurred costa (with one or more lateral costal cells wending into the lamina), one layer of guide cells, and a rudimentary or absent peristome. Like *D. perobtusus* and *Bryoerythrophyllum calcareum* (Thér.) Zand., *D. revolutus* has unicellular gemmae occasionally present in the leaf axils.

7. *Didymodon nigrescens* (Mitt.) Saito, J. Hattori Bot. Lab. 39: 510. 1975.

Barbula nigrescens Mitt., J. Linn. Soc. Bot. Suppl. 1: 36. 1859; *Barbula rufofusca* Lawt. & Herm.

The specimens cited from the Firth River Basin by Steere (1978), det. R. Zander, are actually *D. subandreaeoides*. The distinguishing characters of *D. nigrescens* are the blackish coloration when dry (red in KOH), thin costa, and upper laminal margins minutely crenulate by the small, bulging marginal cells. This and the following two species appear to be closely related.

Didymodon asperifolius is similar but may be distinguished by its longer leaves, straight or reflexed to strongly recurved when wet, upper margins recurved, upper laminal cells larger, 10–13 mm wide, epapillose or papillae simple, and costa usually comparatively wide.

8. *Didymodon perobtusus* Broth., Rev. Bryol. n. ser. 2: 1. 1929.

Barbula perobtusula (Broth.) Chen.

Didymodon perobtusus has several characters in common with *D. revolutus* (Card.) Williams of the southwestern U.S.A. and Mexico, including leaf and laminal papillae shape and unicellular gemmae borne in dense axillary clusters; however, *D. revolutus* differs by the strongly recurved to revolute margins, leaf cells with thin, light yellow walls, and gemmiferous plants uncommon. Both North American collections seen were from stations in which *D. subandreaeoides* is also present, growing in separate or occasionally confluent cushions. The taxonomic position of *D. perobtusus* is not clear. It is placed near *D. subandreaeoides* because of dark, reddish color, and similarity of areolation and laminal papillae. It may, however, turn out to be related to *D. tophaceus*, with which it has a certain resemblance.

9. *Didymodon subandreaeoides* (Kindb.) Zand., Phytologia 41: 23. 1978.

Barbula subandreaeoides Kindb., Rev. Bryol. 32: 36. 1909; *Barbula andreaeoides* Kindb.

The distribution of *D. subandreaeoides* is through inland mountain ranges from the North Slope of Alaska south along the Cordillera into Colorado. It is commonly associated with *Molendoa sendtneriana* (BSG) Limpr. with which it is often mixed in collections, and which apparently has a similar distribution in northwestern North America. The fragile, cochleariform-leaved branchlets may possibly figure in asexual reproduction. *Andreaea rothii* Web. & Mohr lacking sporophytes may be confused with *D. subandreaeoides*, but may be distinguished by the former's autoicous inflorescence, its ecostate, oblong perichaetial leaves, leaves monomorphic, cauline leaves plane, cells with bulging but epapillose bright orange walls, bistratose along the upper margins, middle lamellae often evident between basal cells, and costa not sharply distinguished from laminal cells above midleaf.

10. *Didymodon vinealis* (Brid.) Zand., Phytologia 41: 25. 1978.

Barbula vinealis Brid., Bryol. Univ. 1: 830. 1827; *Barbula bakeri* Card. & Thér.; *Barbula circinnulata* C. Müll. & Kindb.; *Barbula cylindrica* (Tayl.) Schimp. in Boul.; *Barbula fallax* var. *vinealis* (Brid.) Hüb.; *Barbula flexifolia* Hampe; *Barbula horridifolia* C. Müll. & Kindb.; *Barbula laterita* Kindb.; *Barbula pseudorigidula* C. Müll. & Kindb.; *Barbula robustifolia* C. Müll. & Kindb.; *Barbula semitorta* Sull.; *Barbula subcylindrica* Broth.; *Barbula subfallax* C. Müll.; *Barbula subgracilis* C. Müll. & Kindb. in Macoun (syn. nov.); *Barbula tortellifolia* C. Müll. & Kindb.; *Barbula treleasei* Card. & Thér.; *Barbula vinealis* subsp. *cylindrica* (Tayl.) Podp.; *Barbula vinealis* subsp. *cylindrica* (Tayl.) Podp.; *Barbula vinealis* var. *flaccida* BSG; *Barbula vinealis* var. *flaccida* BSG; *Barbula virescens* Lesq.; *Didymodon vinealis* var. *flaccidus* (BSG) Zand.; *Didymodon vinealis* var. *flaccidus* (BSG) Zand.

This species is often difficult to distinguish from sterile forms of *D. rigidulus*, but the red color in nature, the often strongly papillose laminal cells, and the distinct groove down the ventral surface of the leaf along the costa are characteristic features. Some but not all specimens may be quickly assigned to this taxon by the unique deep slit floored by elongate cells on the ventral surface of the costal apex (the ventral epidermis being absent), which is visible as a white window dorsally. *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, though equally bright red in KOH solution, is immediately distinguished by the clear, enlarged basal cells. Like *Bellibarbula recurva* (Griff.) Zand., small forms of *D. vinealis* may have quadrate or very short-rectangular basal cells and a sinuose costa, but the former has thick-walled basal cells and the costa twists laterally (not vertically as in the concave upper portion of the leaf of *D. vinealis*), and the ventral cells of the costa are commonly elongate, 2:1 or more. Two specimens of the new synonym *D. subgracilis*: Canadian Musci, B.C, Yale, on rocks, Coll. Macoun, May 18, 1889, isotype, CANM, and "Canadian Mosses, Collected by John Macoun. Determined by Dr. N. C. Kindberg. 58a. *Barbula subgracilis* Kindb. On rocks, [Casartne?] Bay, [V.I.?], June 24, 1908," CANM, are both *Didymodon vinealis* with typical long, twisted peristomes.

KEY TO VARIETIES OF *DIDYMODON VINEALIS*

1. Peristome present, well developed, cells of operculum twisted 10a. *Didymodon vinealis* var. *vinealis*
1. Peristome absent, cells of operculum straight or nearly so 10b. *Didymodon vinealis* var. *rubiginosus*

10a. *Didymodon vinealis* var. *vinealis*

Some collections have elongate, very fragile leaf apices that are sometimes bistratose, but are not clavate as in *D. anserinocapitatus*. The var. *flaccidus* was synonymized by Sollman (1983), but may be distinguished if needed by the leaves long, often 2.5 mm or longer, crisped when dry, and the upper margins plane. The peristome commonly falls with the operculum in many specimens seen, and may appear to be absent, but the operculum has twisted cells and is thin-walled.

10b. *Didymodon vinealis* var. *rubiginosus* (Mitt.) Zand., *Cryptogamie Bryol. Lichénol.* 2: 379–422. 1981.

Barbula rubiginosa Mitt., *J. Linn. Soc. Bot.* 8: 27. 1864; *Didymodon occidentalis* Zand.

Although the gametophyte of var. *rubiginosus* varies little morphologically, having short-lanceolate to triangular leaves, it is well within the range of variation of the typical variety. It has been reputed (e.g., Zander 1981) to differ in a very narrow upper lamina that is often fragile or notched, or by large upper laminal cells, or by quadrangle basal cells, but these characters are insufficient to distinguish sterile specimens. Although the eperistomate sporophyte is required for accurate identification, var. *rubiginosus* fruits abundantly. The spores are slightly smaller, 8–11 mm, than those of the typical variety. Forms of var. *vinealis* with weakly twisted opercular cells and weak, very fragile peristomes (e.g., California, Flowers 6561, COLO) may be taken as intermediates.

11. *Didymodon nicholsonii* Culm., *Rev. Bryol.* 34: 100. 1907.

Barbula nicholsonii Culm.; *Barbula rigidula* ssp. *nicholsonii* (Culm.) Dix.; *Didymodon rigidulus* var. *nicholsonii* (Culm.) Roth; *Didymodon luridus* ssp. *nicholsonii* (Culm.) Loeske; *Didymodon luridus* var. *nicholsonii* (Culm.) Loeske; *Didymodon vinealis* var. *nicholsonii* (Culm.) Zand.

This species intergrades somewhat with *D. vinealis* but the ovate-lanceolate leaf with a rather broad apex usually is distinctive, as is the tendency toward a partially or completely bistratose upper lamina. The western species *Grimmia cinclidontea* C. Müll. is disconcertingly similar and grows in the same wet habitats, but is autoicous, has smooth leaf cells and a homogeneous costal section.

12. *Didymodon brachyphyllus* (Sull.) Zand., *Phytologia* 41: 24. 1978.

Barbula brachyphylla Sull. in Whipple, *Rept. Pacific R. R. Surv., Bot.* 4: 186. 1856; *Barbula olivacea* (Mitt.) Besch.; *Didymodon reedii* Robins.; *Didymodon vinealis* var. *brachyphyllus* (Sull.) Zand.; *Tortula olivacea* Mitt.

One robust collection of *D. brachyphyllus* (New Mexico: Bartram 99, US), in its stout costa matches European material of *D. cordatus* Jur., while two other collections (Colorado: Hermann 23431, MICH, and the type of *D. reedii*) are similar to the weaker nerved but otherwise identical Asian *D. tectorum* (C. Müll.) Saito. Given the variation seen, all American collections are referred to *D. brachyphyllus*, which is conveniently the earlier epithet. When reduced in size, this

largely aridland species has a more ovate leaf shape, margins less strongly recurved, and costa ends before the apex, which may terminate in a small conical cell or apiculus.

Didymodon luridus Spreng. (see Zander 1978a) does not occur in the range of the flora, though reported by many authors (often as *D. trifarius*, see discussion of Zander 1981). It differs in the triangular leaves and the smooth, more homogeneous and tiny upper laminal cells, 6–9 mm. American collections identified as this are commonly actually *D. brachyphyllus*, *D. nicholsonii*, *D. tophaceus* or *D. vinealis*. Small forms of *D. nicholsonii* have the leaf shape of *D. brachyphyllus* but the lamina is bistratose. Sterile *Grimmia* Hedw. species may be confused with this species, but a small hyaline apex is commonly found on at least some leaves of those. Small forms of *D. vinealis* may be confused with *D. brachyphyllus* but the latter never has lanceolate leaves, and its perichaetial leaves are also short and rather deltoid.

13. *Didymodon nevadensis* Zand. in Zand., Stark & Marrs-Smith, Bryologist 98: 590.

Didymodon nevadensis is similar to *Pseudocrossidium crinitum* (Schultz) Zand. and has much the same appearance under the dissecting microscope. It differs by the somewhat cucullate, acute leaf apex, the costa percurrent (not excurrent as a short awn), smaller upper laminal cells (13–15 mm for *P. crinitum*), and occasional presence of tubers on the basal rhizoids. Like *P. crinitum*, *D. nevadensis* in KOH has blotches of red coloration at midleaf and above, and this irregular red coloration distinguishes it from *Bryoerythrophyllum* Chen species, which are evenly colored red. This species has two layers of guide cells (occasionally to three near the leaf base), while *P. crinitum* is nearly constant in a single layer of guide cells. Unlike *Bryoerythrophyllum columbianum* (Herm. & Lawt.) Zand., which has somewhat the same appearance and rather broad upper costa, the leaf apices of *D. nevadensis* are not fragile and asexual reproduction is by (1–)2(–4)-celled spherical propagula born on rhizoids in the lower leaf axils. *Didymodon australasiae* is similar to *B. nevadensis* but its leaves differ in the thin-walled basal cells and bistratose upper margins. *Tortula atrovirens* (Sm.) Lindb. is very similar in its ventral costal pad but differs in its short oblong leaf shape, broadly channeled leaf apex and strong, rounded stereid band; Flowers (1973, pl. 31) treated and illustrated both species under the name *Desmatodon convolutus* (Brid.) Grout.

14. *Didymodon sinuosus* (Mitt.) Delogn., Bull. Soc. R. Bot. Belg. 12: 423. 1873.

Tortula sinuosa Mitt., J. Bot. 5: 327. 1867; *Barbula sinuosa* (Mitt.) Grav.

On bark of living or fallen trees; low elevations; known from only two stations in southern Alaska.

This species was originally reported (Zander 1978b) from specimens on bark of living or fallen trees at low elevations in southern Alaska. It differs from European material by the smaller leaves, elongate ventral costal cells and deciduous (as opposed to merely fragile) leaf apex, and may prove to be a distinct species. Small, reddish plants of *Trichostomum tenuirostre* (Hook. & Tayl.) Lindb. may occasionally have similar sequentially constricted, fragile leaves, but the leaf cells are papillose and the plane leaf margins are crenulate by projecting walls.

15. *Didymodon fallax* (Hedw.) Zand., Phytologia 41: 28. 1978.

Barbula fallax Hedw., Sp. Musc. 120. 1801.

The elongate cells on the ventral surface of the costa and the usually rounded lumens of the upper laminal cells are characteristic. *Hymenostylium recurvirostrum* (Hedw.) Dix. is similar in these respects and could be mistaken for *D. fallax* when sterile, but that species lacks a stem central strand and the median laminal cells are usually larger than those of the margin. *Ditrichum flexicaule* (Schwaegr.) Hampe may be mistaken for this species but has rather strongly serrulate upper margins, no laminal papillae, and is always clear yellow in KOH, never with an orangish cast. *Didymodon asperifolius* is similar in general morphology but has quadrate or short-rectangular ventral costal cells, and is not hygric in habitat. *Didymodon fallax* intergrades to some extent with *D. ferrugineus* and *D. maximus*. Thick laminal cell walls are correlated with lack of papillae in these species. Robust collections from Newfoundland with long (to 2.5 mm) leaves and basally very broad costae (to 150 mm) have much the appearance of the European *D. spadiceus* (Mitt.) Limpr., but differ by the long (to 800 mm) twisted peristome and margins recurved commonly to near the apex. The leaves of *D. fallax*, being somewhat keeled though not strongly recurved, have the grooved costa of *D. vinealis* but plants may be placed correctly by the elongate ventral costal cells.

16. *Didymodon ferrugineus* (Schimp. ex Besch.) Hill, J. Bryol. 11: 599. 1981 (1982).

Barbula ferruginea Schimp. ex Besch., Mem. Soc. Sci. Nat. Cherbourg 16: 181. 1872; *Barbula fallax* var. *recurvifolia* (Wils.) Husn.; *Barbula reflexa* (Brid.) Brid.; *Didymodon fallax* var. *reflexus* (Brid.) Zand.; *Didymodon rigidicaulis* (C. Müll.) Saito; *Tortula recurvifolia* (Schimp.) Aust., *hom. illeg.*; *Triquetrella ferruginea* (Besch.) Thér.

The sporophyte is rare and similar to, but often smaller than, that of *D. fallax*. This species is easily mistaken for *Triquetrella californica* (Lesq.) Grout, which, however, is quickly distinguished by its triangular stem section, upper leaf margins sharply crenulate by projecting papillae (but not by projecting cell walls as in *D. nigrescens*), and upper medial laminal papillae tall, branching from the base and centered over each lumen. *Didymodon ferrugineus* intergrades with *D. fallax* to some extent but is usually larger, with broader, ovate-lanceolate leaves that are commonly strongly reflexed, and the papillae may be large and strongly evident. The peristome is very fragile and often appears to be missing.

17. *Didymodon michiganensis* (Steere) Saito, J. Hattori Bot. Lab. 39: 517. 1975.

Barbula michiganensis Steere in Grout, Moss Fl. N. Am. 1: 180. 1938; *Barbula catentulata* Dix.; *Barbula catenulata* Dix.

The significant characters are the small size of the leaves, which are catenulate when dry, and the presence of propagula. The laminal cells are arranged in distinct rows but this trait cannot distinguish this species from many congeners.

18. *Didymodon leskeoides* Saito, J. Hattori Bot. Lab. 39: 508. 1975.

Differs from *D. rigidulus* var. *ditrichoides* by the distinctive short and broadly decurrent alar leaf margins (the former has long and narrowly decurrent margins). It is easily distinguished from *Hymenostylium recurvirostrum*, with which it commonly occurs, by its usually olive or orange-brown tinge, as opposed to the green to yellow color of the former. One collection, Canada, N.W.T., Scotter 22277, BUF, has unusually long stems, to 6 cm.

19. *Didymodon maximus* (Syed & Crundw.) Hill, J. Bryol. 11: 599. 1981 [1982].

Barbula maxima Syed & Crundw., J. Bryol. 7: 527. 1973 [1974] nom. nov. for *Barbula reflexa* var. *robusta* Braithw.

This western Arctic taxon is rare and apparently disjunctive to the western British Isles. Is it essentially a very large version of *D. ferrugineus*.

20. *Didymodon giganteus* (Funck) Jur., Laubm. Fl. Oest. Ungarn. 102. 1882.

Geheebia gigantea (Funck) Boul., Musc. France 395. 1884.

Only one specimen, collected in Alaska, has been seen with the combination of characters implied by the above key, being identical with European specimens: Alaska. North slope of DeLong Mts., headwaters of Utukok R., Driftwood Camp, 68° 53'N, 161° 10'W, 1951, Steere 16830 (CANM). Other collections seen that had been previously identified as this are either *D. ferrugineus* or *D. maximus*. Also reported from Europe, the Himalayas of India, China, arctic East Asia, and Japan.

21. *Didymodon tophaceus* (Brid.) Lisa, Elenco Muschi Torino 31. 1837.

Trichostomum tophaceum Brid., Mant. Musc. 84. 1819; *Barbula pringlei* (Card.) Hilp.; *Barbula tophacea* (Brid.) Mitt.; *Dactylhymenium pringlei* Card.; *Desmatodon hendersonii* (Ren. & Card.) Williams in Millsp. & Nutt.; *Husnotiella pringlei* (Card.) Grout.

Although long leaf decurrencies are often considered characteristic of this species, they are not present in a large percentage of specimens. Being rather variable, this species is sometimes difficult to distinguish from *D. fallax*, a species that is seldom found in very hygric habitats. *Didymodon tophaceus* is absent from the Arctic. Like its fellow calciphilic hygrophiles *Hymenostylium recurvirostrum* and *Eucladium verticillatum* (Brid.) BSG, *D. tophaceus* is often encrusted with calcium carbonate; the broad, obtuse leaves and often red costa help distinguish the last. *Barbula ehrenbergii* (Lor.) Fleisch. is quite like *D. tophaceus* but can be immediately distinguished by its large size, 20–30 even rows of thin-walled, often papillose upper laminal cells with quadrate to short-rectangular lumens, and peristome when present long and twisted, while *D. tophaceus* has 10–15 often irregular rows of usually thick-walled, usually smooth upper laminal cells with usually oval lumens, and a short peristome or this occasionally absent.

22. *Didymodon asperifolius* (Mitt.) Crum, Steere & Anders., Bryologist 67: 163. 1964.

Barbula asperifolia Mitt., J. Linn. Soc. London Bot. 1(Supp71.): 34. 1859; *Barbula rufa* (Lor.) Jur., *hom. illeg.*; *Didymodon rufus* Lor.

The ventral surface of the costa may have quadrate or short-rectangular cells. The KOH reaction, as well as the natural color of the lamina, is sometimes light orange, but usually a clear red. This species is quite similar to *D. ferrugineus* but the ventral costal cells are quadrate to short-rectangular.

EVOLUTIONARY EVALUATION

A phyletic study (combining cladistics, phenetics and patristics—see Stuessy 1990: 135) was undertaken. This can demonstrate convergence in combining a hypothetical evolutionary tree with a phenetic distance ordination. A cladistic analysis was done with the data set (Table 1) of 23 morphological characters (Table 2) with *Barbula unguiculata* Hedw. as outgroup. *Barbula* Hedw. is a very closely related genus with a large number of shared morphological characters (Zander 1993); other related genera lack as many comparable characters, possibly through reduction. The parsimony software Hennig86 (Farris 1988) was used to generate the most synapomorphous tree or trees using the commands “mh*;bb*” for heuristic branch-swapping. The data was treated as non-additive (non-ordered) and equal (no) weighting was used. Multiple runs using randomized data sequences found no multiple islands (Maddison, D. 1991) of most-synapomorphous trees. Character state changes were mapped to the strict consensus tree (command “nelson”). The work was exactly duplicated with PAUP (Swofford 1985) using the settings “mulpars,” and likewise no weights or additivity. The relative robustness of the subclades was evaluated by Bremer support (“decay”) analysis in PAUP with the command “bbsave”, where multiple trees were saved with synapomorphy relaxed one, two, three and four steps with note of which clades collapsed at each analysis. This procedure indicates “the number of steps that must be added before each clade present in the minimum length trees is no longer unequivocally supported” (Donoghue et al. 1992).

The study found three equally most-synapomorphous trees, with ambiguity only over which taxon was more basal, *D. nicholsonii* or *D. sinuosus*. Characters were mapped on the consensus tree (Fig. 1), which may be taken as the estimated phylogenetic tree since the polytomy may be seen as modeling evolutionary events that do not greatly affect topology. Character state changes are shown for all branches. Unique and homoplastic synapomorphies are indicated by “u” and “h”, respectively. Salient character states unique to single terminal taxa and also not included in the data set are appended to the listed autapomorphies.

In the phylogenetic tree (Fig. 1) branches ending in *D. perobtusus* and *D. subandreaoides*, and in *D. australasiae* and *D. umbrosus*, had strong Bremer support values (Bremer 1988; Davis 1995), each only collapsing at 4 extra steps, while the remaining branches collapse with one extra step each. The tree is divided into two large branches, with one branch comprised of sect. Fallaces with the *D. nigrescens* group terminal to that lineage, and the species of the other three

previously recognized sections (see above) variously combined in the other branch. The *D. australasiae* group and the *D. nigrescens* group, the latter possibly related to *Didymodon* sect. *Rufidulus* (Chen) Zand. of Asia, may well prove misplaced due to long-branch attraction or are different at the genus level or both, and more extensive study including species of other sections and genera should address these possibilities.

To the extent that a phylogenetic tree of nested sister groups (Fig. 1) actually models ancestor-descendent relationships, it may be termed an evolutionary tree (as in Fig. 5, cf. discussion of Lamboy 1996). Information from interior branches, especially of the more deep ones, has been used to analyze ancestral areas (e.g. Bremer 1995), though Goldman (1990) felt that nodal values at least in maximum likelihood analysis are only “particular realizations of parts of the [analytic] process,” and are unpredictable because in the absence of a model known to be correct they are not inferentially consistent, that is, “it is not possible to increase indefinitely the number of observations (data) pertinent to each.” Although some interior branches of Fig. 1 are based on only one or two homoplastic synapomorphies, there is no reason that the nodes do not model the evolutionarily significant traits of hypothetical, mostly extinct, shared ancestral species. This conclusion is supported in that most extant taxa of *Didymodon* differ little from each other—by only one or two autapomorphies. This implies no large numbers of unmodeled intervening and confounding evolutionary events in the past. According to Mayr (1982: 234), “Whenever a clade (a phyletic lineage) has entered a new adaptive zone, resulting in a drastic reorganization, the transformation may have to be given greater taxonomic weight than the proximity of joint ancestry. The particular importance of the autapomorphies is that they reflect the occupation of new niches and new adaptive zones, which often are of far greater biological significance than the cladistic synapomorphies.” The autapomorphies of ancestors become the synapomorphies of future taxa, and species evolve, not characters (except in an analytic sense). One might then expect uniformitarianism to be a useful guide to modeling ancestor-descendent relationships. The most dubious “synospecies” are the immediate ancestral node of *D. giganteus* and the next most distal node, each based on a single homoplastic, variable (intraspecifically in the terminal taxa of the lineage) shared character state (numbers 10 and 2, respectively). These nodes would not model acceptable ancestors if their patristically close terminal taxa each had more autapomorphies. But, even if these two nodes were collapsed into a hard polytomy (*D. giganteus*, *D. ferrugineus* and *D. maximus* do intergrade to some extent), no great violence would be done to the evolutionary tree of Fig. 5.

Four terminal taxa showed no autapomorphies: *D. australasiae*, *D. fallax*, *D. ferrugineus* and *D. johansenii*. Two other species, *D. rigidulus* and *D. vinealis*, include their respective nearest ancestral node in autapomorphic character variation. These six taxa are proposed as surviving ancestors and are rendered as intercalated, not terminal, in the simplified evolutionary tree that is overlain in the phylogram (Fig. 5). According to Grant (1985) “living fossils” show slow evolution. This is correlated with high adaptation to stable environments, as opposed to such habitats as “impermanent lakes, high mountains, volcanic deposits, active tundra, etc.” The above six species are commonly sexual and are widespread globally. One, *D. johansenii*, is characteristic of northern montane and arctic localities, but the species is apparently quite mobile: collections show little biomass devoted to morphology associated with vegetative growth (perhaps allowed by copious sunlight during long northern days) and much biomass is

given to both sexual and asexual reproduction in the same turfs. Sister group species to the first four of the six taxa either occur rarely and apparently reproduce asexually (*D. anserinocapitatus*, *D. giganteus* and *D. maximus*), or are probably recently widely distributed through inadvertent human agency (*D. umbrosus*).

A cluster dendrogram (Fig. 2) of overall phenetic relationships was produced by a standardized UPGMA analysis (unweighted pair group method using arithmetic averaging) using the software package MVSP (Kovach 1995). The characters and data set are given in Tables 1 and 2. This analysis is sensitive to the distances among the data and leads to grouping closest pairs (Hair et al. 1987). The data set (Table 2) was the same as that used for the cladistic analysis above (thus restricting the phenetic analysis to phylogenetically informative characters) but the entries labeled in that study as “variable” were performed given an exact character state, in this case the commonest state in very well developed “typical” plants. Two species groups (*D. australasiae*, *D. revolutus* and *D. umbrosus*, and *D. nigrescens*, *D. perobtusus* and *D. subandreaeoides*) that were clearly isolated as terminal to phylogenetic lineages (Fig. 1) are also isolated in the cluster analysis with the exception of *D. revolutus*. *Didymodon asperifolius* was shown in the cluster analysis to be overall phenetically similar to *D. ferrugineus* and *D. maximus*, this apparently through convergence: note the large patristic distance (sum of steps in character state changes across intervening nodes) of the first species from the last two in Fig. 1.

A standardized principal component analysis (PCA, Kovach 1995; Sneath & Sokol 1973: 245) was done with the same data set to show similarities in two-dimensional ordination (Fig. 4). There was no variation in results with different data orderings. Other ordination methods, with different optimizations, have also been used in study of patterns in homoplasy, such as detrended correspondence analysis and hybrid multidimensional scaling (Faith 1989; Faith 1997). Axes 1 and 3 were chosen to avoid the distortion of the unusually high score for propagula type on axis 2. Axes 1 and 3 reflect 45 percent of the variation, unrotated to preserve the usual multiple-variable representation of axis 1. Figure 5 is an overlay of the PCA and the evolutionary tree (the terminal taxa are represented by single capital letters, see Table 2). Plots of axes 1 and 2, and of 2 and 3, supported the phylogrammatic analysis below, though individually they were somewhat different.

There were no gaps separating the clusters in the PCA ordination (Fig. 4), confirming that *Didymodon* is, after all, a difficult genus taxonomically. The PCA shows that the same data used for the cluster analysis of distance, giving Fig. 2, a neat dendrogram, does not necessarily produce well-isolated clusters in the ordination, based on a correlation matrix. On the other hand, species of the two main subclades are well distinguished in the PCA. Both the phenetic and cladistic analyses demonstrate a close relationship between *D. ridigulus* and *D. vinealis*, previously placed in different sections. The sect. *Didymodon* and sect. *Fallaces* subclades (Fig. 1 and 5) are fairly well distinguished phenetically in the PCA ordination (Fig. 4) as clusters though there is some interpenetration.

CONVERGENCE

The phylogram (Fig. 5) shows *D. nigrescens* being strongly morphologically convergent towards

D. brachyphyllus of sect. *Didymodon*, and *D. leskeoides* convergent towards *D. rigidulus* and *D. vinealis* of that same section. Although *D. sinuosus* is phenetically close to *D. anserinocapitatus* and *D. johansenii*, the phylogenetic tree (Fig. 1) shows it to be patristically rather distant. In the phylogram, *Didymodon revolutus* is seen to tend morphologically towards the somewhat patristically distant but cladistically related *D. nevadensis* in the same lineage, with overall convergence supported by the cluster dendrogram.

Although in different major subclades and thus different taxonomic sections, *D. tophaceus* and *D. asperifolius* converge morphologically but they are also patristically somewhat near each other at the base of the two subclades. Given certain arguments made below, these two are only doubtfully convergent and may just as well be near each other on the same lineage. The phylogenetically widely divergent species *D. giganteus* and *D. nicholsonii* are shown to be morphologically convergent in the phylogram, and are very closely associated in overall phenetic traits in the cluster dendrogram (Fig. 2). Particular previously suggested (Zander 1978a) parallel trends in speciation in *Didymodon* were supported in this study to some extent where the single shared traits were also reflected in convergence in the phylogram (Fig. 5). For instance, rather distantly related species with propagula present in leaf axils (*D. rigidulus*, *D. brachyphyllus*, and *D. michiganensis*) showed convergence in the phylogram, and two of three species with long-lanceolate leaves (*D. giganteus*, *D. nicholsonii*, *D. vinealis* formae) were also convergent but the other (*D. umbrosus*) was rather isolated in the PCA. Other pairs and trios of unrelated species that shared single salient traits showed less convergence.

Cladistics is here accepted as an adequate basis for general classification, assuming sufficient resolution of the phylogenetic tree, but the major thrust of this evolutionary study is to see if additional relationships may be hypothesized through a phenetic analysis presenting the homoplastic convergence in a cladogram as an evolutionary model. This is acceptable as theory even if maximum parsimony is simply another clustering method, a misnomer when taken to its mathematical limit, and the most likely tree is doubtfully probabilistically the true tree, see discussion below. The conjectures derived from Fig. 5 are logical assuming the methods provide best models of phenetic and phylogenetic relationships assuming maximum synapomorphy. Swofford and W. Maddison (1992) discuss methods using the tree of maximum synapomorphy alone in analysis of paralellisms due to habitat shifts.

RECOVERY OF TRUE TREES: PHENETICS VS. CLADISTICS

It is evident that much information about phylogenetic relationships (e.g. that subject to evolutionary selection or overwritten through saturation) is lost and we are left only with the ability to do approximations. Given the carefully selected small number of characters used in this study (although the consistency index at 0.44 is low), however, it might be expected that the *difference* between the standard phenetic (Fig. 2) and phylogenetic (Fig. 1) analyses reflects convergence (or divergence) between the taxonomic elements belonging to two clades. This remains problematic.

Using artificial phylogenies based on computer-generated data sets, Lamboy (1994, 1996) found that for sets with consistency indexes in the range commonly reported in the literature, maximum

parsimony techniques retrieved the true tree only 0.7–27.8% of the time, while overall, for 85.2% of the simulations accurate retrieval was less than 75%, and for the remainder was much less accurate.

With differently generated artificial phylogenies, Heijerman (1997) demonstrated that certain clustering methods are better at retrieving true trees than parsimony methods of phylogenetic estimation when homoplasy is relatively high. Neither clustering nor parsimony, however, achieved better than 74% similarity with the true tree. In another study using artificial phylogenies (Heijerman 1990), parsimony methods were found to be more accurate than clustering methods when the consistency index is above 0.8, and are fully accurate when $CI = 1.0$ (no homoplasy) though this is not a commendation since the absence of homoplasy must be known beforehand. Usually, however, parsimony methods found shorter trees than true trees.

Moss species usually differ by few, apparently simple, commonly reversed and re-elaborated character states. One might wonder if the differences between the PCA and the parsimony derived tree—that are here attributed to convergence—might be due to artifacts generated by two different and, given the low consistency index, inadequate methods of analyzing complex evolutionary relationships. One could, of course, simply eliminate from the cladistic analysis those states that contribute to homoplasy (see discussion of this by Philippe et al. 1996); but, as Micevich (1982) indicated, convergent characters contributing to homoplasy provide important evolutionary information. As Doyle (1992) pointed out, some characters (e.g. inverted-repeat deletions) may be locally informative and globally have occurred in more than one plant group. With relatively small numbers of character states or relatively large numbers of terminal taxa, a low consistency index is inevitable, and poor retrieval or poor resolution of the true tree must be expected in phenetic and cladistic analyses at least when working at the species level.

In any case, a cluster dendrogram is given in Fig. 3, which reflects the results of one of methods Heijerman found most effective in retrieving at least an approximation of artificial phylogenies with significant homoplasy: UPGMA using unstandardized Pearson product moment correlation coefficient, a similarity measure for linear correlations between all character values of O.T.U.'s, but which is insensitive to variation in character magnitudes (Abbott et al. 1985), and should be robust to outliers. It is much the same as Fig. 2, but reflects the cladogram better in positioning together *D. anserinocapitatus*, *D. johansenii* and *D. sinuosus*, and in a better integration of *D. australasiae* and *D. umbrosus*. *Didymodon michiganensis* is, however, oddly placed in Fig. 3, and *D. revolutus* continues to be removed (as in Fig. 2) from association with *D. australasiae* and *D. umbrosus*. If Heijerman's conclusions are applicable to this data set, then Fig. 3 would be a better reflection of the phylogeny than the estimation procedure using Hennig86 and PAUP (Fig. 1), given the low consistency index.

Because the differences between phylogenetic and phenetic analyses cannot be well evaluated by these techniques when the consistency index is less than about 0.8 according to Heijerman (1990), consilience with other data is needed to decide whether the differences logically attributable to convergence (or divergence) are meaningful.

CONVERGENCE AND HABITAT

One might assume that species that converge morphologically would tend to occupy the same habitats. This is at least true for a demonstrated phenocopy phenomena between *Molendoa sendtneriana* (BSG) Limpr. and *Gymnostomum aeruginosum* Sm. in Colorado (Zander 1977). However, none of the five pairs of apparently converging species in this study are known to occur in the same habitats, and often are not found in the same areas of the world. *Didymodon anserinocapitatus* grows on sandstone cliffs in the American southwest while the convergent *D. sinuosus* (or whatever this name represents in the New World) is found on the bark of trees in the Arctic; *D. asperifolius* is found on calcareous or acid rock, peatland and soil, at high elevations in northern areas while *D. tophaceus* is a hygrophytic calciphile of temperate areas; *D. giganteus* is found on moist soil in the Arctic while *D. nicholsonii* occurs on soil and rock in western temperate areas; *D. leskeoides* is a northern species of waterfall spray zones and wet alpine tundra while *D. vinealis* is a common

ly western-temperate climate species of soil and rock; and *D. nigrescens* is an arctic and far northwestern species of rocky substrates at streams and waterfalls while *D. brachyphyllus* is found on soil and lava in dry areas, especially western steppes but scattered in the North Temperate Zone. Aside from the species shown as convergent in Fig. 5, species with the rare unicellular gemmae, *D. perobtusus* and *D. revolutus*, are found in disparate habitats and different areas of the world, while those with multicellular gemmae, *D. brachyphyllus*, *D. michiganensis*, and *D. rigidulus* var. *rigidulus*, are also of rather different habitats.

Overall, however, there is no doubt that the species shown as apparently convergent in Fig. 5 indeed share more characters between each pair than they do with other species. If the species are evolutionarily convergent, then the characteristics of their habitats as described above are insufficient to explain their similarities of form.

In spite of this study being up against the limits of numerical evolutionary analysis with morphological characters, similar species of North American *Didymodon*, whether or not distantly related, are apparently not evolved to clearly similar niches. Possibly this is because we have not yet done the microhabitat analyses that would clearly define the presumably similar niches, or because other combinations of characters simply are less advantageous in any environment and are now extinct.

STATISTICS, THEORY AND RECONSTRUCTION: A CRITIQUE

A word about cladistics. It has been assumed that phylogenetic classification must reflect an interpretation of derivation from common stock, but apparent synapomorphy in the shortest tree may include convergence (Lyons-Weiler et al. 1996). A phylogeny based on descent from shared ancestors is not logically consistent (Nagel & Newman 1974) as effectuated in maximum synapomorphy techniques in that it is valid parsimoniously only in eliminating grossly unreasonable trees, as discussed below. I am also uncomfortable with the fact that a hypothetical tree derived through phylogenetic analysis may have a low probability that it is the same as the true tree, whether the former is a tree of so-called maximum parsimony or of maximum likelihood (or both). I reassure the reader that the cladogram in Fig. 1 is not intended as a probabilistic

“reconstruction” or “discovery” of the phylogenetic history of *Didymodon*, but, as theory, is yet scientifically valuable. The word probable originally meant ready to be tested (proofable) or “to try the goodness” of one's best efforts (Skeat 1993). Another meaningful definition was “having more evidence for than against” (Harris 1915), but now probable can mean anything from “commonly true” to “possible” (Gove 1976). Harper (1979), however, demanded for scientifically plausible models in phylogenetic analysis that the probability of two taxa sharing closer ancestry to one another than to others in the group, given that the two taxa share one or more uniquely derived advanced character states and the others do not, to be “>.5”, a minimally acceptable definition of probable.

A phylogenetic hypothesis presented, as is common in the literature, as a “reconstruction” resulting from a “discovery process” by implication should have more probabilistic surety associated with it than merely being not contrary to fact, but this is seldom the case.

THE BAYESIAN BET

Early on in cladistic study it was “generally agreed that the reconstruction of evolutionary trees should ideally be regarded as a problem in statistical inference...” (Farris 1973, see also Yang 1997). According to Sober (1986), “the parsimonious hypothesis is the hypothesis of maximum likelihood.” Although Disraeli may have railed quotably against the ease with which statistics can be misused, there is a brand of statistics that even statisticians look on askance, and it is that methodology on which numerical phylogenetic analysis is based. Statistical probability using relative frequency well predicts long-run outcomes of series of instances, but the meaning of “probable” shifts when describing the probabilities involved in a single instance (as discussed by Braithwaite 1953: 118–127, 186–189 and von Mises 1957), and is largely identified with Bayesian analysis techniques in which probability models frequency (Frank & Althoen 1994). Phylogenetic analysis is, at least implicitly, Bayesian.

Many introductory texts emphasize the consequences of the difference between classical frequentist analysis of multiple runs and Bayesian analysis of single instances: Hoel et al. (1971) discuss the former as the “relative frequency interpretation,” while Mosteller et al. (1961) call it the “objective” (as opposed to “personalistic” or “intuitive”) position. That there is a problem is often debated: Winkler (1972) rightly pointed out that intuitive betting on single instances is “operational” (as opposed to “conceptual”) and is the basis for everyday life decisions (though these do not ordinarily involve the special regularity constraints and mathematical compounding issues of the concatenated series of conditional probabilities associated with hypothetical phylogenetic trees). According to Salmon (1971: 56) probabilistic methods can deal with single events because these can be usually be referred to a reference class (see also Pap 1962: 175, 216) of known initial probabilities, specifically the largest homogeneous reference class, which provides the highest posterior probability. Bayesian analysis, for it to work, assigns prior and calculates posterior probabilities of applicable reference classes. That there is a problem of choice of analytical technique is, of course, nonsense, since scientists generally use Bayesian forms of analysis, formal or informal, in initial stages of examination of a phenomenon, then classical frequentist methods as more information becomes available and processes are better understood.

To the classical statistician, a phylogeny, like a single roll of the dice, is a Poincaré system (Braithwaite 1953: 190), in which events that may be assigned equal probabilities when generalized as a series of events (as in J. M. Keynes' *Principle of Indifference*, Pap 1962: 169) are in a single instance actually much affected by unknown, often small differences that make a great difference in final effect—here, in particular, the manifold, non-independent (Sanderson 1993: 241) evolutionary mechanisms contributing to the true phylogeny. A phylogenetic data set is a view of the phylogeny taken at one instant in time, and Bayesian generalizations and inferences are required for thorough analysis (Harper 1979).

A Bayesian bet, in a simple example, might have to do with two hidden dice, a four-sided (tetrahedric) die and an ordinary six-sided (cubic) die, which are rolled randomly by a second person until a “1” turns up (one pip up—or down in the case of the tetrahedron). One must guess which hidden die was used to generate the data set “1”. The initial probability of getting a 1 with a four-sided die is $1/4$, but from a six-sided die it is $1/6$ —these are regularity assumptions that the dice are not loaded and are fairly cast. The likelihood is proportional (in this case 1:1) to the initial probabilities and thus one may conclude that the four-sided die has the maximum likelihood of being the die that was used to generate the data set (in this case with a single datum). This is the best theory and the best bet. By Bayes' Theorem (Harper 1979; Winkler 1972), the posterior probability that one's tetrahedric die hypothesis is correct is 0.6 (while that of a cubic die is 0.4, these adding to “probability 1”). This gives a somewhat better bet than the 0.5 (random) chance one had before knowledge of the additional information (data set). Classical statistics requires multiple throws yielding information on the proportion of 1's to other results to make a well-supported guess, but Bayesian analysis can deal with incomplete information through regularity assumptions. Such assumptions may eventually be proved correct or frequencies may be shown to even out in the long run. But before actual frequency data are known, Bayesian analysis remains the best method of dealing with incomplete information.

On the other hand, a purported reconstruction should certainly not be based on belief-oriented Bayesian analysis of unique phenomena when the bet is poor or at long odds, especially when one must build upon the results, which compounds the effects of being wrong.

In a critical paper discussing the Dollo model, Farris (1977) found that “the more parsimonious of two rooted trees differing by only one in total steps would be at least 4 times as probable as the other.” The probability increases to 16, 64 and 256 times for 2, 3 and 4 steps longer, respectively. Although one assumes that Farris is mathematically correct that “preferring a tree with 4 fewer total steps than an alternative tree for the same data is statistically better justified than preferring an alternative to a null hypothesis when the latter can be rejected at $\alpha = 0.001$,” there are, of course, usually many more than one additional possible longer trees at each of 1, 2, 3, 4 or more steps longer than the shortest. The *sum* of the probabilities of these many trees (if Farris' probability assignments are theoretically acceptable) is generally far greater than that of the shortest tree. Rogers et al. (1967) pointed out much the same problem, to which Kluge and Farris (1969) responded, inadequately (see discussion of the fallacy of irrelevance, Cohen & Nagel 1934: 381), that convergence and parallelism is shown in cladistic homoplasy thus “demonstrating that evolution is not parsimonious.” According to Fischer (1970: 53) “valid empirical proof requires not merely the establishment of possibility, but an estimate of

probability. Moreover, it demands a balanced estimate of probabilities pro and con.”

W. Maddison (1995) calculated the probabilities of single nodes being correctly reconstructed; in the hypothetical case of a binary character with a 0.1 per branch probability of change and a 4-node tree, his calculated probabilities of correct reconstruction of each of the nodes were 0.93, 0.93, 0.90, and 0.79. These values are individually relatively high and fit Harper's (1979) >0.5 criterion of “probable” for each node. For a tree, however, to be probably the true tree, i.e., that all nodes in practice are correctly reconstructed, requires the product of the probabilities of correct reconstruction at each node; seven nodes each at 0.9 probability (assuming single synapomorphies) give the structure a total probability of 0.48. The probability of a correct reconstruction of most large trees based on data sets of morphological data should thus be small in practice. This analysis, of course, assumes the belief-oriented Bayesian stance that characters are random variables, not Poincaré systems, and estimates (being mathematical expectations of relative frequency, Pap 1962: 205) are calculated from probabilistically *modeled* sample data. According to Swofford and W. Maddison (1992): “In general, we accept the use of ‘simple’ assumptions—unordered character states and equal costs for all transformations—as a suitable starting point, loosely analogous to neutral (equal) prior probabilities often used in Bayesian statistical analysis.”

STATISTICAL RELEVANCE

Requiring covariance to be interpreted as based on shared ancestral relationships (not convergence) whenever possible has been hammered into the literature as an equivalence between maximum parsimony and maximum synapomorphy. Though now axiomatic, it is more a convenience for actually obtaining a single tree—on which to base a classification that might prove generally acceptable—then for tree reconstruction, and as such reflects a confusion between practical classification and reconstruction on the part of cladists. There are several methods of phylogenetic analysis, and the two presently commonly used techniques are reviewed below.

A basic concept shared by *maximum likelihood* and *maximum parsimony* techniques of phylogenetic analysis is that of “statistical relevance.” This is only obliquely referred to in the literature, since its application in systematics is faulty. Basically, the more probable one of two or more hypotheses has higher explanatory power, dubbed statistical relevance by Salmon (1971: 11). Salmon showed that a demonstration that a unique event has a probability greater than .5 may not be the appropriate goal of predictive statistical analysis in some cases. His example is of a medical test showing an increase of the chance of a disease in a particular person, from the chance of one member of the general population having that disease to a higher probability (but less than .5) of that particular person having the disease. This increase is certainly reason for concern and further testing in this case.

But Salmon (1971: 56) goes on: “According to Hempel [1965], the basic requirement for an inductive explanation is that the posterior weight...must be high, whereas I have been suggesting that the important characteristic is the increase of the posterior weight over the prior weight as a result of incorporating the event into a homogeneous reference class.... When the posterior

weight of an event is low, it is tempting to think that we have not fully explained it.... [but] when the reference class is epistemically homogeneous in terms of our present knowledge, ...we have provided the most adequate explanation possible in view of the knowledge we possess.” Also: “To explain an event is to provide the best possible grounds we could have had for making predictions concerning it. An explanation does not show that the event was to be expected; it shows what sorts of expectations would have been reasonable and under what circumstances it was to be expected. To explain an event is to show to what degree it was to be expected, and this degree may be translated into practical predictive behavior such as wagering on it. In some cases the explanation will show that the explanandum event was not to be expected, but that does not destroy the symmetry of explanation and prediction. The symmetry consists in the fact that the explanatory facts constitute the fullest possible basis for making a prediction of whether or not the event would occur...” (1971: 79).

Clearly, if Salmon's criterion is applied to phylogenetic analysis, second best hypotheses (and third best, etc.) must be rejected because they involve somewhat less homogeneous reference classes. It is an argument for accepting, at times, an improbable tree as a best hypothesis in phylogenetic analysis because that tree best explains the data (see also Farris 1983; Hull 1974). There is no concern for how badly it explains the data or for the relative quality of second best, third best, etc., explanations. There is also no concern for whether the best explanation is a good Bayesian bet or not *in situations where a good bet is necessary*. Fischer (1970: 50) pointed out, discussing the fallacy of the circular proof, that the best available proof of a historical event may not be good enough to carry the question. Admitting that a correct hypothesis may be an improbable one once it is known, I find problematic the method for selecting as a “reconstruction” one from many nearly equally improbable hypotheses. The single most-adequate explanation can be scientifically inadequate as a hypothesis, and when posterior probability of that one is less than .5, all adequate explanations must be considered.

Maximum likelihood analysis is appropriate in all situations in which loss due to the failure to identify increased risk is very great, and has value in medicine and other critical activities. Statistical relevance in whatever guise has been applied, however, to the results of maximum likelihood and maximum parsimony evolutionary analyses as a justification for presenting the tree of maximum likelihood or maximum posterior probability, or the tree capable of least falsification as the “best” phylogenetic hypothesis. This is a misrepresentation in context, substituting an attainable goal for one that is presently unattainable or rarely attainable, i.e., accepting a most-adequate hypothesis from a number of similar hypotheses instead of an entirely adequate hypothesis that can stand alone. Unless there can be demonstrated more evidence for than against, no one tree can be chosen as a probabilistic hypothesis. In the literature, “best” in the sense of statistically most relevant does not necessarily mean probable, and should not be passed off as probable. All trees with a significant increase in probability or decrease in falsifiability in light of information in a data set are candidates for a reasonable phylogenetic hypothesis, and a more stringent criterion for a single hypothesis is necessary.

These problems are associated with a particular philosophical stance, so-called “realism” whose opposite is “antirealism.” R. Hendry (1996, see also Murphey 1994: 307) compared these opposed scientific world-views as follows: in *Realism*, truth is a criterion, and “if a theory

explains, this is an indication that it is true.... Science is a process of discovery: of truths and entities (electrons, quarks, genes) that were 'there before' [and proposes] extra-empirical criteria for theory choice: explanatory power, simplicity, unity, elegance....” Also, “Theoretical statements, construed literally, make factual claims about the world.... Uses of theoretical terms are attempts to refer to theory-independent entities.... Theoretical statements can be true or false independently of our ability to know their truth-values.... We can have good reasons to believe that our best theories are (approximately) true, and that their theoretical terms refer (i.e. electrons exist)....”

On the other hand, in *Antirealism*, “The only truths that could interest us are the observational ones.... Theories help us predict the observed behavior of the world. In order to do this, they need not be true, they could be convenient schemes for summarizing, classifying, ordering and predicting.... Neither scheme nor concept correspond to anything 'out there in the world.' ...Science is a process of construction: [of] theoretical schemes and concepts that are our creations [and of] prediction: 'saving the phenomena.” Also, “Theoretical statements are just tools, instruments or conventions.... Theoretical statements say no more than their observational consequences.... Truth for theoretical statements is to be identified with either: (i) Verification conditions...; or (ii) The theory that is accepted in the ideal limit of enquiry.... We can have good reasons to believe only that our best theories are empirically adequate (i.e. their observational parts are true).”

It may surprise some systematists that they must in fact choose (in an educated manner or by default) between a realist and an antirealist viewpoint, and that this can make a difference in standards of hypothesis construction. The problems associated with statistical relevance are more easily, but not necessarily, acceptable to the realist viewpoint. Donald Davidson (according to Murphy 1990), building on the well-known (to philosophers) “gavagai” argument of W. V. Quine, defines truth-knowledge as the best interpretation possible that a totally independent interpreter can make of an alien statement with available observational information. This view of truth-knowledge can be used in an overly optimistic manner. Murphey (1994), for instance, argued “...for the form of realism in which the existence of a real world is a postulate to explain our experience rather than a presupposition of inquiry. True knowledge of the real world is possible even though complete knowledge of it is not—that is, we are led to postulate the existence of some states of affairs about which many of the propositions we can formulate will be undecidable. Nevertheless, I argue that science will lead to the best theory which is also a true theory, and that our best confirmed theory is our best present theory. Hence, we can have 'true knowledge'—more strictly, well-confirmed theories that are our best estimate of the true knowledge—about the real world.”

Van Fraassen (1980: 64, italics his), on the other hand, formulated a contrary antirealist stance: “To present a theory is to specify a family of structures, its *models*, and secondly, to specify certain parts of these models (the *empirical substructures*) as candidates for the direct representation of observable phenomena. The structures which can be described in experimental and measurement reports we can call *appearances*: the theory is empirically adequate if it has some model such that all appearances are isomorphic to empirical substructures of that model.” This obtains in phylogenetics, in the case of *any* reasonable tree of a number of reasonable trees

obtained after grossly longer trees (those suggesting close relationships between dissimilar terminal taxa) or statistically improbable trees are eliminated.

Perspective on the Platonic realism implicit in mathematical “discovery” is provided by Scott-Ram (1990) and Nagel and Newman (1974), and such belief has long been a problem in human endeavors. John Stuart Mill (s.d.) responded to William Whewell's “Germanic” philosophy with “The notion that truths external to the mind may be known by intuition or consciousness, independently of observation and experience, is, I am persuaded, in these times, the great intellectual support of false doctrines and bad institutions.... And the chief strength of this false philosophy...lies in the appeal which it is accustomed to make to the evidence of mathematics and of the cognate branches of physical science. To expel it from these is to drive it from its stronghold....” Whewell (1847) promoted research into progress and change over time, devised the hypothetico-deductive method (conjecture and refutation) though also strongly supporting the inductive method, and coined the term “palaetiology” for the so-called historical sciences (O'Hara 1997), these being a unified inferential study of antecedent events of present-day phenomena in many intellectual fields with “certain principles, maxims, and rules of procedure in common.” Mill declared that inductive conclusions are capable of complete certainty, but William S. Jevons (in 1874 *vide* Kiernan 1965) found that scientists' informally devised hypotheses that were subsequently evaluated through the calculus of probability were never more than “just barely certain.”

More modernly, the empiricist/pragmatist W. V. Quine (1953, 1993) argued that all observational sentences are theory-laden (see also discussion of the Baconian fallacy by Fischer 1970), and (as explained by Murphy 1990: 81) there is no clear difference between statements grounded in fact and those grounded in meaning independent of fact; while, equally true, “there is no place for *a priori* philosophy” (in Murphy 1990: 96). It is in inadvertent or purposeful reification (e.g. that synapomorphies and phylogenetic patterns are real) that I see idealism sneaking into realism and thus supporting the misuse of statistical relevance in phylogenetic analysis. Van Fraassen (1980: 40) has posited a kind of natural selection of theories: “Only the successful theories survive—the ones which *in fact* latched on to actual regularities in nature.” This implies that the theory (from cladistics, phenetics or maximum likelihood) that predicts best by ongoing external verification (e.g. value in prediction) is the best theory, and this may be a brute force solution to the problems associated with choosing methodologies and with verification of inductive generalizations. The problem of whether the best theory is also an adequate theory may be approached this way: is it predictive enough, by some independent measure, to be scientifically useful? According to Hendry (1996), the “pessimistic meta-inductivist” philosophical position cautions that false scientific theories in the past have been predictive successes, which is, however, an argument for, not against, antirealism.

MAXIMUM LIKELIHOOD

Maximum likelihood estimation is often considered superior to parsimony methods. According to Yang (1997): “Under quite general regularity conditions, maximum-likelihood estimators have desirable large-sample properties: they are consistent, asymptotically unbiased, and most efficient....” Some cladists, however, find it philosophically antithetical to hypothetico-

deductivism and corroboration through congruence alone. Kluge (1997) argued that, as a verificationist methodology, likelihood techniques are opposed to Popperian falsificationism, and cladists (here apparently meaning those using parsimony techniques) are “not preoccupied with knowing the absolute truth, unlike verificationists.” Siddall and Wenzel (1997) admonished phylogeneticists “to abandon neojustificationist statistical interpretations.” On the other hand, Yang (1997), a statistical phylogeneticist and partisan of maximum likelihood methods, referred to maximum parsimony and similar methods as studies using “intuitive clustering algorithms for phylogeny reconstruction, which lack a rigorous statistical basis.” Refreshingly, H. E. Ballard, Jr. (pers. comm.) found that maximum likelihood analysis of ITS molecular data may generate more parsimonious explanations of evolution than do parsimony methods in that for oceanic island groups fewer biogeographic dispersal events or ecological shifts are required. In the present paper, I argue that both methods can produce unacceptable results, at least from an antirealist viewpoint.

A phylogenetic tree may be viewed stochastically as a martingale (Goldman 1990; Williams 1991), consisting of branching Markov chains (Sanderson 1993) of conditional probabilities. Each event is dependent only on the event immediately preceding it in the chain. The abstruse mathematics of maximum likelihood analysis in the literature is a result of having to deal with many parameters. Variables are treated as continuous (just as the bell-shaped curve associated with the Central Limit Theorem may be of use when working with discrete data in frequentist statistics). Maximum likelihood is the point on the curve of probability density where the slope of a tangent line is zero, i.e., the top of the curve, and thus recourse can be made to the infinitesimal calculus. For computational reasons, maximum likelihood analysis has been limited to small data sets until recently. Much of the research in efficiency (computational speed) is in devising ways around having to solve complex, high order (powers) differential equations, such as reducing them to binomials or modeling solutions with Monte Carlo methods. Log likelihoods are used as measures, in part, because they are easily distinguished to the left of the decimal point, while actual likelihood values are often very small decimal fractions; also, log likelihoods are conveniently monotonic (the values are unaltered).

Because gene mutations are readily calculated as stochastic events, maximum likelihood is presently a much used method of molecular phylogenetic analysis. The rate of evolutionary change of morphological characters is difficult to estimate (Martins 1994). With maximum synapomorphy, in addition, all identical character states are considered to have been caused by a single mutation unless forced to be interpreted otherwise in the shortest tree, thus there is no independent measure of mutation rate outside of the method itself. Kluge and Farris (1969) have suggested weighting by the degree of variation of a character within a taxon, a position abandoned by them and most cladists since (though occasionally mentioned wistfully in the literature).

Likelihood analysis simulates DNA sequences by calculating probabilities of oligonucleotides by correlation between base frequencies in various positions of the sequence (Bralley 1996). Functional gene sequences expressed in the mRNA may also be affected by evolutionary selection (their mutations thus are mainly only base substitutions since functionality may be impaired by other changes) and are commonly related to other genes through duplication, while

non-translated intervening spacers and other non-functional genomic elements (Lewin 1985: 333; Suzuki et al. 1981: 524), are better bets for stochastic analysis of changes (deletions, insertions and base substitutions) accumulated through phylogenetic time—assuming rates may be well estimated in speed and variability or if the method is somehow robust to variation in such. Portions of the genome that are (theoretically) most isolated from direct evolutionary selection are, for instance, almost absent from the mtDNA genome though common in chloroplast DNA, but where there is also a high level of homoplasy (Avice 1994: 337). The neutralist-selectionist debate continues, however, as to relative isolation from natural selection of different genomic elements (reviewed by Avice 1994), but likelihood analyses generally include no coefficients of selection. Another problem is expected quantity of information: e.g. the much ballyhooed ITS (internal transcriber spacers) region of the nuclear ribosomal DNA may have no intrapopulational variation and almost no useful phylogenetic information for morphologically very different species in the same genus (Soltis & Kuzoff 1993).

EXAMPLES

Markov chains tend toward a steady state or an equilibrium (Rolf & Williams 1991) which allows analysis of long-term trends. A maximum likelihood method using a Markov chain Monte Carlo method was used by Mau et al. (1997) to estimate the phylogeny of nine species of *Clarkia* Pursh (Onagraceae) on the basis of cpDNA restriction-site data. The tree of maximum likelihood was chosen as the best phylogenetic hypothesis. This is commonly justified as being a correct method in the Bayesian sense because the more probable one of two or more hypotheses has higher explanatory power (or statistical relevance, Salmon 1971: 11). Posterior probabilities (the actual chance that the hypothesis is true) can easily be calculated from likelihood values via the Bayes Theorem. Marginalized posterior probabilities of the five most likely phylogenies were reported as 0.649 (the tree of maximum likelihood as usual has highest posterior probability), 0.179, 0.168, 0.002 and 0.001. This means in classical frequentist terms that if this exact, same data set were to occur many times, the tree of maximum likelihood will also be the true tree in about 13 out of every 20 duplications. Rannala and Yang (1996) used much the same technique with primate pseudogenes to select a (((human, chimpanzee), gorilla), orangutan) tree with a posterior probability of 0.84. This same paper reported a similar study of 11 mitochondrial tRNA genes in a slightly larger set of primates giving the (((common chimpanzee, pygmy chimpanzee), human) gorilla) orangutan tree a posterior probability close to one (0.9999). A study of mitochondrial genome segments, being “parts of two protein-coding genes and three tRNA genes,” by Yang and Rannala (1997) found a high posterior probability for nine primates: ((((((human, chimpanzee) gorilla) orangutan) gibbon) crab-eating macaque) squirrel monkey)(tarsier, lemur) of between 0.95 to 0.96 depending on the evolutionary model used, all models obtaining the same tree.

The curves of probability density in these studies are high-peaked. These particular Bayesian probabilistic bets are, however, for small and thus limited data sets, and assume that no other data (sharing significant numbers of advanced characters) applies. As to this, Yang and Rannala (1997) asserted that posterior probabilities did not change much among different analytical variations, and their method “is robust to variations in the prior” because “most information concerning phylogeny derives from the data.” In any case, the analyses appear to have

successfully established good gene tree hypotheses for the primate data sets, given the regularity assumptions, neutralist expectation toward gene selection, the logic of treating character states as independent and uniformly distributed random variables in these particular genes, the amount of sampling for intraspecific variation in traits, and pending congruence with trees based on other, independent genes. There may be eventual selection of a species tree in the pool of reasonable parsimony results as a good phylogenetic hypothesis of evolution in the group.

In the same Mau et al. (1997) paper above, mitochondrial DNA for 31 species of African cichlid fish (plus an outgroup) was reported as having been analyzed at 1044 aligned sites. The posterior probabilities of the five most likely phylogenies were 0.11, 0.07, 0.06, 0.04 and 0.03. Here the curve of probability density is much flattened. The chance, with this larger data set, is about 1 in 10 that the most likely tree is the true tree. This is about the same posterior probability of guessing correctly that the tetrahedric die generated the data set “1” when one tetrahedric die and an additional 14 cubic dice are cast randomly until a “1” appears. The very strong Bayesian bet is that the most likely tree is *not* the true tree—one of the cubic dice (statistics does not tell us which one) most probably generated the “1” because the effect of the number of dice involved outweighed that of the likelihoods. Though the best theory available (of the 15 dice the tetrahedric die has maximum likelihood of generating the data set), this is hardly the kind of probabilistic evaluation from which, say, outgroups should be selected for analyses of taxa higher in the tree of life, unless perhaps the pertinent subclades in the several most likely clades are identical and their trees add to a strong posterior probability (most did not).

Avise (1994: 350) suggested that “In the foreseeable future, it should be possible to assemble molecular (and other) data into a grand phylogenetic encyclopedia—a universal Tapestry linking all life forms.” Sections could be “stored and referenced as nested series of phylogenies of increasing evolutionary depths.... Different molecules and assay procedures will have to be employed at different levels of the hierarchy, due to the varying windows of resolution provided.” This vision is impressive and possibly eventually achievable in part and in various degrees of confidence. Clearly, one can foresee weak links due to poorly supported maximum synapomorphy or low posterior probability causing false branches in this deeply conditional chain of life. Rice et al. (1997) review problems with analysis of massive data, where “maximum parsimony (at run times within reach of today's hardware) has poor asymptotic performance...” with large data sets, and recommend adding more characters rather than more taxa, and trying new methods, such as parsimony jackknifing and the inferred ancestral states approach (a hypothetical exemplar ancestor replacing a large presumptive clade). They allow that abandoning maximum parsimony and maximum likelihood as optimality criteria “requires that we rethink the hypotheticodeductive or probabilistic underpinnings of the discipline...,” as is encouraged in the present paper. A grand cladogram of life is thus limited by analytical techniques for single large data sets and by gradual lowering of probabilities of being correct when separately derived cladograms are logically concatenated.

There are more than 38 million possible tree arrangements for a mere 10 taxa (according to Doyle 1993). Of course, of these, one could eliminate perhaps 37 million trees as unreasonably different from dendrograms of phenetic analyses (based on the same data), which certainly reflect natural selection to a considerable extent (Yablokov 1986), but what of the remainder?

Although Mau et al. (1997) eliminated in the cichlid study above most of ca. 10^{40} trees to get the 250 trees that comprised their “95 percent credible zone” (the most likely trees with posterior probabilities adding to 95%), one would have to somehow eliminate all but the two most likely trees to make the one most likely tree a good bet to be the true tree. It is this “somehow” that is the proper focus of new research in phylogenetic methodology and is reflected in some papers cited here. Taking a mathematical elimination process to the limit may be wrong if the justification for eliminating the majority of possibilities (phylogenetically grossly long trees or improbable trees) is different from the justification (mathematically projecting theoretical requirements maximally) of eliminating all but one from the pool of credible trees. In maximum likelihood studies this is done perhaps to get a single tree as a result, to match the apparent success of maximum synapomorphy results. On the analogy with reports of radiocarbon dating of anthropological artifacts where a measure of plus or minus a number of years is given to reflect different sigma values, a strict or majority-rule consensus tree of how trees in the 95% credible zone actually agree would seem to be the better interpretive result in likelihood analyses.

A comparison of a consensus gene tree from the .5 and .95 credibility zones obtained with statistical methods with the gene tree of maximum synapomorphy (from the same data set) might throw light on what the word “approaches” means when cladists assert that a particular result approaches, approximates or converges on the true tree, and on what Bremer support really signifies. Hendry's (1996) account of “convergence realism” includes a caution that the expectation of science converging on the truth is only applicable to mature sciences—this is hardly a description of phylogenetic systematics.

It is important to grasp that at least with larger phylogenetic data sets the most probable tree is not “probably the true tree.” Few papers using maximum likelihood to date discuss relevant posterior probabilities: Bohs and Olmstead (1997) do not mention them, Huelsenbeck and Rannala (1997) promoted the use of likelihood ratio tests (e.g. as used by Yang 1996) instead and did not mention posterior probabilities. I agree with Rannala and Yang (1996) that “the posterior probability provides a natural measure of the reliability of the estimated phylogeny” given the various assumptions required for it to be calculated, but it must be used relative to the sum of the alternative probabilities, not relative to the next highest value.

MAXIMUM PARSIMONY

Maximum parsimony analyses are parsimonious in eliminating myriads of unreasonable trees of overly complex hypotheses. This leaves a pool of tens or hundreds of trees (similar to the “credible zone” above) that are acceptably reasonable under Darwinian theory, thus the phrase “maximum parsimony” as used in the literature is a semantic distortion. The explanation of descent from common stock applies to all plausible trees, whether common descent is maximized or not. Maximum parsimony methods require that *all* covariance where possible must be interpreted as due to shared ancestors, something not required by Darwinian theory—this problem is also discussed by Lyons-Weiler et al. (1996).

In fact, *contra* Farris (1983) and Kluge (1997), eliminating longer trees to the mathematical limit from the pool of credible or reasonable trees is based on unjustifiable *ad hoc* assumptions about

the degree of joint ancestry of terminal taxa. At the point that the method goes beyond elimination of grossly unreasonable trees, and the number of synapomorphies (as assumptions against convergence) is needlessly increased, the method becomes antiparsimonious and overly interpretive. A tree selected as that one with all covariance possible treated as ancestrally based is not a phylogenetic reconstruction through parsimony, but is the theoretical tree of maximum (interpreted) synapomorphy or, alternately, of minimum convergence, a concept not unmentioned in the literature but the significance of which is little discussed. The shortest tree may be used for classification if it is understood that all plausible evolutionarily convergent alternative trees have been eliminated, to which extent the fine structure is artificial and reflects a too-simple theory of evolution. Those who insist on the original *ad hoc* argument should consider the second, third, fourth, etc., least falsifiable trees, which compete as reasonable explanations in quantity if not in quality. Here again, philosophical realism can introduce low standards for hypotheses.

The hypotheses of homology and of independence of traits necessary for phylogenetic analysis in practice are (1) almost always to some extent wrong (even if homologies are apparently more easily identified in molecular data—Avice 1994, but according to Philippe et al. 1996 because there are only four nucleotide states, this makes convergence very likely) and (2) evolutionary homoplasy is, as is well known, apparently common and introduces ambiguities into the data set, both leading to data sets that may be interpreted easily in various ways as different, often slightly longer trees. Like the incorrect assumption that the Winter Solstice must be the coldest moment of the year, the shortest tree is only doubtfully similar to the true tree unless, perhaps, Bremer support (1988) extends through the pool of plausible trees. Though Bremer support for subclades might help with this problem, the characters involved must be shown to be independent variables, because suites of characters that evolve in concert cannot be acceptable as multiple support.

In sum, congruence in the tree of maximum synapomorphy is not corroborative, it is methodologically based coincidence and based on unjustified rejection of plausible alternative interpretations on the basis of convergence (including parallelism).

MOLECULAR ANALYSIS

Molecular data may conflict among sources, or between molecular data and morphological data (Avice 1994: 314; Philippe et al. 1996; Seberg et al. 1997); “diverse data sets do not always yield the same estimates of phylogeny for the same organisms” (Sites et al. 1996). Hasegawa (1997) discussed the differing results of various researchers in mammalian evolution (citing examples in whales and among eutheria, marsupials and monotremes) when using different genes; Hasegawa thought a total evidence (Carnap 1962; Kluge 1989) approach using maximum likelihood techniques might solve this problem. Total evidence means that there should be no more data available whose addition to the data set might change the degree to which a conclusion is supported. Sites et al. (1996) presented a method of approaching a total evidence analysis of discordant molecular and morphological data sets using parsimony analysis; they found that deleting homoplastic characters produced a better (more parsimonious than previously published trees) result but part of the tree structure collapsed, being “an unacceptable loss of phylogenetic

information.” They instructively discussed several critical problems with molecular phylogenetic analysis that apparently affected their results. In line with this, Philippe et al. (1996) warned that “A character may contain reliable phylogenetic information whatever the number of extra steps it requires. As a result, discarding the more variable characters leads to an increase in the number of multifurcations, demonstrating that information was lost.... Thus, the more a character changes the more it is subject to homoplasy, but also the more information it potentially contributes.... Removal of the sites for which more steps are required in the true tree than in the most parsimonious tree does not result in the true tree....”

Milinkovitch et al. (1996) found that “different phylogenetic analyses of the same genetic data set can yield conflicting results, depending on the choice of parameter settings and included taxa,” and used a sensitivity analysis to identify “portions of the multidimensional parameter space where phylogenetic signal is most reliably recovered.” Naylor and Brown (1997), dealt with the “notion that historical ‘signal’ will rise above misleading ‘noise’ as more sequence is gathered.” They found that a poor match between a bootstrap consensus parsimony tree based on “the entire protein-coding portion (12,234 base pairs) of the mitochondrial genome of 19 taxa whose interrelationships are widely accepted...” with the accepted tree was due to, for instance, among codons, poor fit of nucleotides at third positions (see also Felsenstein & Churchill 1997: 100); among genes, NADH2; and among amino acids, isoleucine, leucine and valine. The retention index was used to determine phylogenetically reliable functional classes of sites, though it was recognized that using the expected tree to discover resilient sites was not an independent test. On the other hand, they pointed out that molecular data may show a similar covariation due to both shared history *and* functional requirements as have morphological characters, resulting in a need to ascertain the “relative importance of particular co-varying combinations of residues for protein structure, function and folding.”

Sometimes a single tree may represent the pool of reasonable trees if the terminal taxa are disparate and all have reference groups of intermediate taxa. Philippe et al. (1996) used an “accepted” tree of 29 Vertebrata as the “true tree” for comparative purposes. With data sets concerning a few taxa for which all but two have clearly different traits (say human, chimpanzee, fox, cow, fish), maximum synapomorphy yields a reasonable and parsimonious estimate of phylogenetic relationships because there are many shared traits and reference groups of intermediate taxa, contributing patristic distance, are known. This yields a so-called “accepted” tree. Intermediate lineages contribute as reasonable hypotheses but may not be resolvable in fine structure. It is the relationships of the intermediate taxa in the data set that should not be blithely considered adequately resolved by maximum synapomorphy methods because at some point, similarity of the taxa and lack of intermediates allow perfectly reasonable alternative evolutionary hypotheses; a *probabilistic* result of an analysis based on multiple independent genes that supports a reasonable species tree seems a necessary requirement for a hypothesis in such cases.

ADDITIONAL ASSUMPTIONS

In cladistic analysis, it is, for now, rather improbable that either the shortest tree or the most likely tree is likely to be the same as the true tree, that is, the results of phylogenetic analysis of

substantial groups cannot be expected to have more evidence for than against. Thus, those willing to attempt a statistical analysis of a unique past phenomenon of concatenated events are given short odds on recovering fine tree structure. There is apparently a pool of trees similar to the so-called most parsimonious, maximally likely, and best phenetic cluster dendrograms, that include, probabilistically, the true tree, but which can all be almost equally easily explained through Darwinian theory (assuming convergence is an option, and grossly unreasonable trees are eliminated). Swofford and W. Maddison evaluated the effect of underestimation of character state changes, especially in regard to evaluation of parallelism, but only as to the effect on mapping state changes on the tree of maximum synapomorphy.

In a new field, thoroughness in initial broad analyses is often sacrificed in the excitement of discovery, but eventually this must be corrected. Doyle (1992) questioned the present privileged status of molecular systematics studies, which are commonly exempt from testing for variation in gene characters within an OTU; see also discussion of intraspecific cpDNA polymorphism by Rodriguez and Spooner (1997).

Rzhetsky and Sitnikova (1996) found that recognition of a set of unreasonable trees was important—in that selection, reliability and efficiency of the correct complex mathematical model of molecular evolution can be facilitated through “estimation of the prior distribution of phylogenetic parameters” of alternative tree topologies. They indicated that it “is rather intuitive that different tree topologies and different combinations of parameter values may have very different likelihoods of being encountered in real phylogenetic analysis and therefore the vast majority of possible tree topologies and parameter values should not be considered in the real data analysis....” Also, they point out that such estimation of “prior probabilities” is done in any case by simply focusing on a particular taxonomic group for study. Milinkovitch et al. (1996) increased efficiency of parsimony analysis by reducing degrees of freedom for “uncontested groups” with a constraint tree based on “reasonable assumptions because of strong support from numerous morphological characters.” Molecularly based “nonsensical” trees that violated the morphologically based constraint were found to be few.

According to Felsenstein and Churchill (1997): “It has long been recognized that the assumption of equal rate of evolution implicit in many methods of analyzing phylogenies from molecular data is unrealistic.” They offered a method of introducing particular assignments of rates to sites, but relied on maximum likelihood and relative posterior probabilities. Philippe et al. (1996), however, showed that the evolutionary rate of a given position apparently varies throughout time and “substitution models should incorporate variation in evolutionary rate at a given site....”

The consistency argument in maximum likelihood analysis and other probabilistic studies is that the method ensures that the tree of, for instance, maximum likelihood must converge probabilistically to 1 as data increase to infinity (Shenton & Bowman 1977), in other words, in Keynes' theory of induction “it can be demonstrated by means of the calculus of probability that the probability of a generalization g increases with its confirmations and approaches certainty as the limit...” (Pap 1962: 167). This is merely intuitive and liable to sampling errors according to Yang (1994), and was flatly denied by Sober (1983, 1986) as impractical, echoing an argument (attributed to J. Nicod by Pap 1962: 166) that the resultant certain generalization would be

useless because it would be monstrously complex in having to reflect all confirming instances. Belief-oriented analytical methods require rigid, precise regularity constraints that surely require investigation, e.g. equal prior probabilities and selective neutrality of evolutionary events, and whether supposedly independent and uniformly distributed random variables do even out in the long run. “Most of the models used in evolutionary analyses describe a gene as a collection of *independent* sites each being an instance of the same random process, a Markov chain,” according to Rzhetsky and Sitnikova (1996). Also, the numbers of species supplying increasing data are limited (Sanderson 1993).

If data conflict, bias and sample error are negligible, the chance of the maximum tree converging to probability 1 and also of being the true tree is also limited by the chance that the assumed model mirrors the manner of gene modification; “Any model of a process as complicated as evolution will necessarily be a simplification of the true situation” (Goldman 1990). There are several (relatively simple) models (Schöniger & von Haeseler 1995) of gene modification so the most likely tree is again only the best theory since one must intuitively choose the theoretically best model and apply it across the board (but see Yang 1997). On the other hand, “A method assuming a wrong model may still be consistent and may have smaller sampling errors than one using the right model” (Yang et al. 1995); while, apropos of this problem, Hendry (1996) remarked “Approximate truth is a difficult concept. On any reasonable construal, approximate truth does *not* explain predictive success....”

Morphological characters, as they change evolutionarily, are of particular value because they are often recognizable as transformation series, but gene sequencing has promise of providing many phylogenetically informative data, with an expected redundancy of data among different genes at similar levels of taxonomic resolution that helps cut through “phylogenetic noise.” (Note, however, that Rice et al. 1997 demonstrated that “branch lengths should not be used as a measure of confidence or robustness...” at least in large data sets.) Such data may have high consistency indexes (showing low estimated homoplasy on parsimony trees) commonly between 0.45 and 0.85, with many studies at the high end, assuming no inflation of CI by “hidden autapomorphies”—Nixon 1991—in the data). Another reason molecular systematics is very attractive is because morphological character states of ancestors that are selected against in environments that the terminal taxa no longer inhabit are (at least in part) no longer in the data set. Likewise, morphological character states of ancestral nodes (in other words, the branches below the vertices) in any one lineage that are expressly adaptive to environments in which the extant terminal taxa of the lineage are not found have been eliminated (at least in part). This is may occur by anagenetic change, identical reversal(s) in daughter taxa, or identical reversal(s) and an extinction in daughter taxa, as daughter taxa adapt to environments sufficiently different than that of their shared ancestor. Only if the synapomorphy to autapomorphy ratio (as relative mean numbers of traits per terminal taxon or node) is near 1 can one hope for good retention of morphological ancestral characters.

In molecular systematics, this may be also true to some extent for exons, but apparently non-functional genomic elements are not expected to lose phylogenetic information through selection (eventual saturation, however being a problem). According to Avise (1994: 8), although there is much homoplasy due to apparent parallelism, convergence, and reversals in molecular

characters, “any widespread and intricate similarities [in the genome] that appear are unlikely to have arisen by convergent evolution...” and (Avice 1994: 28) “...nucleotide positions or genic regions that are functionally less constrained are those most likely to harbor neutral variation and to exhibit the most rapid pace of allelic substitution.” If selection has indeed eliminated many important ancestral molecular character states, it is possible that recently evolved traits (essentially autapomorphies) are sometimes incorrectly resolved as synapomorphies on a random basis. There is no need for such speculation in cases of a general agreement of analyses using apparently adaptive morphological and non-adaptive molecular traits (when grossly unreasonable trees have been eliminated and the trees of maximum likelihood and maximum synapomorphy which generally represent the credible pools are compared). There are, however, still many additional problems with molecular systematics.

According to Doyle (1992), because a gene tree may be uncoupled from a species tree by introgression, lineage sorting, or mistaken orthology, molecular systematics has many of the faults of one-character taxonomy—unless many genes are tested in a cladogram—and molecular analysis is not alone a better alternative to morphological analysis (this contested by Olmstead & Palmer 1997 for relatively distant relationships they studied in in Solanaceae); Doyle added: “...additional data for any particular gene, while it may produce a better gene tree, cannot increase confidence in that gene as representative of the species phylogeny.” Some recent studies have begun to use several genes in analysis for just this reason (e.g. Nei & Takezaki 1996 who used a genetic distance measure). Also, Avice (1994: 314 ff.) reviewed many cases of apparently successful application of molecular techniques to solution or clarification of intransigent systematic problems, often accomplished with congruent results from analysis of more than one genic element. Avice (1994: 354) recommended multiple lines of evidence as important in addressing such problems as “shared retention of ancestral states by the taxa in question, extreme molecular rate heterogeneities across lineages, convergent evolution to a shared molecular condition, introgressive hybridization, and a mistaken assumption of orthology when the loci in question might truly be paralogous...” and he reviewed apparently well supported evidence for at least occasional horizontal transmission of particular genes, which may be mediated by parasites.

RELATIVE CERTAINTY

In spite of much discussion in the literature about technical consistency and eliminating *ad hoc* assumptions, certainty is never attainable in scientific applications even though the method is consistent, or an ideal data set matching an ideal model may ensure it (as in Heijerman's 1990 finding that phylogenies generated from his artificial data sets are fully retrievable with maximum synapomorphy methods when there is no homoplasy), or in the face of the sanguine enthusiasm over the “virtually infinite number of [gene] characters available” (Doyle 1992). Also, a consistency index even as high as 0.85 means that there is still considerable cladistic homoplasy (CI is essentially the number of observed steps divided by the necessary steps, Kluge & Farris 1969, though it has subsequently been variously calculated), which implies a similar amount of evolutionary convergence “hidden” among the synapomorphies of the tree of interpreted maximum synapomorphy. Patristically distant convergence is identifiable as cladistic homoplasy, but patristically close convergence, in morphological or gene data, is lost among trees a few steps longer than the shortest tree.

Because of the nature of the strongly belief-oriented probabilistic analysis used in phylogenetics and the poor results in practice, the degree of assurance that frequency-based long-run statistical analyses give to other scientific studies may never be attained. It is paradoxical that some of those using the above intuitive numerical analysis techniques should deprecate previous evolutionary theorization (the “New Systematics”) as being intuitive. For instance: “...patterns of functional evolution should be founded on a corroborated set of statements about phylogenetic patterns of structural features. The emphasis on theories of process and evolutionary transformation, for example, has obfuscated the analysis of tetrapod origins throughout this century...” (Lauder & Liem 1983: 187; see also Crowe 1994). (Apparently, the major problem with evolutionary theory ca. 1950–1980 was a mistaken expectation of little genetic variability in species, excepting balanced polymorphism, because of strong selection forces, Avise 1994; the problem was not the fact of theorization itself but a basic assumption later proved mistaken.)

The supposedly “standard evolutionary theory” that is inherent in the synapomorphy criterion (pointed out by various authors, including Scott-Ram 1990: 175) adduces an expectation that the shortest tree is the best hypothesis of evolutionary relationships explained though derivation by common ancestral stock alone, and thus it cannot contribute to an acceptable theoretical reconstruction even if there were such a thing as a discovery process for Platonic realities.

The shortest or most likely tree may be seen as having a pragmatic (Pap 1962: 228) scientific value in that, if a choice *must* be made from among very many hypotheses, even on the basis of a less-than-probabilistic reductionism, the perceived risk is then lowest. In many sciences, one can devise an immediate test of the correctness of the most-likely hypothesis, or each of the several most likely. The expectation of the success of *post hoc* testing for correctness may be the psychological justification of the otherwise illogical (Wittgenstein 1961: 70) idea of simplicity (Sober 1975) or Occam's Razor (Jefferys & Berger 1992). This is not so in systematics, where immediate, clear-cut tests of correctness are unavailable. One rejoices, instead, in the expectation that at least one “least wrong” hypothesis is probably truly correct every, say, ten or twenty published papers—which was the breakthrough paper, however, is unknown. Cohen and Nagel (1934) discuss the fallacy of exclusive particularity in science, one example of which is a confusion of a sufficient condition for a necessary one. The best hypothesis as “least wrong” in maximum synapomorphy or maximum likelihood analysis is not necessarily a scientifically acceptable result. This reminds one of the casino gambler, who, when asked how luck was holding out, replied: “Fine! I have not won in two hours, but my friend here has not won in four hours.”

Though risk-based losses (incorrect predictions) may now be greater than gains, with additional information and better methods over time one may begin to probabilistically model the past with Whewellian consilience, but only to the extent it is indeed retrievable. If one has a species trees, with many gene trees congruent to it, and there are many of such examples, the method may be seen to have general value; one requires such overwhelming evidence in the face of presently overwhelming regularity assumptions.

This paper's cladogram (Fig. 1) shows minimum phylogenetic distance (as summed steps) of the

ensemble terminal taxa from a hypothetical shared ancestor (here determined by an outgroup), and as such is valuable as a clustering technique (Barker 1996; Yang 1997: 107) that maximally interprets character covariance as due to shared ancestors. Even if we accept, however, the assumption-laden (summarized well by Farris 1973 and Swofford & W. Maddison 1992) regularity strictures of computerized evolutionary analysis, the cladogram's explanatory power (as per Farris 1983; Hull 1974) is restricted to evolutionary theory that eliminates or renders as improbable the possibility of convergence other than that implied by cladistic homoplasy. My previous cladistic work (Zander 1993, 1995, 1996), along this same line, should be interpreted as cluster analyses (the distance measure summing state changes minimized globally) supportive of the derived general classification alone, given the few steps per node and the simple character states, and the fine structure of the maximum synapomorphy trees remains rather dubious as an estimate of true relationships.

It is possible that molecular systematics can provide data for evolutionary trees of high probability (as at least good Bayesian bets), but there is as yet successful demonstration for only a few small data sets and the problems involved are immense. Further advancement in evolutionary analysis must concern ways of distinguishing synapomorphies in the shortest tree that are due to shared ancestry from those due to evolutionary convergence. An ingenious method of distinguishing at least some apparent synapomorphy from evolutionary synapomorphy was proposed by Lyons-Weiler et al. (1996), for instance, based on identifying fidelity of phylogenetic signal by “how much unique similarity exists between two taxa with no redundant information added.” According to J. Lyons-Weiler (pers. comm.) “...in the absence of fidelity of phylogenetic signal, a high degree of covariation of character changes along branches in parsimony trees is not expected.” Apropos of this, a totally random data set may be used to generate highly resolved cladograms of maximum parsimony.

A MORE STRINGENT REQUIREMENT

In my opinion, a probabilistic estimate of species phylogeny addressing fine tree structure must (at least) use a model incorporating variable evolutionary rates if possible in Bayesian statistical analysis of data sets of several selectively neutral, independent genes (total evidence is better) resulting in a gene tree with posterior probability greater than .5 (greater than .95 is better if the results are to be used as a basis for analyzing concatenated trees higher in the tree of life) that is congruent to a short tree derived from a morphological data set that passes at least a fidelity of phylogenetic signal test.

The species tree should be within the pool of reasonable parsimony trees, and may even turn out to be same as the so-called tree of maximum parsimony. A pool of candidate reasonable species trees might be developed through a parsimony analysis of non-gene characters with “accepted” relationships constrained (as per Milinkovitch et al. 1996) and then the shortest tree and all trees one step longer (at least) retained. This produces a set of trees with grossly unreasonable trees eliminated. It remains a problem that the only test of such a hypothesis is congruence of the model with information about the past obtained from other sources, since the essentially Bayesian bet on a single (chained) past evolutionary event can have no direct corroboration.

Ways of estimating confidence sets for cladistics studies have been suggested by, e.g., Sanderson (1989) using bootstrap replicates, and Faith (1991) using random character correlation, but these use the tree of maximum synapomorphy as methodologically central. According to Swofford and W. Maddison (1992): “One way to minimize the impact of incorrect assumptions regarding the phylogeny when examining hypotheses of character evolution is to reconstruct the character(s) on a variety of reasonable trees, ideally a large enough set of trees that the probability of including the true tree is relatively high.” Felsenstein (1985) cautioned, in the case of multiple equally shortest trees, against the assumption of good support for those subclades appearing identically in all trees: “the confidence interval on phylogenies appears to be much larger than the set of all most parsimonious trees.” Bremer (1988) concluded, with protein sequence data, “Not only the shortest cladograms, but also those with an increasing number of steps should be combined into strict-consensus trees.... Only those groups present in the consensus trees may be hypothesized to be monophyletic with any confidence. There is no easy way to determine how many extra steps should be allowed....”

Along the lines of these suggestions, the results of the present analysis were reinterpreted from a set of trees one step longer than the shortest (but including the shortest). First, the two main subclades were constrained as “uncontested” by being analyzed separately with PAUP (*B. unguiculata* as outgroup, unordered, “bbsave” set to one step more than the number of steps in the shortest tree). For a true parsimony analysis, the number of extra steps to include reasonable trees might be estimated as the average number of steps per node (length per branch). Only the sect. *Fallaces* subclade produced a set of trees that did not overrun computer memory. The 48 resulting trees were analyzed by majority-rule techniques (CONSENSE, Felsenstein 1995; MAJORITY, Wilkinson 1995). Clusters of terminal taxa in the following exact topologies appearing in greater than 50 percent of the total number of trees (48) were (*D. nigrescens* (*D. perobtusus*, *D. subandreaeoides*)) 100%; (*D. leskeoides*, *D. tophaceus*) 96%; (*D. ferruginascens*, *D. maximus*) 88%; and (*D. michiganensis* (*D. nigrescens* (*D. perobtusus*, *D. subandreaeoides*))) 63%. The cluster (*D. leskeoides*, *D. tophaceus*) was at the base of the tree in 54% of the trees. Of the 48, there were 22 trees in this pool of reasonable trees that include all three subclades. Thus, even if the tree of maximum synapomorphy is excluded as less parsimonious, true parsimony analysis (given the above assumptions) results in poor resolution at least with this particular data set.

If the 48 trees examined constitute a confidence interval, the particular majority rule subclades have probabilistic support, but if not, then this is another example of unuseful statistical relevance. Which obtains remains uncertain. The .44 consistency index of the cladogram in Fig. 1 is evidence for at least minor convergence that affects topology (of course, some minor convergence does not affect tree structure) and is to some extent modeled in the reinterpretation. Major convergence would be, for example, nodes of one of the two subclades (sect. *Didymodon* and sect. *Fallaces*) being derived in parallel from several nodes of the other subclade through immediate elaboration of several states of a suite of character states associated with adaptation to a particular, different environment—but no evidence of different environments (plus clear cut environmentally associated traits) associated with the two subclades is at hand. This exercise, in dealing with an “accepted” subclade, does not challenge the phylogrammatic results.

A disenchantment with statistics (as improper use of null hypothesis testing) has recently developed in the psychological sciences where "...more theoretical courage" is called for (J. Kagan in Bower 1997). In modern systematics, acceptance of maximum synapomorphy trees as provisional "best" reconstructions just because they are least falsified or are best explanations is a philosophically realist too-low standard. Least falsification here is similar to the concept of "power of the test" in classical statistics (Rawlings 1988: 100; Tabachnick & Fidell 1989), which is the probability of rejecting a false null hypothesis (e.g. by large *F*-ratios). Likelihood ratios with low posterior probabilities are not acceptable simply because no other more probable tree has come to light. Requirements for null hypotheses in phylogenetics are discussed by Wollenberg et al. (1996), among others, especially Faith and Cranston (1992).

That a great deal is presently expected from phylogenetic analysis is clear from many university positions presently being offered for phylogenetic systematists (especially those using molecular techniques) and from the amount of U.S. National Science Foundation grant support. As to the latter, for the year 1997 (National Science Foundation 1997), more than \$14 million was awarded in 96 grants for systematic research. Of these, 55 awards (57%) had the words "phylogeny" or "cladistic" or "molecular systematics" or some variant in their title: these grants totalled about \$7.5 million, averaging \$135,000 per grant. An additional 16 grants (16%) had the word "evolution" or a variant in their title: these grants totalled about \$1.5 million, averaging \$97,000 per grant. The 23 remaining systematics research grants (23%) totalled about \$5.3 million, averaging \$250,000 per grant; for these, any emphasis on phylogenetics could not be told from their titles. If one combines the phylogenetic and evolution categories (evolution in systematics studies being almost certainly used in the sense of phylogenetics), support for modern computerized evolutionary analysis by NSF in just the one year 1997 is conservatively estimated at about \$9 million (of a \$14 million pot), taking at least 70% of the awards. Now there are two kinds of phylogenetic studies presently common in the literature: (1) those that methodologically wrongly equate maximum parsimony with maximum synapomorphy, and wrongly substitute ratios of maximum likelihood and maximum posterior probabilities for posterior probability greater than .5 (i.e. more evidence for than against); and (2) those that treat their results as steps along the way in building a modern method for probabilistically estimating phylogenetic relationships for at least some groups (as do many of the theoretical studies cited in the present paper). Clearly little scientific advance can be expected from support given funded projects like the former, other than the generation of data sets. One might hope that, in view of the well-known world-wide critical status of biological diversity, alpha taxonomic studies (keys, descriptions, nomenclature, typification, discussion of range and variation, illustration, etc.) are part of morphologically based phylogenetic projects, as is sometimes the case, that are supported by NSF.

CONCLUSIONS

There are three major problems with phylogenetic analysis as currently practiced that are outlined in this paper. (1) A difficulty shared by all phylogenetic analysis is the extensive regularity assumptions necessary for modeling frequencies in Bayesian-style analysis of unique events. (2) A second problem is that analysis through maximum synapomorphy is evidently not probabilistic at all beyond eliminating evolutionary scenarios that appear to be grossly

unreasonable, or at least calculation of such probabilities are highly dubious. Also, the posterior probability of a tree of maximum likelihood selected through likelihood ratio (or similar linear rank) techniques may be very low and then does not reflect more evidence for than against when compared with other reasonable trees in the pool or “credible zone.” (3) Third is over-interpretation through computer algorithms of the idea of descent from common stock. A pool of somewhat short trees that are each a reasonable evolutionary hypothesis are improperly reduced to one tree by maximum synapomorphy, thus falsely (in view of consistency indexes seldom higher than .85 and usually much lower) “reconstructing” a phylogeny by the assumption of no evolutionary convergence unless it is shown in cladistic homoplasy.

Recognizing that the result of parsimony analysis is merely a best theoretical model for classification by common descent alone avoids the idea implied in the literature that such analysis is a statistical method producing concrete, confidence-inspiring reconstructions, but instead reflects the powerful ability of computerized analysis to interpret large, complex data sets on the basis of a simplistic theory of common descent. If we do base classification on explanations that are merely best of a number of competing explanations requiring in addition a host of regularity assumptions, then this is the sorry burden of systematics that has not been alleviated to any significant extent by modern computerized evolutionary analysis. A similar problem exists in vicariance biogeography, where scenarios involving long-distance dispersal, except where obvious, are largely ignored, and the results are valuable as heuristic constructions but not as reconstructions.

I justify this phyletic study of North American *Didymodon* species in three ways. (1) The cladogram provides an acceptable general classification as there are many terminal taxa of similar morphology intermediate between extreme morphotypes, and the two identified clades are reasonable interpretations for this particular data set. (2) The lineages seem to be good hypotheses in the distal areas of the tree because there are relatively many ancestral nodes that approximate the morphological complexity of the terminal taxa, allowing identification of possible surviving ancestors (which themselves are generalist). Though most nodes do model ancestors, the existence of such ancestors as characterized by the state combinations at the nodes is only theoretical. Most nodes collapse at one additional step (but see majority-rule analysis above), and the fine structure, certainly that deeper in the tree, is thus questionable. (3) The tree of maximum synapomorphy can be considered in its alternate guise as the tree of theoretically minimum convergence in a trait-polarized, phylogenetic context. The phenetic ordination is related, then, to the broad patristic distances between terminal taxa (not the fine structure in lineages) and the phylogram helps identify species that may be evolutionarily convergent in the genus.

The theoretical phylogeny (at least as a cluster dendrogram) suggested by the phylogenetic estimation (Fig. 1) is useful for classification purposes also because it is reasonable, and agrees with intuitive evaluations involving “look and feel” characters not easily scored, and of apparent transformation series (the robust species *D. giganteus* and *D. nicholsonii* are clearly part of two different stature-gradient series as suggested in figures 1 and 2). Further analytical exploration, given the increased agreement of figures 1 and 3 over that of figures 1 and 2, is warranted, with study of additional species and data.

Phylogrammatic analysis can provide explicit phenetic information as an interpretive classificatory aid for cladistically poorly resolved groups or poorly supported subclades, though this was not needed in the present study in which the major lineages for these very similar taxa are well resolved in the tree of maximum (interpreted) synapomorphy. The two relatively least supported nodes or vertices of the phylogenetic cluster dendrogram (discussed above) are, in fact, supported by the PCA analysis. Theoretically, the phylogram (Fig. 5) demonstrates that cladistically evinced evolutionary convergence in *Didymodon* would have adversely affected supraspecific classification by phenetic analysis in only a few species. Principal component analysis was less affected by apparent convergence than cluster analysis when both are compared with the results of cladistic analysis. To the extent that phenogram and cladogram agree, the possibility of potentially confounding convergence identified by cladistic homoplasy in classification is minimized.

TAXONOMIC RESULTS

Based on the results of the evolutionary analysis, species in *Didymodon* sect. *Asteriscium* (C. Müll.) Zand. and *Didymodon* sect. *Vineales* (Steere) Zand. are better associated with *Didymodon* sect. *Didymodon*. Given the high synapomorphy to autapomorphy ratio and the similarity of the terminal taxa (relatively few autapomorphies per taxon contributing to low patristic distance), at least the sectional classification may be considered a parsimonious hypothesis. That this supra-specific arrangement will obtain for the genus worldwide is doubtful, however, especially concerning the distinctive *D. nigrescens* and *D. australasiae* groups that terminate long branches, and further study is, of course, needed. But, in any case, based on the available information, the species of *Didymodon* in North American can be distributed as follows:

Sect. *Didymodon*: *D. anserinocapitatus* (L.-j. Li) Zand., *D. australasiae* (Hook. & Grev.) Zand., *D. brachyphyllus* Sull., *D. johansenii* (Williams) Crum, *D. nevadensis* Zand., *D. nicholsonii* Culm., *D. perobtusus* Broth., *D. revolutus* (Card.) Williams, *D. rigidulus* Hedw., *D. sinuosus* (Mitt.) Delong., *D. umbrosus* (C. Müll.) Zand., *D. vinealis* (Brid.) Zand.

Sect. *Fallaces* Steere: *D. asperifolius* (Mitt.) Crum, *D. fallax* Hedw., *D. ferrugineus* (Besch.) Hill., *D. giganteus* (Funck) Jur., *D. leskeoides* Saito, *D. maximus* (Syed & Crundw.) Hill., *D. michiganensis* (Steere) Saito, *D. nigrescens* (Mitt.) Saito, *D. subandreaeoides* (Kindb.) Zand., *D. topiaceus* (Brid.) Lisa.

ACKNOWLEDGEMENTS

I thank Patricia M. Eckel, Wayne K. Gall, James Lyons-Weiler, Charles A. Maynard, Gert S. Mogensen, Lloyd R. Stark, Kevin P. Smith and Tod Stuessy for helpful comments on early drafts or particular portions of this work, or who have been otherwise helpful. Through the Taxacom listserver (see archives for September through December 1997, http://kaw.keil.ukans.edu/mail_archives/taxacom) I profited from the shared perspectives accompanying the illuminating James Lyons-Weiler/Tom DiBenedetto debate, that included Sylvia Hope, Ted Schultz and others. Lyons-Weiler provided especially helpful comments, suggestions, and encouragement on

probabilistic aspects of phylogenetic analysis. Warren Kovach suggested methods of cluster analysis. For loans of *Didymodon* over the years, I thank the curators at many herbaria, especially ALA, BM, C, CANM, COLO, DUKE, F, FH, H, MICH, NY, PC, S, UBC, US, and WTU. Gratitude is extended to George F. Goodyear for the support he has given the Museum and its scientific divisions over the years.

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Note in Proof: Scotland (1997) recently argued that parsimony algorithms do not necessarily maximize character congruence or minimize homoplasy, through there remain problems with the definition of congruence. Parsimony minimizes the number of interpretations of synapomorphy (as steps per branch) but maximizes the number of terminal taxa affected by each synapomorphy. The phrase “tree of maximum synapomorphy” in the present paper, however, may be replaced with “the shortest tree” with little violence to my arguments against optimality criteria as these are used in phylogenetic inference.

(Scotland, R. W. 1997. Parsimony neither maximizes congruence nor minimizes incongruence or homoplasy. *Taxon* 46: 743–746).

Note added, December 29, 2008: Pianka (1986) diagrammed a PCA and phylogram combination detailing evolutionary ecomorphology of certain desert lizards. His phylogram is also available in his well-known text book (Pianka 1999: 343).

(Pianka, E. R. 1986. Ecology and Natural History of Desert Lizards. Analyses of the Ecological Niche and Community Structure. Princeton University Press.

Pianka, E. R. 1999. Evolutionary Ecology. Sixth Edition. Addison Wesley Longman, Inc., San Francisco.

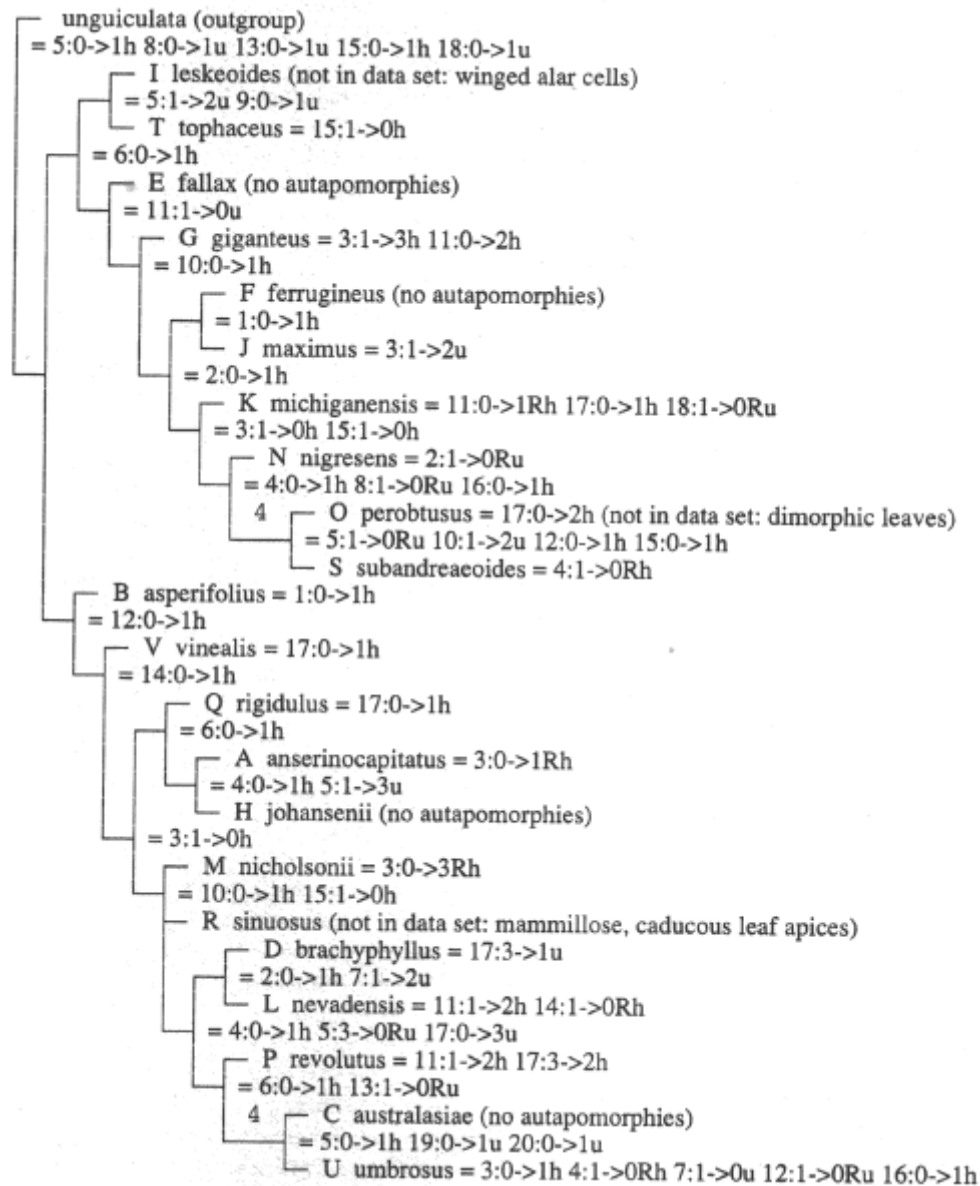


Figure 1. Phylogenetic tree of 22 species of *Didymodon*. Characters were mapped on the

consensus tree of 3 trees of maximum synapomorphy with tree length 63, consistency index 0.44. The outgroup is *Barbula unguiculata* Hedw. The capital letters correspond to these same species on the PCA diagram and Table 2. R = reversal; u = unique, appearing once in cladogram; h = homoplasy. Bremer support values are indicated above the branches where greater than 1.

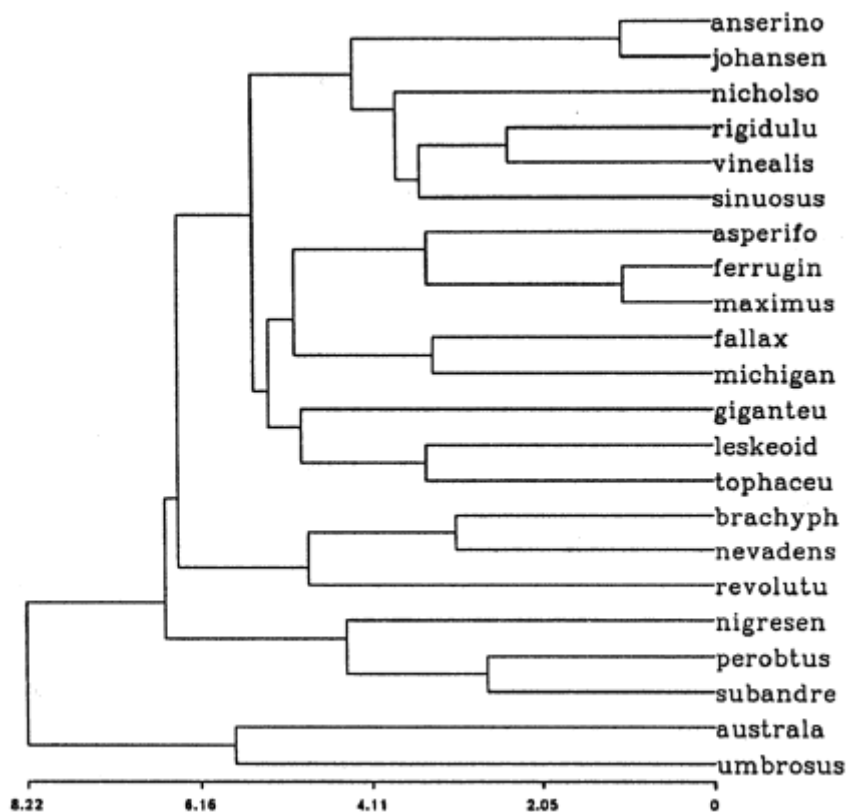


Figure 2. Dendrogram of UPGMA cluster analysis of 22 species of *Didymodon*, using standardized Euclidean distance.

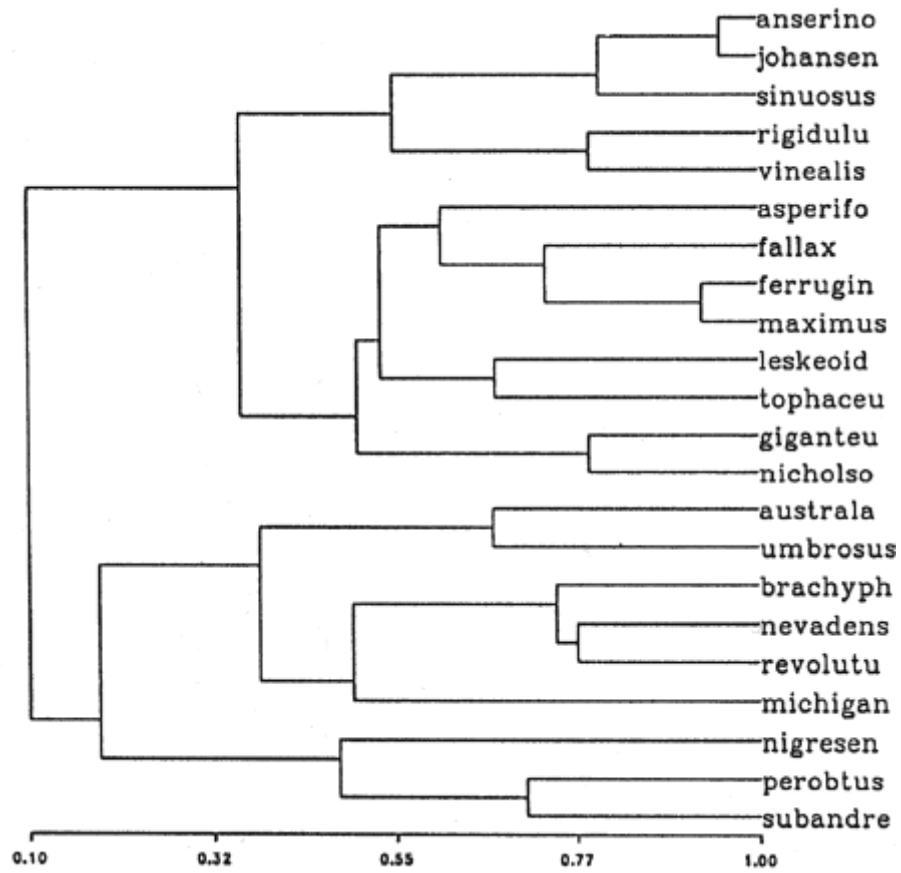


Figure 3. Dendrogram of UPGMA cluster analysis of 22 species of *Didymodon*, using an unstandardized Pearson product moment correlation coefficient.

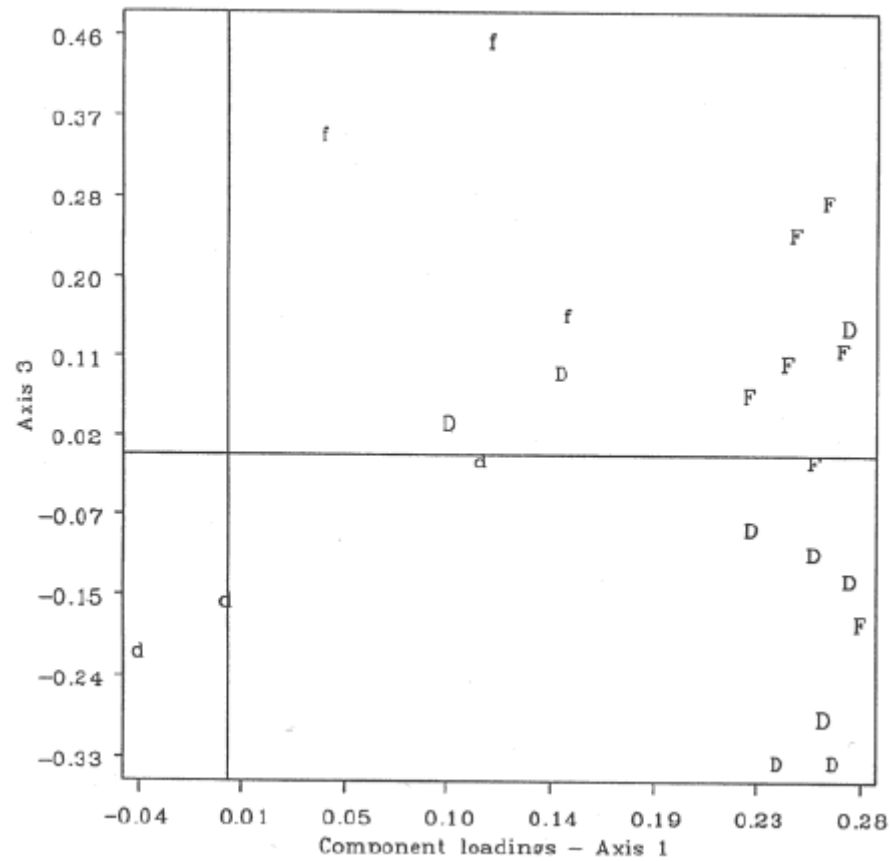


Figure 4. Principal component analysis of the data set, axes 1 and 3, Euclidean distance, standardized. D and d = species of *Didymodon* sect. *Didymodon*; F and f = species of *D.* sect. *Fallaces*. Lower case “d” refers to *D. australasiae* group, lower case “f” to *D. nigrescens* group. There is little interpenetration between the two sectional clusters.

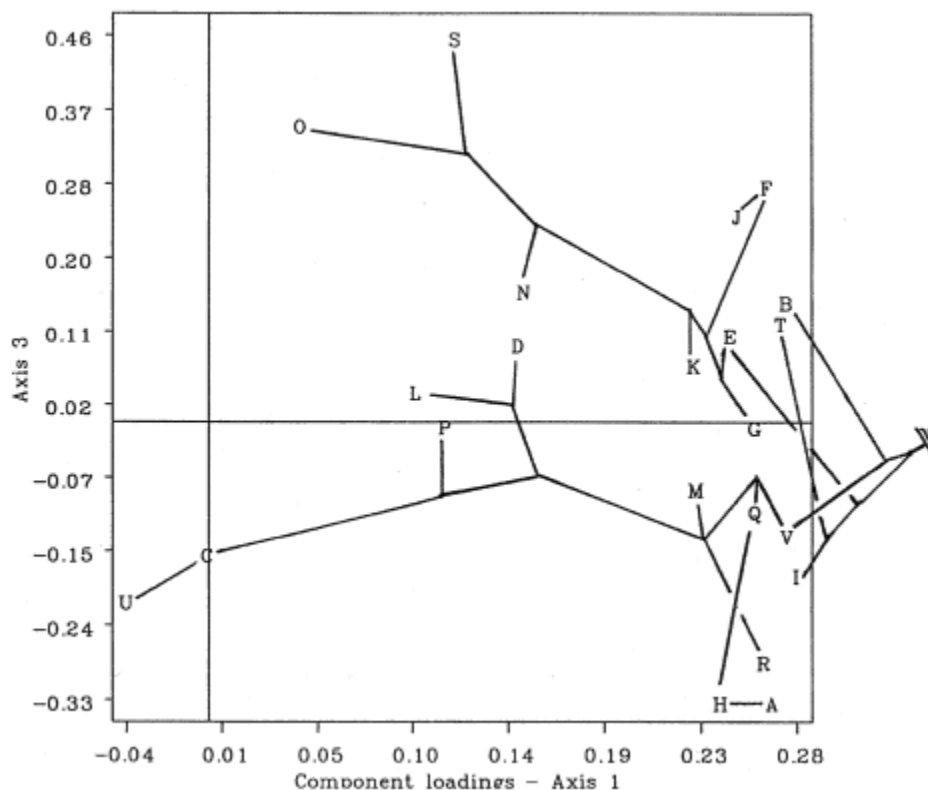


Figure 5. Phylogram combining principal component analysis and an evolutionary tree of maximum synapomorphy simplified from Fig. 1. The tree is rooted outside the square at the “ground” symbol. Letters correspond to list of species in Table 2 (see also Fig. 1). Species “C”, “E”, “F”, “H”, “Q” and “V” are possible surviving ancestors. The two main subclades branching from the root are sect. *Didymodon* and sect. *Fallaces*. The phylogram shows morphological convergence (length of branches are not significant), especially between the species pairs “A” and “R”, “B” and “T”, “G” and “M”, “I” and “V”, “D” and “N”.

Table 1. States of twenty characters scored in the data set of 22 *Didymodon* species.

1. Leaf stance when moist:
 0. spreading to weakly recurved, commonly lying flat when removed.
 1. strongly recurved, lying on their sides when removed.
2. Leaf shape:
 0. short- to long-lanceolate.
 1. deltoid to ovate-lanceolate.
3. Leaf length:
 0. 0.9–1.5 mm.
 1. 1.2–2.5 mm.
 2. 2.0–3.5 mm
 3. 3.5–5.0 mm
4. Leaf channeling above midleaf:

- 0. with a narrow groove along ventral surface of costa.
- 1. broadly channeled to nearly plane.
- 5. Leaf apex shape:
 - 0. rounded or obtuse (occasionally broadly acute).
 - 1. broadly to narrowly acute.
 - 2. very long acuminate, whiplike.
 - 3. swollen as a propagulum.
- 6. Leaf apex cells:
 - 0. of a clear conical cell or mucro:
 - 1. rounded and obscure.
- 7. Leaf margin flexion:
 - 0. plane or nearly so.
 - 1. recurved in lower 1/2 or 3/4.
 - 2. recurved or revolute to apex.
- 8. Leaf upper margin ornamentation:
 - 0. minutely crenulate.
 - 1. smooth or papillose.
- 9. Leaf base:
 - 0. gradually or quickly narrowed to the insertion.
 - 1. winged or auriculate.
- 10. Costa ending:
 - 0. clearly excurrent, usually as a short mucro.
 - 1. percurrent or ending to 2 cells before the apex
 - 2. ending more than 2 cells before the apex.
- 11. Costa width at midleaf:
 - 0. 2–3(–4) cells.
 - 1. 4–5(–6) cells.
 - 2. (5–)6–9 cells.
- 12. Costa superficial ventral cells:
 - 0. elongate, more than 2:1.
 - 1. quadrate or very short-rectangular (at least near apex).
- 13. Costa hydroids:
 - 0. present.
 - 1. absent.
- 14. Cells, upper laminal, layering:
 - 0. unistratose, rarely bistratose in patches.
 - 1. bistratose along margins, at apex, or often bistratose in patches.
- 15. Upper laminal cell lumens:
 - 0. mostly rounded.
 - 1. mostly angular.
- 16. Upper laminal papillae:
 - 0. absent or simple, bifid or multifid.
 - 1. low, massive and lens-shaped.
- 17. Propagula:
 - 0. absent.
 - 1. present, axillary, multicellular.
 - 2. present, axillary, unicellular.
 - 3. tubers present on rhizoids.
- 18. KOH color reaction of upper laminal cells:
 - 0. yellow or orange, occasionally negative.
 - 1. brick-red, seldom red-orange.
- 19. Basal cell walls:

0. firm, thin to thickened.
 1. very thin, hyaline.
 20. Well developed specimens with ventral costal stereid band:
 0. present.
 1. absent
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Table 2. Data set of 20 characters for 22 species of *Didymodon* and the outgroup *Barbula unguiculata*. Character states that were scored as variable in the cladistic analysis are underlined, otherwise they are as used in the PCA and cluster analyses. The capital letters map to the PCA ordination.

unguiculata	00100	01000	10000	00000
A anserinocapitatus	00113	11100	11111	00 <u>1</u> 00
B asperifolius	<u>1</u> 1101	0110 <u>1</u>	11101	00100
C australasii	0 <u>1</u> 011	11101	11010	03 <u>1</u> 11
D brachyphyllus	01010	02101	11110	01100
E fallax	0 <u>1</u> 101	11100	00101	00000
F ferrugineus	<u>1</u> 1101	1110 <u>1</u>	00101	00100
G giganteus	00301	11101	20101	00100
H johansenii	00013	11100	11111	00100
I leskeoides	00102	11110	10101	00100
J maximus	11201	1110 <u>1</u>	00101	00100
K michiganensis	01001	11101	10100	01000
L nevadensis	0101 <u>0</u>	02101	21100	03100
M nicholsonii	00301	01101	11110	00100
N nigresens	00011	11001	00100	10100
O perobtusus	01010	11002	01101	12100
P revolutus	00010	<u>1</u> <u>2</u> <u>1</u> <u>0</u> <u>2</u>	21010	0 <u>2</u> <u>1</u> 00
Q rigidulus	00001	1110 <u>1</u>	11111	01100
R sinuosus	00003	0110 <u>1</u>	11110	00100
S subandreaeoides	01000	11002	01101	10100
T tophaceus	0 <u>1</u> <u>1</u> <u>0</u> <u>1</u>	1111 <u>1</u>	10100	00 <u>1</u> 00
U umbrosus	00101	10101	10010	13 <u>0</u> 11

V vinealis

00101 01101 11111 01100
