

Systematics of North American *Petasites* (Asteraceae: Senecioneae). I. Morphometric analyses

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Abstract: *Petasites* Mill. (Asteraceae: Senecioneae) is a taxonomically difficult genus of polygamodioecious, perennial clonal herbs distributed across Canada, Alaska, and the northern contiguous United States. The taxonomic confusion surrounding the genus is reflected in the ambiguity of the various classification systems currently used. As many as ten species and as few as two species have been recognized (*Petasites sagittatus* (Banks ex Pursh) Gray and *Petasites frigidus* (L.) Fries with three varieties), in addition to one hybrid taxon. To determine if discrete groups could be recognized according to a combination of vegetative and (or) reproductive characters and thereby clarify the phenetic relationships among the taxa of *Petasites*, morphological data were subjected to principal components and discriminant analyses. Particular emphasis was placed on *P. frigidus* var. *frigidus*, *P. frigidus* var. *nivalis* sensu Bogle, and the purported hybrid between these taxa, which exhibits an intermediate morphology (the *frigidus* complex). Additionally, the specific status of *P. sagittatus* was investigated. Evidence obtained from multivariate morphometric analyses indicates that North American *Petasites* is comprised of four closely related polymorphic entities. While morphological variation among different taxa of *Petasites* is continuous for most reproductive characters, leaf characters were determined to be the most taxonomically discriminating. The entities of the *frigidus* complex form a cohesive group somewhat distinct from the other taxa. The morphological differentiation between *P. sagittatus* and other taxa of *Petasites* is not considered sufficient to warrant recognition of specific status. Therefore, we recommend that only one polymorphic species of *Petasites* in North America be recognized (*P. frigidus* with three varieties) in addition to one hybrid taxon originating from a cross between two of the varieties.

Key words: *Petasites*, Asteraceae, North America, systematics, principal components analysis, discriminant analysis.

Résumé : Le genre *Petasites* Mill. (Asteraceae: Senecioneae) est un genre taxonomiquement difficile d'herbacées pérennes polygamodioïques, distribuées à travers le Canada, l'Alaska et la partie nordique contiguë des États-Unis. La confusion taxonomique qui entoure ce genre est illustrée par l'ambiguïté des différents systèmes de classification présentement utilisés. On a reconnu autant que dix et aussi peu que deux espèces (*Petasites sagittatus* (Banks ex Pursh) Gray et *Petasites frigidus* (L.) Fries avec trois variétés), en plus d'un taxon hybride. Pour déterminer si on pourrait reconnaître des groupes distincts selon une combinaison de caractères végétatifs et (ou) reproductifs, et ainsi clarifier les relations phénétiques entre les taxons de *Petasites*, des données morphologiques ont été soumises à des analyses en composantes principales et par discrimination. On a mis une emphase particulière sur les *P. frigidus* var. *frigidus*, *P. frigidus* var. *nivalis* sensu Bogle, et le présumé hybride entre ces taxons, lequel montre une morphologie intermédiaire (le complexe *frigidus*). De plus, le statut spécial du *P. sagittatus* a été examiné. La preuve obtenue par les analyses morphométriques multivariées indique que le genre *Petasites* nord-américain comporte quatre entités polymorphiques étroitement reliées. Alors que la variation morphologique entre les différents taxons de *Petasites* est continue pour la plupart des caractères reproductifs, les caractéristiques foliaires apparaissent comme les plus discriminantes taxonomiquement. Les entités du complexe *frigidus* forment un groupe cohérent, quelque peu distinct des autres taxons. La différenciation morphologique entre le *P. sagittatus* et les autres taxons de *Petasites* n'est pas considérée suffisante pour reconnaître un statut spécifique. Conséquemment, les auteurs recommandent de ne reconnaître qu'une seule espèce polymorphique de *Petasites* pour l'Amérique du nord (*P. frigidus* avec trois variétés) en plus d'un taxon hybride provenant d'un croisement entre deux des variétés.

Mots clés : *Petasites*, Asteraceae, Amérique du nord, systématique, analyse en composantes principales, analyse par discrimination.

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Introduction

Petasites Mill. (Asteraceae: Senecioneae) is a taxonomically difficult genus in North America. Individuals are polygamodioecious, perennial, clonal herbs that are widely distributed, extending across Canada, Alaska, and the northern contiguous United States as far south as California. All North American taxa of *Petasites* have sympatric ranges in north-western North America.

Historically, North American species of *Petasites* have been recognized under two other generic names. Of the seven species of *Tussilago*, described by Linnaeus (1753), only *T. frigida* occurs in North America. Hooker (1833) transferred this taxon to *Nardosmia* and Fries (1845) later transferred it to *Petasites*. Similarly, many other North American taxa of *Petasites* were originally named as species of *Tussilago*, then *Nardosmia*, and then *Petasites*.

Numerous systematic treatments of *Petasites* have been generated since Linnaeus' time. Herder (1865) and Toman (1972) studied primarily Eurasian *Petasites*, while Pursh (1814), Hooker (1833), Gray (1876), Rydberg (1927), Hultén (1937; 1950; 1968), Cronquist (1946; 1953; 1978a), Bogle (1961; 1968), Scoggan (1979), Porsild and Cody (1980), and Packer (1983) examined primarily North American *Petasites*. A major difficulty has been the exclusive use of minor differences in leaf morphology for species definition and recognition. This has proven to be problematic, because the leaves exhibit a high degree of plasticity; therefore, the differences used to distinguish taxa are far from constant. The relationships between leaf form and taxon delimitation have not been uniquely defined, and this is reflected in such commonly used classifications as those of Rydberg (1927), Cronquist (1978a), Hultén (1950), Bogle (1968), Scoggan (1979), Porsild and Cody (1980), and Packer (1983). Figure 1 compares their systematic treatments. The species circumscription of *Petasites* has varied substantially, with as many as ten (Rydberg 1927) and as few as two (Cronquist 1978a; Bogle 1968) species described in North America.

Although the circumscription of *Petasites sagittatus* (Banks ex Pursh) Gray appears to exhibit the highest degree of integrity of all taxa across the various systematic treatments (Fig. 1), the intergrading morphological links between it and other taxa in the genus have prompted questions about its taxonomic status as a species. Hooker (1833) first recognized that the species in this group were distinguished by minute differences only, and although he maintained the taxa as separate species, he suggested that they all might be conspecific. Bogle (1968) did not discard such a possibility, but recommended additional research to test this hypothesis.

Although intergradation of the various leaf forms was acknowledged by most authors, few accounted for it in their systematic treatments. Only Bogle (1968) and Hultén (1937; 1950; 1968) attempted to describe and explain the origin of these intergrading leaf forms. Hultén (1950; 1968) indicated the occurrence of hybrid swarms of *Petasites frigidus* (L.) Fries – *P. sagittatus* and *P. frigidus* – *Petasites hyperboreus* Rydb. where their ranges overlapped. He designated the latter as *P. frigidus* var. *hyperboreoides* in 1937. Bogle (1961) agreed with Hultén's circumscriptions for the most part, although he ranked the taxa at the varietal level and chose to designate the hybrids with a hybrid formula.

The various circumscriptions of *Petasites warrenii* St. John, *Petasites trigonophylla* Greene, and *Petasites vitifolius* Greene are also depicted in Fig. 1. Unexpected findings emerged from Bogle's (1961) investigation of *P. warrenii*, a supposed endemic of Washington State. By performing a series of crossing studies, he elucidated the relationship of this species with the other taxa of *Petasites*. He concluded that *P. warrenii*, *P. vitifolius*, and *P. trigonophylla* were all members of a large, diverse group originating from hybridization between *P. sagittatus* and *Petasites frigidus* var. *palmatus* (Ait.) Cronq. The hybrid designation *P. xvitifolius* was proposed by Bogle (1968) to include the various members of this group (Fig. 1). Although Porsild and Cody (1980) and Packer (1983) acknowledged Bogle's research, they continued to retain this taxon at the specific rank.

Except for crossing studies (Bogle 1961) and chromosome number determinations (Cherniawsky 1994; Morton 1981; Löve 1975; Johnson and Packer 1968; Ornduff et al. 1963) no other biosystematic research has been performed on the North American taxa of *Petasites*.

Working classification of North American *Petasites*

Our working classification of *Petasites* was based on our interpretation of the various authors' keys, descriptions, type specimens, and annotations on herbarium specimens. It most closely follows Bogle (1968) and recognizes six groups. We use specific epithets only (refer to Fig. 1). Our concept of *frigidus* and *nivalis* is in accordance with Bogle's (1968) for *P. frigidus* var. *frigidus* and var. *nivalis*, respectively. These two taxa and the forms intermediate in morphology between them are collectively referred to as the *frigidus* complex. The intermediate forms are denoted simply as "intermediates". The taxa *palmatus*, *sagittatus*, and *vitifolius* are recognized sensu Bogle's *P. frigidus* var. *palmatus*, *P. sagittatus*, and *P. xvitifolius*, respectively. Figure 2 provides comparative illustrations of the leaves of the six groups.

The taxon *frigidus* is characterized by sagittate, deltoid to cordate leaf blades, which are regularly or irregularly dentate, or very shallowly or deeply, equally or unequally lobed (Figs. 2a–2c). The geographical range of this taxon includes North America and Eurasia. Compared with the other taxa of *Petasites* in North America, *frigidus* exhibits the most restricted range, being common in Alaska, the Yukon, the Northwest Territories, and several Arctic islands and extending into more southern limits in mountainous regions of British Columbia and Alberta.

The highest degree of leaf dissection of all North American taxa is exhibited by *nivalis*. The most extreme forms are five parted and shallowly to deeply lobed. Many lobes have at least two lateral triangular teeth that frequently overlap, and sinuses are oblong and closed. Figure 2d is a representative of this leaf form, which exhibits a moderate degree of dissection. Figure 2e exhibits a lesser degree of dissection than Fig. 2d. As does *frigidus*, *nivalis* inhabits moist alpine to subalpine slopes, although it also occurs at much lower altitudes (1050 m; Bogle 1961). The geographic range of *nivalis* is considered to be concurrent with much of the range of *frigidus*. However, *nivalis* is absent from arctic Canada and the eastern Keewatin District and extends southward to British Columbia, Alberta, and Washington.

Figures 2f and 2g represent leaf forms intermediate between

Fig. 1. Comparative systematic treatments of North American *Petasites*. The squares denote the circumscription of the various taxa. The absence of squares indicates that the author has not included that particular taxon in his treatment.

Rydberg 1927	Cronquist 1978a	Hultén 1950	Bogle 1968	Scoggan 1979	Porsild & Cody 1980	Packer 1983
<i>P. sagittatus</i> = <i>P. dentatus</i>	<i>P. sagittatus</i>	<i>P. sagittatus</i>	<i>P. sagittatus</i>	<i>P. sagittatus</i>	<i>P. sagittatus</i>	<i>P. sagittatus</i>
		* <i>P. frigidus</i> X <i>P. sagittatus</i>	* <i>P. f. var. frigidus</i> X <i>P. sagittatus</i>			
<i>P. alaskanus</i> ¹	<i>P. frigidus</i> var. <i>frigidus</i>	<i>P. frigidus</i>	<i>P. frigidus</i> var. <i>frigidus</i>	<i>P. frigidus</i>		
<i>P. gracilis</i> ²						
<i>P. frigidus</i>					<i>P. frigidus</i>	
		** <i>P. frigidus</i> X <i>P. hyperboreus</i> = <i>P. f. var.</i> <i>hyperboreoides</i> = 1, 2, 3	** <i>P. f. var. frigidus</i> X <i>P. f. var. nivalis</i>			
<i>P. nivalis</i>	<i>P. frigidus</i> var. <i>nivalis</i> incl. <i>P. warrenii</i>	<i>P. hyperboreus</i>	<i>P. frigidus</i> var. <i>nivalis</i>	<i>P. vitifolius</i>		<i>P. nivalis</i>
<i>P. hyperboreus</i>						<i>P. hyperboreus</i>
<i>P. vitifolius</i> = <i>P. trigonophylla</i>						<i>P. vitifolius</i> = <i>P. f. var.</i> <i>palmatus</i> X <i>P. sagittatus</i>
<i>P. hookerianus</i>	<i>P. frigidus</i> var. <i>palmatus</i> = <i>P. arcticus</i> ³	<i>P. palmatus</i>	<i>P. frigidus</i> var. <i>palmatus</i>	<i>P. palmatus</i>	<i>P. palmatus</i>	<i>P. palmatus</i>
<i>P. palmatus</i>						
<i>P. speciosus</i>						
					<i>P. arcticus</i>	<i>P. arcticus</i>

* denotes the hybridization between *P. frigidus* and *P. sagittatus* as proposed by Hultén (1950) and supported by Bogle (1968).

** denotes the hybridization between *P. frigidus* and *P. hyperboreus* as proposed by Hultén (1950). Hultén designated this hybrid as *P. frigidus* var. *hyperboreoides* and included *P. alaskanus*, *P. gracilis*, and *P. arcticus* as additional products of such hybridization events. This proposal has been supported by Bogle (1968), in part, although he preferred to recognize *P. frigidus* as the typical variety of this species, *P. hyperboreus* as *P. frigidus* var. *nivalis*, and *P. arcticus* as a synonym of *P. frigidus* var. *palmatus*.

frigidus and *nivalis* (*P. frigidus* × *P. nivalis* sensu Hultén 1950; 1968). Taxa with these leaf forms, are, by far, the most confusing to identify because of their morphological intermediacy. Figure 2*h* illustrates a plant with leaves characteristic of both *frigidus* and *nivalis*. Figure 2*i* shows a plant possessing leaves typically associated with both *frigidus* and *frigidus* × *nivalis*.

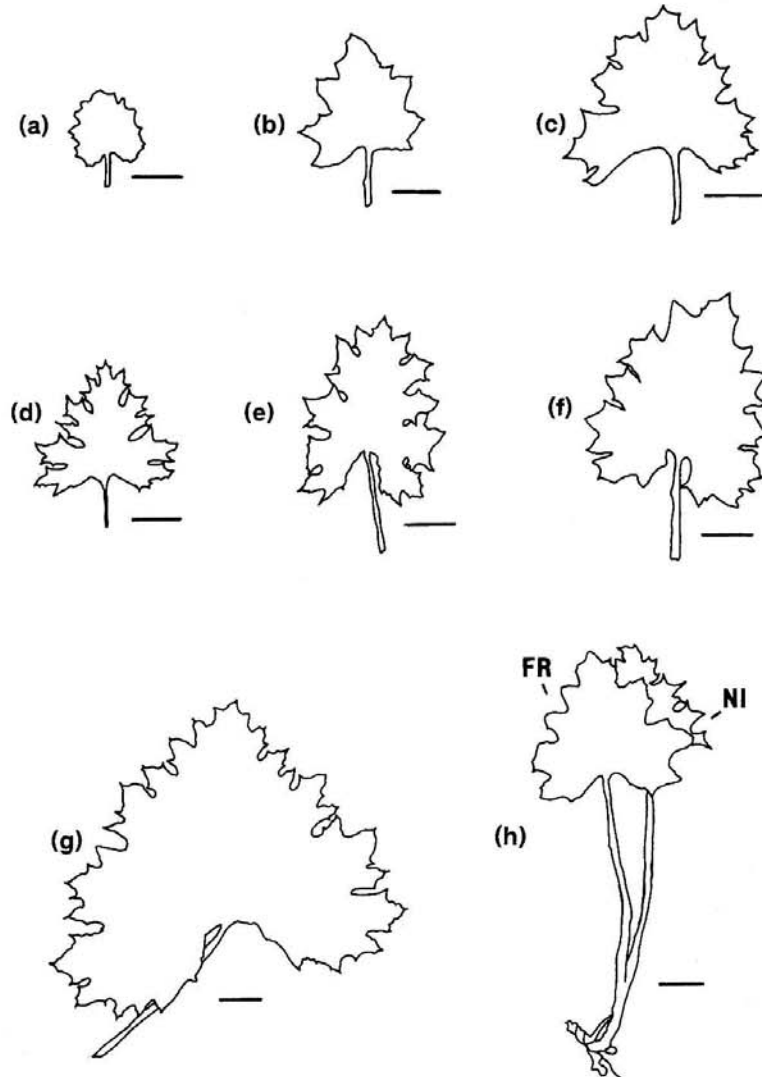
The taxon *palmatus* is characterized by orbicular to reniform leaf blades with palmately divided foliage of five to nine entire or dentate lobes usually divided more than half way to the leaf base (Fig. 2*j*). Like the others, the highly variable size and stature of this taxon has resulted in the naming of several different segregates (Fig. 1). Of all taxa of *Petasites*, *palmatus* is the most widely distributed in North America, although it is

absent from Alaska and arctic Canada. It extends from the northwestern Yukon Territory to the western Mackenzie District and across all provinces of Canada. Its range extends southward to Maine, Massachusetts, and New York and continues westward to Michigan, Wisconsin, Minnesota, Washington, Oregon, and as far south as Monterey County, California.

The taxon *sagittatus* is characterized by sagittate (Fig. 2*k*) and hastate (Fig. 2*l*) to cordate leaf blades that are entire to dentate, varying from wavy to conspicuously dentate. This taxon is often found growing in association with *palmatus* and *vitifolius*. The geographic range of *sagittatus* is similar to that of *palmatus* although it extends into Alaska but not California.

The hybrid taxon *vitifolius* exhibits a morphology interme-

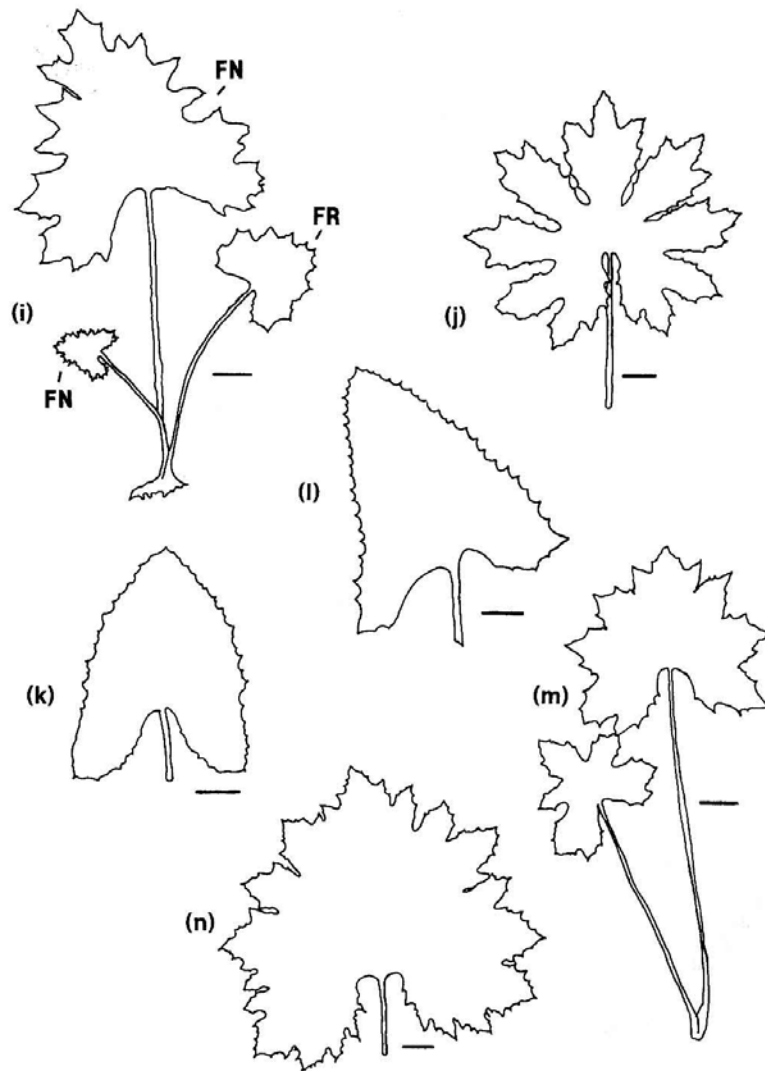
Fig. 2. A comparative illustration of the vegetative morphology for the six groups recognized in *Petasites*. Scale bar = 2 cm. (a) Leaf of *frigidus* exhibiting typical morphology, A.R. Batten 226 (ALA-52583); (b) leaf of *frigidus* exhibiting typical morphology, S.G. Aiken and K.I. McLachlan 87-144 (CAN-530972); (c) leaf of *frigidus* exhibiting typical morphology, R.T. Porsild 1384 (CAN-318264); (d) leaf of *nivalis* exhibiting a moderate degree of dissection, W.C. McCalla 9307 (ALTA-67297); (e) leaf of *nivalis* exhibiting a lesser degree of dissection than in Fig. 2d, D.J. Cooper 1080 (ALA-98624); (f) leaf exhibiting morphology intermediate between *frigidus* and *nivalis*, F.W. True and D.W. Prentis, Jr. 37 (US-241413); (g) leaf exhibiting morphology intermediate between *frigidus* and *nivalis*, C. Schweger 178 (ALA-3422);



diolate to its parental taxa, *palmatus* and *sagittatus*. It is characterized by reniform to deltoid or, more frequently, cordate leaf blades, which are usually widest at the base with convex-curved edges (Figs. 2m and 2n). There are 4–14 shallow, entire to dentate triangular primary lobes and as many as 11 secondary lobes. Many juvenile forms closely resemble *frigidus*

(Bogle 1961), causing further taxonomic confusion in *Petasites*. Commonly found in wet conditions preferred by *sagittatus*, *vitifolius* also lives in drier regions in association with both *palmatus* and *sagittatus*. The geographical range of this hybrid extends somewhat beyond the sympatry zone of *palmatus* and *sagittatus* but is less extensive than the range

(h) specimen possessing leaves characteristic of both *frigidus* (FR) and *nivalis* (NI), R. Brockman 25 (ALA-28549); (i) specimen possessing leaves characteristic of both *frigidus* (FR) and *frigidus* × *nivalis* (FN), A. Batten 76-134 (ALA-78703); (j) leaf of *palmatus* exhibiting typical morphology, W.C. McCalla 11308 (ALTA-67285); (k) leaf of *sagittatus* with sagittate shape, W.C. McCalla 2530 (ALTA-67301); (l) leaf of *sagittatus* with hastate shape, S.S. Talbot 2186 (ALTA-49620); (m) plant of *vitifolius*, W.C. McCalla 3704 (ALTA-6728); and (n) leaf of *vitifolius*, W.C. McCalla 9367 (ALTA-76767).



of either parent. Its distribution includes the south-eastern Yukon Territory, the southwestern Mackenzie District, British Columbia, the prairie provinces of Canada, Ontario, central Quebec, Labrador, and south to northern Michigan, northern Minnesota, and Washington State.

Research objectives

The primary objective for the first part of this research is to redefine the phenetic relationships among the different morphological entities of *Petasites* native to North America. Particular attention is focused on the *frigidus* complex because of

the high degree of morphological intergradation among its entities and its inconsistent circumscription across the various systematic treatments. Additionally, *sagittatus* is investigated to determine if its morphological differentiation from the other taxa warrants specific taxonomic recognition.

This will be accomplished using multivariate morphometric analyses, including principal components analysis (PCA) and discriminant analysis (DA). This is the first study that utilizes these techniques to examine phenetic relationships among North American taxa of *Petasites*. Multivariate morphometric analyses provide an assessment of morphological relationships of various taxa. A PCA can indicate which characters provide the greatest contribution to differences among taxa. It is used to show if distinct groups can be recognized without designation of a priori groups (Wiley 1981). In contrast, a DA assigns individuals to groups a priori. It estimates the correct classification rates of the individuals assigned to these groups and determines the discriminating characters among the different taxa. A set of morphological characters that delimits the various taxa will be determined and then integrated into a key, which will be provided in a future publication (D.M. Cherniawsky and R.J. Bayer, unpublished).

Materials and methods

Data for the morphological studies were obtained from pressed specimens collected in the spring of 1991 from 51 populations in Alberta, British Columbia, the Yukon Territory, and Alaska (vouchers are deposited at ALTA). Due to the rhizomatous habit of *Petasites*, plants were collected a few metres apart to avoid sampling from the same vegetative clone. Herbarium specimens were selected to represent the entire geographical range of *Petasites* and to reflect the morphological variability present within each taxon. These were borrowed from various herbaria including the University of Alaska (ALA), the University of Alberta (ALTA), the National Museum of Canada (CAN), the University of British Columbia (UBC), the United States National Herbarium (US), the University of Wisconsin (WIS), and Washington State University (WS). Illustrations of the leaf morphologies for the various taxa of *Petasites* were created by drawing the traced outlines of photocopied herbarium specimens (Fig. 2).

Characters selected for analyses included those most frequently utilized in keys and diagnoses of the various taxa. Characters considered useful by the authors in reliable identification were also selected.

All specimens used in the analyses were in a mature stage of development: leaves fully expanded; anthers of the functionally staminate florets (from here on "staminate") with abundant pollen; and styles of the functionally pistillate florets (from here on "pistillate") elongated. The outermost series of phyllaries of the inflorescences were not measured because of observable damage; therefore, the next inner series of phyllaries were used instead. Measurements were taken with a hand ruler and an ocular micrometer.

Leaf form, described in terms of lobes and teeth, is defined for this study by the authors as follows. A primary lobe is the leaf region separated by two sinuses (a sinus must extend at least one quarter of the distance between the leaf margin and midrib). Secondary lobes are defined as protuberances on the primary lobes that are at least one third the length of the primary lobe. Teeth are defined as protuberances of the leaf margin that are less than one third the length of the primary lobes. If there are no lobes, any protuberances are regarded as teeth.

As a result of the polygamodioecious nature of *Petasites* and the tendency to produce short-lived reproductive inflorescences before emergence of the leaves, most specimens possessed only one kind of inflorescence (functionally staminate or functionally pistillate) or only leaves. Therefore, it was necessary to compile separate data sets

for individuals with pistillate heads, staminate heads, and leaves. To circumvent the problem of misidentifying taxa based on floral morphology alone, only those specimens with both flowers and leaves were used in the pistillate or staminate data set. However, in most specimens where both leaves and flowers were present, the leaves were in an immature stage of development and could not be included in the leaf data set. The initial data matrices were constructed from 17 vegetative characters, 24 staminate characters, and 25 pistillate characters, in addition to latitude and longitude (Table 1). One mature leaf per plant and one staminate or pistillate floret per inflorescence per plant represented one individual. In total, 271 leaves, 150 staminate florets, and 132 pistillate florets were measured for the various attributes (Cherniawsky 1994).

Morphological variation within and among taxa of *Petasites* was assessed using univariate statistics (mean, standard deviation, variance) and multivariate morphometric analyses (PCAs and DAs). The same data matrices constructed for leaf, staminate, and pistillate characters of *Petasites* were used for both PCAs and DAs, except that latitude and longitude were excluded from the DA. Latitude and longitude were removed to determine the most discriminating morphological characters without the influence of these two variables. The PCAs were produced with the NTSYS program, version 1.2 of Rohlf (1987). The STAND, SIMINT, EIGEN, and PROJ subcommands were employed to complete the analyses. The DAs (direct method) and univariate statistics were generated by SPSS for Microsoft Windows, release 6.0. The subcommands DESCRIPTIVES, GROUPS, VARIABLES, STATISTICS, MISSING (individuals with missing data were included), and PLOT were used to execute these analyses. Three-dimensional coordinates obtained from the DAs and PCAs were plotted by Sigmaplot graphics for Windows, version 2.01 (Jan-del Corporation 1994) to produce scatter diagrams.

Results

Univariate statistics, in addition to the minimum and maximum values for each character for each taxon in *Petasites*, are shown in Cherniawsky (1994). Values overlap extensively for all characters across all taxa.

Principal components analyses

Leaves

The first three principal components (PCs) account for 60.54% of the total variance of the data (27.0, 24.2, and 9.4% for PC1, PC2, and PC3, respectively). In decreasing order, PC1 has highest loadings for sinus depth, perimeter, maximum width, and pubescence on the abaxial surface; PC2 has the highest loadings for number of teeth, maximum length, sinus shape, and distance from apex to widest portion of leaf; and PC3 has the highest loadings for longitude and shape.

The scatter diagram of the leaf results is presented in Fig. 3. The best separation of groups is obtained when the first two PCs are plotted (only these results are presented). Two distinct groups are evident. One group consists of *sagittatus*, and the other includes all other taxa, except for four individuals of *frigidus* that are closely associated with *sagittatus*. The similarity that unites these individuals to *sagittatus* is the lack of sinuses; these individuals are merely toothed. The taxa *palmasus* and *vitifolius* are virtually inseparable.

Staminate inflorescences

The first three PCs account for 34.02% of the total variance of the data (13.2, 12.0, and 8.8% for PC1, PC2, and PC3, respectively). No specific characters provide a substantial contribu-

Table 1. Morphological characters and character states for leaves, staminate inflorescences, and pistillate inflorescences of *Petasites* used in principal components analyses and discriminant analyses.

Characters (character state)	Abbreviation
Leaves	
Shape of leaf: (1) sagittate, (2) deltoid, (3) reniform, (4) cordate-reniform, (5) cordate, (6) orbicular	SHAPE
Maximum leaf width (cm)	MAXW
Maximum leaf length (cm)	MAXL
Distance from apex to widest portion of leaf (cm)	APWID
Angle between apex and closest lobe of leaf (degrees)	APANGL
Angle between leaf base and petiole (degrees)	BAPANGL
No. of primary lobes	NO1LOB
No. of secondary lobes	NO2LOB
Apex shape of primary lobes: (1) obtuse, (1.5) intermediate, (2) acute, (3) both	LBAPSHP
No. of teeth	NOTETH
Teeth shape: (1) crenate, (2) dentate, (3) minute	TETHSHIP
Depth of deepest sinus (cm)	SINDEP
Width of deepest sinus (cm)	SINWID
Base shape of deepest sinus: (1) rounded, (2) pointed	SINSHP
Perimeter of leaf (cm)	PERI
Pubescence of adaxial surface: (0) glabrous to (4) tomentose	PUBAD
Pubescence of abaxial surface: (0) glabrous to (5) villose	PUBAB
Latitude	LAT
Longitude	LONG
Staminate inflorescences	
No. of heads	NOHEADS
Phyllary width (mm)	PHYLWI
Phyllary length (mm)	PHYLLEN
Margin of phyllaries: (1) entire, (2) serrate, (2.5) intermediate	PHYLMAR
No. of ray florets/head	NORF
Position of ray florets: (1) peripheral, (2) central	POSRF
Ray length (mm)	RL
Ray width (mm)	RW
Style length (mm)	STYLEN
Length of style branches (mm)	LENSTBR
Texture of style surface: (1) papillose, (2) hairy	STYTEX
Pappus length of ray florets (mm)	PAPLENRF
No. of disc florets/head	NODF
Position of disc florets: (1) peripheral, (1.5) both, (2) central	POSDF
Corolla length (mm)	CORLEN
Corolla lobe width (mm)	CORLBWI
Style length (mm)	STYLENG
Length of style branches (mm)	LENGSTBR
Texture of style surface: (1) papillose, (1.5) intermediate, (2) hairy	STYLTEX
Length of anthers (mm)	LENANTH
Shape of anther apical appendage: (1) round, (2) triangular, (3) intermediate	SHPANAPP
Shape of corolla lobes: (1) rounded, (1.5) intermediate, (2) triangular, (3) both	SHPCORLB

Table 1. (concluded).

Characters (character state)	Abbreviation
Pappus length of disc florets (mm)	PAPLENDF
Disc corolla lobe length (mm)	DCLL
Latitude	LAT
Longitude	LONG
Pistillate inflorescences	
No. of heads	NOHEADS
Phyllary width (mm)	PHYLWI
Phyllary length (mm)	PHYLLEN
Margin of phyllaries: (1) entire, (2) serrate, (2.5) intermediate	PHYLMAR
No. of ray florets/head	NORF
Position of ray florets: (1) peripheral, (1.5) both, (2) central	POSRF
Ray length (mm)	RL
Ray width (mm)	RW
Style length (mm)	STYLEN
Length of style branches (mm)	LENSTBR
Texture of style surface: (1) papillose, (2) hairy	STYTEX
Pappus length of ray florets (mm)	PAPLENRF
Achene length (mm)	ACHLEN
No. of disc florets/head	NODF
Position of disc florets: (1) peripheral, (2) central	POSDF
Corolla length (mm)	CORLEN
Corolla lobe width (mm)	CORLBWI
Style length (mm)	STYLENG
Length of style branches (mm)	LENGSTBR
Texture of style surface: (1) papillose, (2) hairy	STYLTEX
Length of anthers (mm)	LENANTH
Shape of anther apical appendage: (1) round, (2) triangular, (3) intermediate	SHPANAPP
Shape of corolla lobes: (1) rounded, (1.5) intermediate, (2) triangular	SHPCORLB
Pappus length of disc florets (mm)	PAPLENDF
Disc corolla lobe length (mm)	DCLL
Latitude	LAT
Longitude	LONG

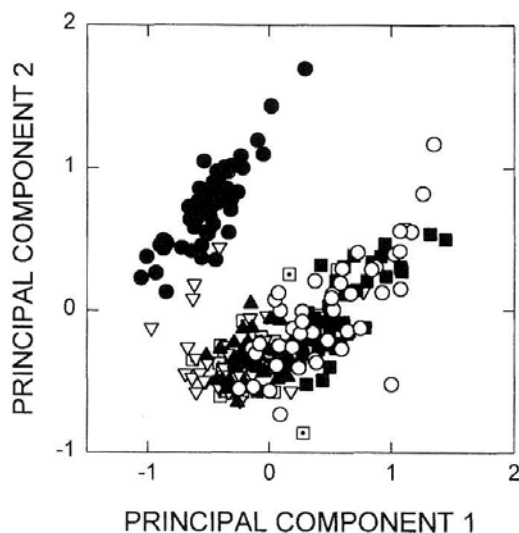
Note: Units of measurement are given in parentheses. Latitude and longitude were excluded from the discriminant analyses.

tion to the total variance. PC1 has the highest loadings for ray length, style length of ray florets, texture of style of disc florets, number of heads, and latitude; PC2 has the highest loadings for disc corolla lobe length, pappus length of disc florets, and phyllary length; and PC3 has the highest loadings for length of anther apical appendage and longitude. The best separation of groups occurs with the ordination of the first two principal components; therefore, only they are shown (Fig. 4).

No strong discontinuities exist among taxa of *Petasites* with respect to staminate characters. Much overlap among all taxa occurs in the central region of the scatter diagram. Although outliers of *frigidus* and *palmatus* aid in the separation of these taxa, many members of *frigidus*, in addition to *sagittatus* and *vitifolius*, are intermediate between these two extremes.

PC1 provides better separation of *frigidus* and *palmatus* than does PC2. Ray length and latitude are important characters that permit the differentiation of these taxa. Plants of *pal-*

Fig. 3. Scatter diagram from principal components analysis results of leaf characters for taxa of *Petasites*. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.



matus have some of the shortest rays, whereas plants of *frigidus* have some of the longest rays and also occur at higher latitudes than *palmatus*. Some individuals of *palmatus* are greatly separated from the rest of this taxon, because they possess the longest disc corolla lobes, the longest pappus of disc florets, and the longest phyllaries. Similar to the results for leaf morphology (Fig. 3), there is a large proportion of overlap for staminate characters among taxa of the *frigidus* complex.

Pistillate inflorescences

The first three PCs account for 33.46% of the total variance of the data (13.6, 11.0, and 8.8% for PC1, PC2, and PC3, respectively). PC1 has the highest loadings for style length of ray florets, style length of disc florets, phyllary length, phyllary width, and longitude; PC2 has the highest loadings for ray length, number of heads, and latitude; and PC3 has the highest loadings for pappus length of ray florets and achene length.

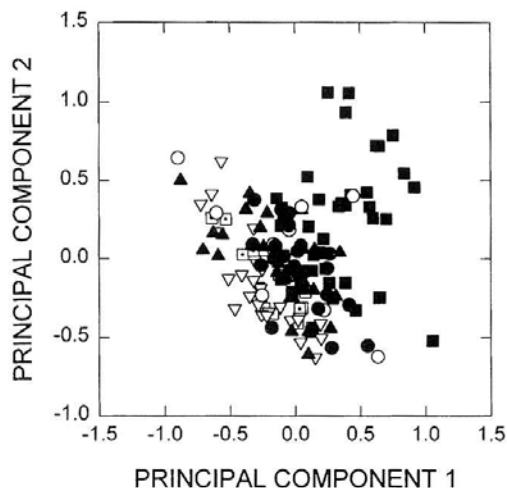
The ordination of PC1 and PC2 is presented in Fig. 5. There is virtually no separation of taxa, although extremes of *frigidus* and *palmatus* separate to some degree along PC2. This separation may be attributed to the wide range of ray lengths for *palmatus* (Cherniawsky 1994). Additionally, *palmatus* possesses the greatest number of heads, whereas *frigidus* possesses the fewest number and occurs at higher latitudes than *palmatus*.

Discriminant analyses

Leaves

Results from significance tests for the equality of group means for each character are computed as *F* ratios. Characters with

Fig. 4. Scatter diagram from principal components analysis results of staminate characters for taxa of *Petasites*. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.

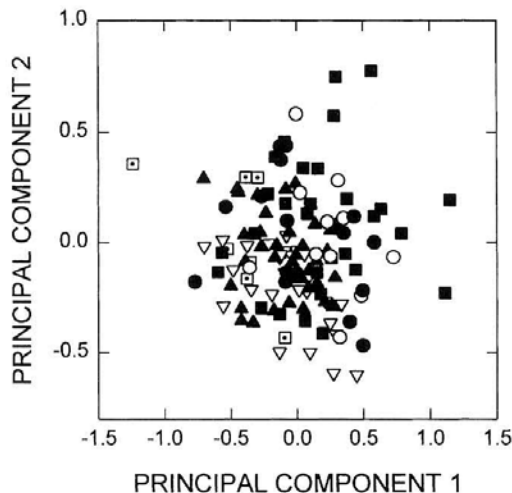


the highest *F* ratios are, in decreasing order, number of primary lobes, sinus shape, sinus depth, number of teeth, shape, and number of secondary lobes. Group means for characters except lobe apex shape, teeth shape, adaxial pubescence, and abaxial pubescence are significantly different.

The percentages of between-group variances for functions 1–5 is 69.2, 18.9, 8.2, 3.5, and 0.2%, respectively. The correlation coefficients between discriminating characters and canonical discriminant functions show that the number of primary lobes and sinus shape are the most discriminating characters for function 1. These are the same characters with the highest *F* ratios. The characters that best discriminate taxa for function 2 are number of teeth, shape, and sinus depth. These characters are the same ones that had the highest loadings for PC1–PC3 in the PCA. The number of secondary lobes, angle from apex to nearest lobe, and sinus width are the characters with the most discriminating power along function 3. Several characters that also show relatively high coefficients are not included, because they are highly correlated with one another (Cherniawsky 1994). This presupposes them to carry more weight as discriminating characters, when in fact, they may not be meaningful (Norusis 1988). These character relationships include perimeter, maximum width, maximum length, and distance from apex to widest portion of leaf.

The discriminant scores of the individuals and centroids are plotted in Fig. 6. A centroid represents the average individual computed from all the means of characters for that particular taxon. Results from functions 1 and 2 are presented, because they account for most of the variation and yield the best separation of taxa. The DA provides greater separation of taxa than the PCA. The reason for this is that the DA is constrained by forcing it to recognize the existence of six groups, whereas the PCA is not constrained in this manner. Three groups are evident in Fig. 6a. The first group, comprised of *sagittatus* indi-

Fig. 5. Scatter diagram from principal components analysis results of pistillate characters for taxa of *Petasites*. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.



viduals, appears to be the most distinct. It achieves its best separation from the other taxa along function 1. The second group, the *frigidus* complex, and the third group, including *palmatus* and *vitifolius*, are more weakly defined along function 2.

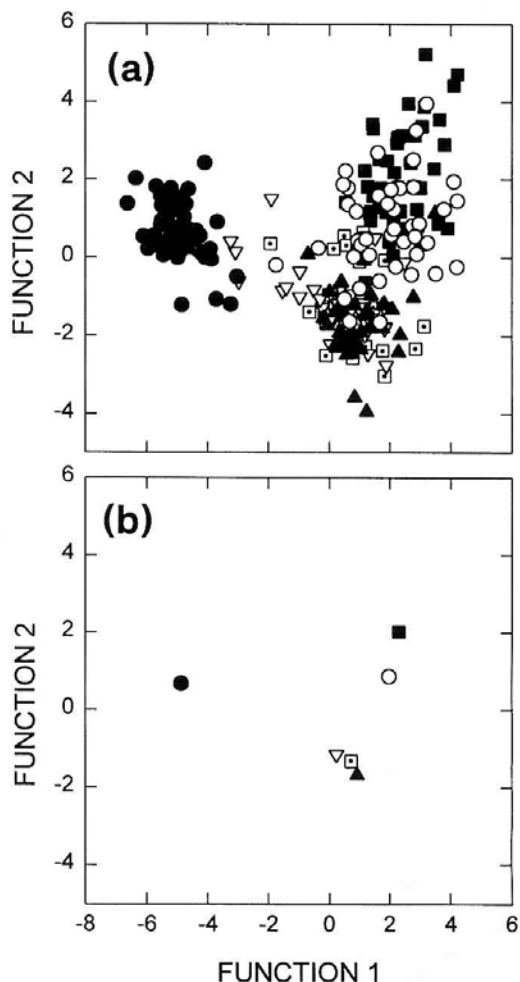
The separation of *sagittatus* from the other taxa along function 1 is mostly due to a lack of lobes and sinuses. As in the PCA, the absence of lobes in some individuals of *frigidus* places them closer to *sagittatus* than to other members of *frigidus*.

The possession of the smallest number of teeth (0–32) and the shallowest sinuses (0–5.20 mm) segregates the *frigidus* complex from the other taxa. The possession of the deepest sinuses in *palmatus* and *vitifolius* (0.38–8.90 and 0.40–6.90, respectively) promotes their close association. Additionally, being the only taxon with orbicular shaped leaves, *palmatus* is further removed from the other taxa.

The overlapping range of values for discriminating characters within the *frigidus* complex illustrates the morphological similarity among its three entities. A comparison of values for the *frigidus* complex is given in Table 2. The proximity of the centroids in this complex clearly shows their close association (Fig. 6b).

Correct classification rates for *frigidus* × *nivalis*, *frigidus*, *nivalis*, *palmatus*, and *vitifolius* are 35.9, 72.7, 66.0, 83.0, and 76.1%, respectively (Table 3). All individuals of *sagittatus* were correctly classified, indicating that it is the most morphologically distinct taxon. The *frigidus* complex appears cohesive, as misclassified operational taxonomic units (OTUs) are more likely to be assigned to another taxon within the complex than to a taxon outside the complex. For *frigidus*, however, the rate of misclassification within the complex is the same as it is outside the complex.

Fig. 6. Scatter diagrams from discriminant analysis results of leaf characters for taxa of *Petasites* including (a) all individuals and (b) centroids only. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.



Staminate inflorescences

Results from significance tests for the equality of group means show that characters with the highest *F* ratios are, in decreasing order, number of heads, style texture of disc florets, number of ray florets, and length of style branches of disc florets. The characters that had significantly different group means in addition to those mentioned above were disc corolla lobe length, phyllary margin, ray width, length of style branches of ray florets, and pappus length of disc florets. The percentages of between-group variances for functions 1–5 are 65.2, 16.4, 10.4, 5.6, and 2.5%, respectively.

The correlation coefficients between discriminating char-

Table 2. Values for the most discriminating characters for leaves, staminate inflorescences, and pistillate inflorescences for the entities of the *frigidus* complex.

Discriminating characters	Predicted taxon membership		
	FN	FR	NI
Leaves			
NOILOB	0–12	3–14	5–13
SINSHP	0–2	1–2	1–2
SINDEP	0.00–1.60	0.50–4.00	0.14–5.20
SHAPE	1–5	1–5	1–5
NOTETH	0–22	2–32	3–32
NOHEADS	3–12	3–13	2–20
Staminate inflorescences			
NORF	1–13	5–12	2–12
STYLTEX	1.5–2	1.5–2	1–3
PHYLMAR	2–2.5	2–2.5	1–2.5
LENGSTBR	0.06–1.60	0.76–2.00	0.05–1.40
NOHEADS	8–13	5–18	6–19
Pistillate inflorescences			
PHYLMAR	0.56–1.24	0.00–1.04	0.00–1.00
LENGSTBR	2–2.5	2–2.5	2–2.5
STYLTEX	2–2	1–2	1–2
DCLL	0.88–1.56	0.52–4.40	0.36–2.08

Note: Character abbreviations are given in Table 1. Taxon codes: FN, *frigidus* × *nivalis*; FR, *frigidus*; NI, *nivalis*.

acters and canonical discriminant functions indicate that the number of heads, the number of ray florets, style texture of disc florets, and length of style branches of disc florets are the most discriminating characters for function 1. These characters also have high *F* ratios.

The number of heads and style texture of disc florets are the only characters common to both the DA and PCA that provided a large contribution to the total variance. The taxon *frigidus* has the fewest heads (2–20) and fewest ray florets (1–13), while *palmatus* has a moderate number of heads (4–32) and the highest number of ray florets (5–70). The greatest number of heads (8–35), of all taxa, with relatively few ray florets (4–19) characterizes *sagittatus*. The taxon *vitifolius* possesses values for these characters that are intermediate to those of *sagittatus* and *palmatus*.

The characters that best discriminate taxa along function 2 are number of heads, phyllary margin, length of style branches of disc florets, pappus length of disc florets, and style texture of disc florets. The best separation between *sagittatus* and the other taxa is achieved along function 2. As previously mentioned, *sagittatus* has the highest number of heads in addition to the longest style branches of disc florets (0.5–2.3) and a consistently hairy style texture of disc florets.

For function 3, corolla length, phyllary width, and number of disc florets are the most discriminating characters. Style texture of disc florets and phyllary margin are moderately correlated (Cherniawsky 1994); therefore, their value as discriminating characters may not be as important as they appear.

The ordinations of the discriminant scores of the individual cases and centroids for the six taxa are shown in Fig. 7. Results from functions 1 and 2 showed the best separation of taxa and are presented here. Three weakly defined groups can be distinguished: *palmatus*, the *frigidus* complex, and *sagittatus*. Individuals of *vitifolius* do not form a cohesive group but are

Table 3. Classification results from the discriminant analysis for leaves of *Petasites*.

Actual taxon	No. of cases	Predicted taxon membership					
		FN	FR	NI	PA	PV	SA
FN	31	11	9	5	1	5	0
		35.9%	29.0%	16.1%	3.2%	16.1%	0.0%
FR	44	6	32	0	0	2	4
		13.6%	72.7%	0.0%	0.0%	4.5%	9.1%
NI	47	7	8	31	1	0	0
		14.9%	17.0%	66.0%	2.1%	0.0%	0.0%
PA	47	0	3	1	39	4	0
		0.0%	6.4%	2.1%	83.0%	8.5%	0.0%
PV	46	2	4	1	4	35	0
		4.3%	8.7%	2.2%	8.7%	76.1%	0.0%
SA	56	0	0	0	0	0	56
		0.0%	0.0%	0.0%	0.0%	0.0%	100.0%

Note: Values given in boldface are the numbers and percentages of correct classifications. Overall correct classification rate is 75.3%. Taxon codes: FN, *frigidus* × *nivalis*; FR, *frigidus*; NI, *nivalis*; PA, *palmatus*; PV, *vitifolius*; SA, *sagittatus*.

scattered throughout the loose groups of the other taxa. Along function 1, *palmatus* is clearly separated from *sagittatus* and the *frigidus* complex. The differentiation of *sagittatus* and the other taxa occurs along function 2. As mentioned earlier, *sagittatus* has the highest number of heads, in addition to a consistently hairy style texture of disc florets, and the longest style branches of disc florets (0.5–2.3).

Similar to the leaf results, the close association of the centroids in the *frigidus* complex (Fig. 7b) supports their unification. The discriminating character values along functions 1 and 2 (Table 2) provide a numerical illustration of the close relationship among the entities in the *frigidus* complex.

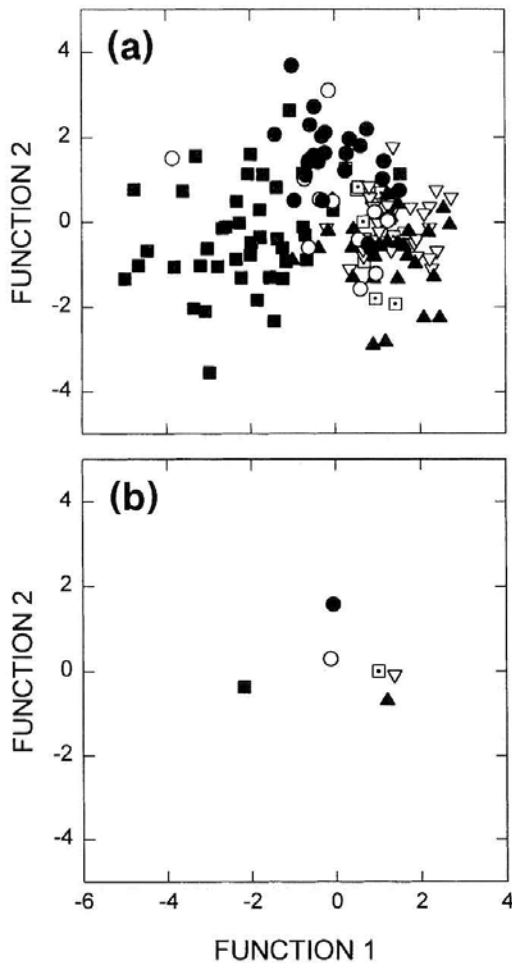
The correct classification rates are 66.7, 58.6, 58.1, 85.4, 54.5, and 82.6% for *frigidus* × *nivalis*, *frigidus*, *nivalis*, *palmatus*, *vitifolius*, and *sagittatus*, respectively (Table 4). As with the leaf results, the *frigidus* complex appears cohesive, as misclassified OTUs are more likely to be assigned to another taxon within the complex than to a taxon outside of it.

Pistillate inflorescences

Results from significance tests for the equality of group means show that characters with the highest *F* ratios are, in decreasing order, number of heads, length of style branches of disc florets, phyllary margin, and disc corolla lobe length. The number of heads is the most significant character of these. The other characters that had significantly different group means include phyllary margin, anther length, style texture of disc florets, phyllary width, number of ray florets, style length of ray florets, and number of disc florets.

The percentages of between-group variances for functions 1–5 is 56.3, 18.3, 13.7, 7.5, and 4.2%, respectively. The correlation coefficients between discriminating characters and canonical discriminant functions show that the number of heads, length of style branches of disc florets, length of anthers, disc corolla lobe length, and phyllary margin provide the most discrimination among taxa for function 1. These are the same characters with the highest *F* ratios. For function 2, the number of heads, length of style branches of disc florets, phyllary margin, and style texture of disc florets are the best

Fig. 7. Scatter diagrams from discriminant analysis results of staminate characters for taxa of *Petasites* including (a) all individuals and (b) centroids only. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.



discriminating characters. Discriminating characters for function 3 include style length of ray florets, style texture of disc florets, number of ray florets, and corolla length. The number of heads and style length of ray florets are the only characters common to both the DA and PCA that provided a high contribution to the total variance. Correlation coefficients of pistillate characters are available in Cherniawsky (1994).

The ordinations of the discriminant scores of the individual cases and centroids for the six taxa are shown in Fig. 8. Results from functions 1 and 2 showed the best separation of taxa and

Table 4. Classification results from the discriminant analysis for staminate inflorescences of *Petasites*.

Actual taxon	No. of cases	Predicted taxon membership					
		FN	FR	NI	PA	PV	SA
FN	15	10	2	2	0	0	1
		66.7%	13.3%	13.3%	0.0%	0.0%	6.7%
FR	29	6	17	3	0	1	2
		20.7%	58.6%	10.3%	0.0%	3.4%	6.9%
NI	31	5	4	18	1	2	1
		16.1%	12.9%	58.1%	3.2%	6.5%	3.2%
PA	41	2	1	0	35	1	2
		4.9%	2.4%	0.0%	85.4%	2.4%	4.9%
PV	11	0	1	1	1	6	2
		0.0%	9.1%	9.1%	9.1%	54.5%	18.2%
SA	23	0	2	0	0	2	19
		0.0%	8.7%	0.0%	0.0%	8.7%	82.6%

Note: Values given in boldface are the numbers and percentages of correct classifications. Overall correct classification rate is 70.0%. Taxon codes: FN, *frigidus* × *nivalis*; FR, *frigidus*; NI, *nivalis*; PA, *palmatus*; PV, *vitifolius*; SA, *sagittatus*.

they are presented here. In Fig. 8a, four weakly defined groups are evident: *palmatus*, *sagittatus*, *vitifolius*, and the *frigidus* complex. The best separation between *palmatus* and the other taxa occurs along function 1. A weak separation between *sagittatus* and *vitifolius* and the *frigidus* complex and *palmatus* occurs along function 2.

The *frigidus* complex possesses the fewest heads (5–19) and *palmatus* possesses the highest number of heads (8–42). Both *sagittatus* and *vitifolius* exhibit values that are intermediate between the former two groups. The longest style branches of disc florets (0.3–1.3 mm) are found in *sagittatus*. The largest disc corolla lobe length occurs in *frigidus* (0.4–4.4 mm), and the smallest occurs in *sagittatus* (0.40–1.84 mm). The phyllary margin in *palmatus* is distinguished from the other taxa by the presence of completely entire phyllary margins in some individuals.

The centroids of the six taxa (Fig. 8b) indicate the presence of four groups. The close association of the three entities of the *frigidus* complex favors their amalgamation into one. Again, Table 2 provides a numerical depiction of their close morphological similarity.

Correct classification rates for *frigidus* × *nivalis*, *frigidus*, *nivalis*, *palmatus*, *vitifolius*, and *sagittatus* are 75.0, 76.9, 76.3, 72.7, 72.7, and 62.5%, respectively (Table 5). With the exception of *nivalis*, the *frigidus* complex appears cohesive, as misclassified OTUs are more likely to be assigned to another taxon within the complex than to a taxon outside of it.

Discussion

The morphometric analyses indicate that North American *Petasites* is comprised of four similar polymorphic entities including the *frigidus* complex, *palmatus*, *sagittatus*, and the hybrid entity *vitifolius*. They also demonstrate that taxa of *Petasites* cannot be delimited with the use of reproductive characters alone. Morphological variation for most staminate and pistillate characters is continuous with a high degree of overlap across taxa. It has been shown that the most reliable characters for delimiting taxa of *Petasites* in North America

Table 5. Classification results from the discriminant analysis for pistillate inflorescences of *Petasites*.

Actual taxon	No. of cases	Predicted taxon membership					
		FN	FR	NI	PA	PV	SA
FN	8	6	2	0	0	0	0
		75.0%	25.0%	0.0%	0.0%	0.0%	0.0%
FR	26	2	20	3	0	1	0
		7.7%	76.9%	11.5%	0.0%	3.8%	0.0%
NI	38	1	3	29	0	1	4
		2.6%	7.9%	76.3%	0.0%	2.6%	10.8%
PA	33	1	0	3	24	5	0
		3.0%	0.0%	9.1%	72.7%	15.2%	0.0%
PV	11	0	1	1	1	8	0
		0.0%	9.1%	9.1%	9.1%	72.7%	0.0%
SA	16	1	0	3	1	1	10
		6.3%	0.0%	18.8%	6.3%	6.3%	62.5%

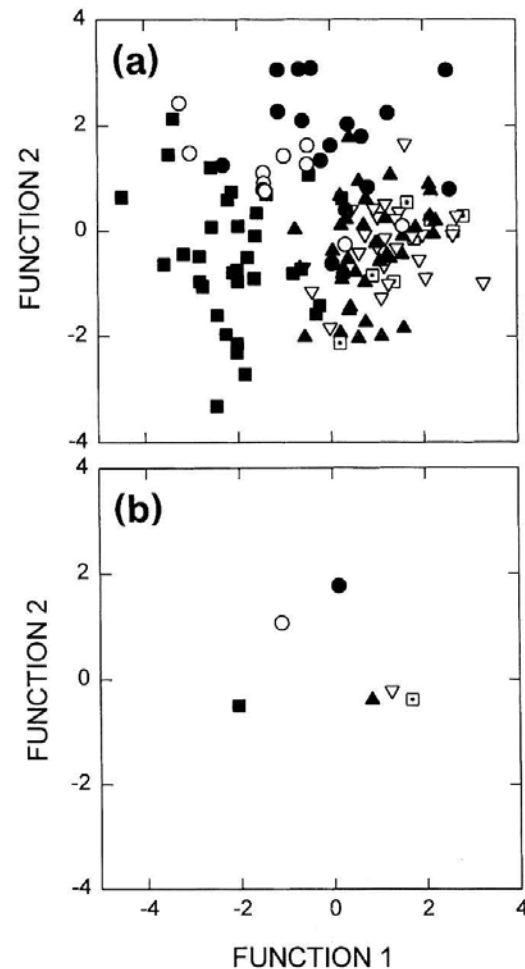
Note: Values given in boldface are the numbers and percentages of correct classifications. Overall correct classification rate is 73.5%. Taxon codes: FN, *frigidus* × *nivalis*; FR, *frigidus*; NI, *nivalis*; PA, *palmatus*; PV, *vitifolius*; SA, *sagittatus*.

can be obtained from leaf morphology. Due to the absence of lobes and sinuses, the leaf form of *sagittatus* emerges as the most distinct. However, inspection of minimum and maximum values for leaf characters (Cherniawsky 1994) reveals that there is extensive overlap among taxa, similar to the overlap observed with staminate and pistillate characters. Therefore, the use of leaf characters to discriminate among taxa of *Petasites* is not absolutely reliable. With additional information on habitat and geographical coordinates, however, the reliability of both vegetative and reproductive characters as discriminators is greatly improved.

The recognition of a close morphological relationship in North American taxa of *Petasites* is consistent with the results from the isozyme analysis (D.M. Cherniawsky and R.J. Bayer, unpublished), which show that morphological divergence of the different taxa is not correlated with divergence at isozyme loci. Therefore, we interpret the close association of morphological characters, in conjunction with the similarity in isozymes, and chromosome number ($x = 30$) as evidence of a close relationship among all taxa of *Petasites* in North America.

Our systematic interpretation of North American *Petasites* is in agreement with the suspicions of Hooker (1833). *Petasites* is recognized as one polymorphic species. Our circumscription of *Petasites* reflects the taxonomic species concept utilized in this study: "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1978a). By comparing the morphometric results with the criteria required for the recognition of this taxonomic species, we outline our reasons for treating North American *Petasites* as one morphologically variable species.

The smallest groups criterion in this species definition requires that groups cannot be further subdivided into smaller groups that meet the remaining tests. This criterion is not met for taxa of *Petasites* when considering reproductive morphology. Individual inflorescences without associated leaves could be readily distinguished as *Petasites*, but it would be difficult to recognize less inclusive groups. Therefore, the smallest

Fig. 8. Scatter diagrams from discriminant analysis results of pistillate characters for taxa of *Petasites* including (a) all individuals and (b) centroids only. Taxon symbols are as follows: □, *frigidus* × *nivalis*; ▽, *frigidus*; ▲, *nivalis*; ■, *palmatus*; ○, *vitifolius*; ●, *sagittatus*.

group would be the species *Petasites frigidus* sensu Cronquist (1978a) and Bogle (1968).

The second criterion of being consistently distinct maintains that consistent features in an individual must conform to the range of variation within the group and that the variation in this group must be continuous with the variation exhibited by other groups. All the individuals in question must clearly belong to one group and not the other. The species criterion for consistency cannot be fulfilled for *Petasites* using reproductive morphology. Although extreme values for certain characters are specific to some taxa, none of these taxa can be

reliably and consistently identified with the use of reproductive characters alone. Variation between the groups is not discontinuous; therefore, individuals do not clearly belong to one group and not the other.

The third criterion, being persistently distinct, specifies reproductive isolation (Cronquist 1978b). There must be certainty that the offspring of a species will also belong to that species. Hybridization reduces the degree to which this persistence criterion can be fulfilled; therefore, this species criterion is also unsatisfied in *Petasites*. Due to the absence of reproductive barriers, hybridization commonly occurs among all taxa of *Petasites* (Hultén 1968). Consequently, phenetic discontinuity is not persistent among the different groups.

The last criterion of distinguishing taxa by ordinary means is not satisfied for reproductive morphology in *Petasites*. Even with a dissecting microscope, it is usually difficult to distinguish taxa of *Petasites* using reproductive morphology alone.

On the basis of vegetative morphology, there is enough variation in *Petasites* for further subdivision into taxonomic groups; therefore, these taxa could reasonably be considered to be the smallest groups. However, the discontinuity in variation between five of these groups is too small to prevent misidentification. Consequently, the consistency criterion is not met. As with reproductive morphology, the persistency criterion is not fulfilled with leaf morphology because of hybridization among taxa. The ordinary means criterion is met for some taxa of *Petasites*; all that is needed for accurate identification is the naked eye. However, entities in the *frigidus* complex cannot be reliably separated. Therefore, the conclusion is that, on the basis of leaf morphology, discontinuity between groups is insufficient to warrant their recognition at the rank of species.

The most cohesive vegetative morphology, exhibited by *sagittatus* (Table 3), is largely due to the low level of variability expressed in the leaves. On the basis of morphological distinction of the leaves, it might be argued that *sagittatus* should remain at the rank of species. Members of this group cannot be further divided into smaller groups, thereby meeting the smallest groups species criterion. Leaf morphology of *sagittatus* also exhibits the highest discontinuity with the other groups (Table 3). Hence, for this taxon, the species criterion for consistency is also fulfilled. However, the ability to hybridize with all other taxa prevents *sagittatus* from meeting the requirement for persistency.

Moreover, since vegetative characters in *Petasites* tend to exhibit more environmental plasticity than reproductive characters, both kinds of characters must be considered. The pistillate morphology of *sagittatus* received the lowest rates of correct classification (Table 5) indicating a slight discontinuity with the other taxa. Additionally, the low levels of variability in pistillate and staminate characters for all taxa and the lack of reproductive barriers suggests that they are all closely related. Variation in *sagittatus* is not sufficiently discontinuous in both vegetative and reproductive morphology to meet the species criterion of consistency.

The entities that comprise the *frigidus* complex exhibit widely overlapping ranges in all morphological attributes. Consequently, each entity cannot be considered to be consistently distinct, as is evident by the rates of misclassification in Tables 3, 4, and 5. The PCAs and DAs have shown that the entities of the *frigidus* complex maintain a certain degree of

morphological integrity, while remaining somewhat distinct from the other taxa. However, the *frigidus* complex is not considered to be sufficiently differentiated from the other taxa to warrant the designation of the rank of species. Therefore, a plausible suggestion is that the entities of this group be united and recognized under one taxon. The possession of both *frigidus* and *nivalis* leaf forms on the same plant (Fig. 1) lends support to this interpretation.

In summary, based on our results from the morphometric analyses, North American *Petasites* is interpreted as one species, *P. frigidus*, with infraspecific taxa. The circumscription of *palmatus* is maintained in the sense of Bogle (1968) and Cronquist (1978a) (Fig. 1) as var. *palmatus*. Based on the very close relationship of members of the *frigidus* complex, it is proposed that the previously recognized taxon, *nivalis*, be united with *frigidus* along with forms intermediate in morphology between these two taxa, as the polymorphic typical variety originally described as *T. frigida* (Linnaeus 1753). This circumscription differs from any other treatment of *Petasites*. The close morphological association of reproductive inflorescences, absence of reproductive barriers, and isozymic similarity indicates that *sagittatus* is only weakly differentiated from the other taxa of *Petasites*. Therefore, also contrary to any previous treatment, we recommend that *sagittatus* be circumscribed as a variety of *P. frigidus* (D.M. Cherniawsky and R.J. Bayer, unpublished). The circumscription of the hybrid taxon, *vitifolius*, resulting from the hybridization events between var. *palmatus* and "var. *sagittatus*" is also maintained in the sense of Bogle (Bogle 1968). However, in accordance with the new combination of one of its parental taxa, *P. frigidus* var. *sagittatus*, the new combination *P. frigidus* var. *xvitifolius* is proposed (D.M. Cherniawsky and R.J. Bayer, unpublished).

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