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A TAXONOMIC INVESTIGATION
OF THE *CAREX MACLOVIANA* D'URV. AGGREGATE
IN WESTERN CANADA AND ALASKA

by

Richard Whitkus

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A Taxonomic Investigation of the *Carex macloviana* D'Urv. Aggregate in Western Canada and Alaska submitted by Richard Whitkus in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

The *Carex maclovimna* aggregate is comprised of several phenetically similar taxa in western Canada and Alaska. The slight morphological differences among the taxa has led to treatments recognizing one more inclusive, or, six less inclusive species. Since the group had not been intensely studied before, a detailed morpho-taxonomic investigation was initiated to delimit species and describe phenetic relationships among them. Results from study of herbarium speciemns from the entire geographic range of each taxon, and various numerical analyses of Canadian and Alaskan material, indicated the taxa *C. microptera* Mack., *C. festivella* Mack. and *C. limnophila* Hermann comprise one species, *C. haydeniana* Olney another species, phenetically similar to the first, anc that *C. macloviana* D'Urv. and *C. pachystachya* Cham. *ex* Steud. are two similar but distinct species. A statistical analysis of 47 quantitative characters indicated that the species do not differ appreciably from one another but there are a few characters which either alone or correlated with others, can be used to diagnose each species. The species were also determined to have different chromosome numbers, geographic distributions; and ecological preferences. During the course of the investigation, a previously unrecognized taxon, designated 'stubby', was found and included in all the analyses to determine its phenetic position within the aggregate. It was concluded that 'stubby' represents an extreme form of the variable *C. pachystachya*, differing not only in morphology but in chromosome number as well.

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INTRODUCTION

The genus *Carex* L.[1] is the largest and most widespread genus in the family Cyperaceae with approximately 1500-2000 species. Like most genera in the family, *Carex* is comprised of grass-like perennial herbs with highly reduced, wind pollinated flowers. Along with the genera *Kobresia* Willd., *Schoenoxiphium* Nees, and *Uncinia* Pers., *Carex* is a member of the tribe Cariceae Nees of the subfamily Caricoideae and is interpreted as having true unisexual flowers which are laterally arranged in spiciform inflorescence units, and as possessing a prophyll which partially to completely surrounds the gynoecium (Holttum, 1948; Koyama, 1969; Eiten, 1976). These features, which have proved useful in the classification of the family, distinguish the tribe Cariceae from other members of the Cyperaceae. The remaining tribes of the subfamily Caricoideae have terminally disposed flowers and a bract which surrounds the female flower that is not homologous to the prophyll (Koyama, 1965; Eiten, 1976; Meert and Goetghbeur, 1979). The subfamily Cyperoideae possess pseudanthia in the form of bisexual flowers (Koyama, 1969), while the subfamily Mapanioideae possess pseudanthia and cymose inflorescence units (Koyama, 1969).

Within the tribe Cariceae, the genus *Carex* is distinguished by possessing a completely fused perigynium and a rachilla which does not extend beyond the perigynium. Since the reproductive structures of *Carex* are unique in relation to other angiosperms and play an important role in the taxonomy of the genus, it is desirable to first review these structures and the terms which apply to them.

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[1] Derived from Greek *charaktos*, meaning toothed, *karcharos*, meaning jagged, and *keirin*, meaning to cut (Robertson, 1979).

The flowers of the genus *Carex* are unisexual and most species are monoecious. The flowers, adapted for wind pollination, are highly reduced and lack a perianth. The male flower simply oonsists of three stamens subtended by a scale. Although this is the common interpretation, evidence based on anatomical studies has shown the male flowers may actually be pseudanthia composed of three single-stamen flowers (Smith, 1966; Smith and Faulkner, 1976). The female flower consists of a bi- or tricarpellate, unilocular, single ovuled, superior gynoecium completely surrounded by a sac-like organ, the pergynium, and the whole structure subtended by a scale. It has long been thought that the female 'flower' is a reduced inflorescence, consisting of the gynoecium, placed laterally on the floral axis, the rachilla, and the perigynium which is homologous to a prophyll, a reduced leaf found at branch bases in many monocots (Blaser, 1944; Holttum, 1948; Eiten, 1976). In *Carex*, the rachilla aborts and does not extend beyond the perigynium, except in one species, *C. microglochin* Wahlenb. However, in other genera of the tribe Cariceae, the rachilla extends beyond the perigynium, and in *Kobresia* and *Schoenoxiphium* has one to several distal male flowers. Thus the 'flowers' of *Carex* are actually spikelets reduced to such a degree that they appear and function as true flowers (Smith and Faulkner, 1976). For taxonomic purposes, however, the interpretation of these structures is not a serious matter and throughout the present investigation they are referred to in the vernacular sense as flowers, a convention used by most workers in the genus.

The flowers are variously arranged into spike-like structures, which are subtended by a bract which may be reduced. These spike-like structures are secondarily arranged into spiciform or racemose inflorescences, or they may be single and terminal on the culm or stem. In those instances where the inflorescence is capitate, it is usually referred to as a head. The spike-like structures are sometimes called spikelets (Lawrence, 1951; Smith, 1977), however, as discussed above, this is erroneous, and for the purposes of this work, these structures are referred to as spikes.[2] The spikes may contain flowers of only one sex or may have both. Bisexual spikes which have female flowers above the male are called gynecandrous, and those with male above the female are called androgynous. In species with unisexual spikes, the distal spikes are usually male and the proximal female.

Description and Taxonomy of the Genus

CAREX L.[3]

> Grass-like perennial herbs. Culms (stems) solid, triangular or terete. Leaves narrow, linear, three-ranked, with closed sheaths. Plants monoecious or rarely dioecious. Flowers borne in spikes; spikes one to many, unisexual or bisexual, when bisexual, staminate flowers terminal (spikes androgynous) or basal (spikes gynecandrous), subtended by a large and leafy to much reduced bract, or bract wanting, sessile or pedunculate, racemosely arranged in a loose to compact terminal inflorescence, sometimes, some well removed from others and axillary to leaves near base of culm. Flowers unisexual, subtended by a scarious bract (scale); perianth none; staminate flowers of three, rarely two stamens, filaments free; pistillate flowers surrounded by a sac-like structure (perigynium) from the mouth of which the style or stigmas protrude; pistil one, superior, of two or three united carpels, locule one, ovule one, style one, stigmas accordingly two or three. Achenes lenticular or triangular, sessile or stipulate, completely surrounded by perigynium or rupturing it in ripening. (Mackenzie, 1931-35; Lawrence, 1951; Cronquist, 1969).

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[2] Again, following convention, although it is realized that since the flowers are really spikelets, then the spikes are really reduced panicles.

[3] See Appendix 1 for synonymy.

> A cosmopolitan genus with over 1500 species, most abundant in the North Temperate zone and Arctic; the tropical species occur mostly in montane habitats (Cronquist, 1969). There are 504 species currently recognized in North America and Greenland (Kartesz and Kartesz, 1980).

Linnaeus included twenty-nine *Carex* species in his *Species Plantarum*. By the mid 19th century, however more than 500 were described by F. Boott, through four publications (cf. Robertson, 1979). With this increase in the number of species, the need to arrange the included species into less inclusive taxa became evident. In 1819, Beauvois, in Lestiboudois's *Essai sur la Famille de Cyperacees* (cited by Bailey, 1866), working with European material, placed the species in two genera: *Vignea*, with bistigmatic ovaries and lenticular achenes, and *Carex*, with tristigmatic ovaries and trigonous achenes. These taxa were later accepted by workers as subgenera (cf. Bailey, 1886). Kükenthal (1909), who was the first to monograph the genus *Carex* on a world-wide basis, recognized four subgenera: *Primocarex* Kükenth., with single, terminal spikes and bi- or tristigmatic ovaries; *Vignea* (Beauv.) Nees, with several bisexual sessile spikes, and bistigmatic ovaries; *Indocarex* Baillon, with several pedunculate, bisexual, and terminal staminate spikes, and tristigmatic ovaries; and *Eucarex* Cosson *et* Germain, with several pedunculate, unisexula spikes,and bi- or tristigmatic ovaries. Kukenthal's system is still in use, although Smith and Faulkner (1976) have pointed out that there is a tendency to recognize two subgenera, only, with *Eucarex, Indocarex,* and most *Primocarex* (those with tristigmatic ovaries) placed in the subgenus *Carex*, and the *Vignea* of Kükenthal, plus the remaining *Primocarex* (those with bistigmatic ovaries) placed in the subgenus *Vignea*.

In addition to subgenera, numerous sections have been proposed as a way of grouping species into what appear to represent natural assemblages, based primarily on the reproductive structures. The first attempt to classify the genus *Carex* in this way, was that of Tuckerman in 1883, in *Enumeratio Methodica Caricum Quarundam* (cited by Bailey, 1886). Although previous workers had proposed sections, these were considered more or less artifical since they were based primarily on the sex of the spikes (Holm, 1908; Robertson, 1979). An alternate system of sections or 'greges' was proposed by Drejer in 1884, in *Symbolae Caricologicae* (cited by Holm, 1908), and completed by Holm in 1903. However, Drejer's system, considered natural and unique for its discussion of natural affinities among the various 'greges', has not been accepted. Robertson (1979) points out that Drejer's discussion of natural affinities was one of evolution influenced by Lamarckism and not fully understood by contempory carciologists. This is a possible reason why Drejer's system has been over-shadowed by the slightly earlier system of Tuckerman.

Systematic and Biosystematic Research in the Genus

Research in *Carex* has been concerned, to a large part, with morphological investigations, from which information useful for classification has been attained. However, additional data for classification and for understanding interrelationships among the taxa have become avaiable.

Initial cytological studies reported chromosome numbers (Heilborn, 1922, 1924, 1928, 1939; Tanaka, 1939; Wahl, 1940) but these showed pecularities. Among these, three are important in understanding the cytology of *Carex*.

The first pecularity concerns the behavior of the chromosomes during meiosis. This was first documented for *Carex* by Wahl (1940) and later described as post-reductional meiosis by Bataglia and Boyes (1955). In this process, the first anaphase of meiosis is characterized by the homologous chromosomes remaining paired while the sister chromatids of each homologue separates, thus giving an equatorial division. During the second anaphase, the homologous chromosomes separate, resulting in a reductional division. This method of meiosis is the reversed condition for most organisms where the first anaphase is a reductional division, splitting homologous chromosomes, and the second is an equatorial division, separating sister chromatids (Bataglia and Boyes, 1955). This method of meiosis is possible because of a second pecularity of *Carex* cytology: the presence of diffuse centromeres, a feature shared by some of the other genera of the Cyperaceae, the Juncaceae and the insect orders Heteroptera and Hemiptera (Grant, 1971).

The chromosomes of most organisms possess a localized constricted region, the centromere. The centromere attaches to the spindle apparatus during mitosis and meiosis and splits during anaphase, dragging behind the sister chromatids towards opposite poles of the spindle (Strickberger, 1976). In those organisms with diffuse centromeres, there is no differentiated centromeric region; instead the chromosomes align themselves at the equator during metaphase, and the entire length of the chromatid migrates toward the poles of the spindle during anaphase (Bataglia and Boyes, 1955). Because the whole chromosome possesses centromeric activity, fragments are not lost during meiosis, but migrate along with the rest of the chromatids, and cells with fragments remain vaible, but possess different chromosome numbers.[4] This leads to the third pecularity of *Carex* cytology: the aneuploid chromosome numbers exhibited by the genus.

A series of haploid chromosome numbers from n=6 to n=56 with every gametic number from n=12 to n=43 is represented in *Carex* (Davies, 1956). Basic numbers of x=5,6,7,8 and 9 have been proposed for the genus (Wahl, 1940; Löve, Löve and Raymond, 1957). Following the lead of Grant (1971), a number of authors prefer to limit the term aneuploidy and exclude aneuploid series produced through the action of diffuse centromeres. Thus, strict aneuploidy refers to numerical differences with respect to individual chromosomes, while the differences in the number of independently assorting pairs of chromosome fragments is referred to as agmatoploidy(Malheiros-Gardé and Gardé, 1951).

It is generally held that agmatoploidy has played a major role in the evolution of the genome of *Carex* (Davies, 1956; Grant, 1971; Faulkner, 1972). The series of numbers observed for the genus is a result of successive fragmentation of the chromosomes. This is corroborated by the fact that those species with low numbers have the largest chromosomes, while those with higher numbers have successively smaller chromosomes (Heilborn, 1932, 1939; Tanaka, 1949; Davies, 1956; Wahl, 1940). In addition, normal polyploidy and hybridization have been demonstrated (Löve, Löve, and Raymond, 1957), but are considered to have played minor roles in the evolution of the karyotype of the genus (Grant, 1971; Faulkner, 1972). Faulkner (1972) concludes that the presence of unlocalized centromeres imparts a great deal of flexibility to the

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[4] This ability has been demonstrated experimentally by inducing fragments with X-ray treatment and observing their activity. This was first accomplished by Håkansson (1954, 1958) with the genus *Eleocharis* in the Cyperaceae.

genome of *Carex* by allowing fragments and interchange heterozygotes to remain chromosomally balanced. Thus the large number of species in the genus as well as in the *C. maclovіana* aggregate, may be due, in part, to this genetic flexibility.

Many workers have studied reproductive structures in *Carex*, but usually as part of a study of the systematics of the Cyperaceae (see Koyama, 1965, 1969; Eiten, 1976; etc.). Walter (1975) has used scanning electron microscopy to study the achene epidermis, in characterizing the sections *Pseudo-Cypereae* and *Vesicariae*, and placed into them two problematic species, *C. schweinitzii* Dewey and *C. lurida* Wahl., respectively. In another study using SEM, Toivonen and Timonen (1976) included the perigynium epidermis in characterizing some northern European sections in the subgenus *Vignea*. In both investigations some characters proved useful at the supraspecific level, while some perigynia characters (i.e. teeth on beak or perigynium) were species distinct (Walter, 1975; Toivonen and Timonen, 1976). Vegetative structure has been studied by Metcalf (1971). He suggested that some characters, such as prickle variation, distribution of papillae, and sclerenchyma patterns, may be useful at the species level, but called for further investigation. Chemical studies have been initiated by Clifford and Harborne (1969), Harborne (1971), Kukkonen (1971) and Williams and Harborne (1977) to characterize the flavonoids in the genus and the family. Biosystematic studies by Toivonen (1974) have used flavonoid spotting patterns of two dimensional paper chromatograms to identify the parents of putative *C. canesces* L. hybrids and in characterizing other species in the section *Heleonastes*.

Northwest European species of the section *Acutae* have been investigated biosystematically by Faulkner (1972, 1973). In conjunction with cytotaxonomic studies, Faulkner hybridized species of the section *Acutae* and compared seed set, pollen grain viability and seed germination results. The most notable results of this work showed that *C. juncella* (Fr.) T. Fr. and *C. nigra* (L.) Reichard are conspecific, even though they are separated by a distinct morphological character, the lack of creeping rhizomes in *C. juncella*. However, the two species share the same chromosome number ($2n=84$), and their F_1 hybrids showed completely regular meitoic pairing. A second result of this study showed *C. recta* Boott to be a hybrid taxon between *C. acuta* L. and *C. paleacea* Wahl., with F_1 hybrid of *C. acuta* X *C. paleacea* indistinguishable on morphological and cytological grounds.

Classification of the Section Ovales

In Mackenzie's (1931-35) monograph of the genus *Carex* for North America, the largest section recognized was the *Ovales* Kunth with 73 species. Since then, a number of these names have been synonymized and a number of new species have been described, leaving the *Ovales* with approximately 70 species. Mackenzie subdivided the *Ovales*, gave each subdivision a name with the stem taken from presumably typical species, and added a plural adjective ending, thus ranking his subdivisions equivalent to subsections or series. This lead had been followed by Hermann (1970, 1974), who followed Mackenzie's treatment closely, by ranking Mackenzie's subdivisions as subsections. However, since Mackenzie had not specified rank, nor had he, or anyone else validly published the names, they cannot be given nomenclatural recognition at present.

The species of the section *Ovales* are fairly distinct and like other members of the subgenus *Vignea* possess several sessile, bisexual spikes in the inflorescence, perigynia which are incompletely fused towards the apex, forming a suture on the dorsal (abaxial) side, and bistigmatic ovaries which mature into lenticular achenes. The section *Ovales* is separated from other sections in the subgenus *Vignea* by cespitose growth form, gynecandrous spikes, and flat to plano-convex, beaked perigynia which are noticeably winged margined. The section shows its best development in North America, with several speices reaching into or occurring in Central and South America, three species extending to Greenland and Eurasia, two in Japan, one in Siberia and one in Hawaii (Kukenthal, 1909; Hultén, 1927; Mackenzie, 1931-35; Krauss, 1950; Hermann, 1974).

Although the species in the *Ovales* comprise a distinct section, they are not clearly separated from one another. While the species of *Carex* are separated by small, differences, the differences are distinct and consistent, resulting in sharply defined species. However, it has been noted that in some sections, most notably the *Ovales*, the distinctions between species are vague and tend to overlap, resulting in a series of taxa in which specific status of the members is questionable (see discussions in Cronquist, 1969; Hudson, 1977; and Boivin, 1979). One such group of taxa in the section *Ovales* is the *Carex macloviana* aggregate.

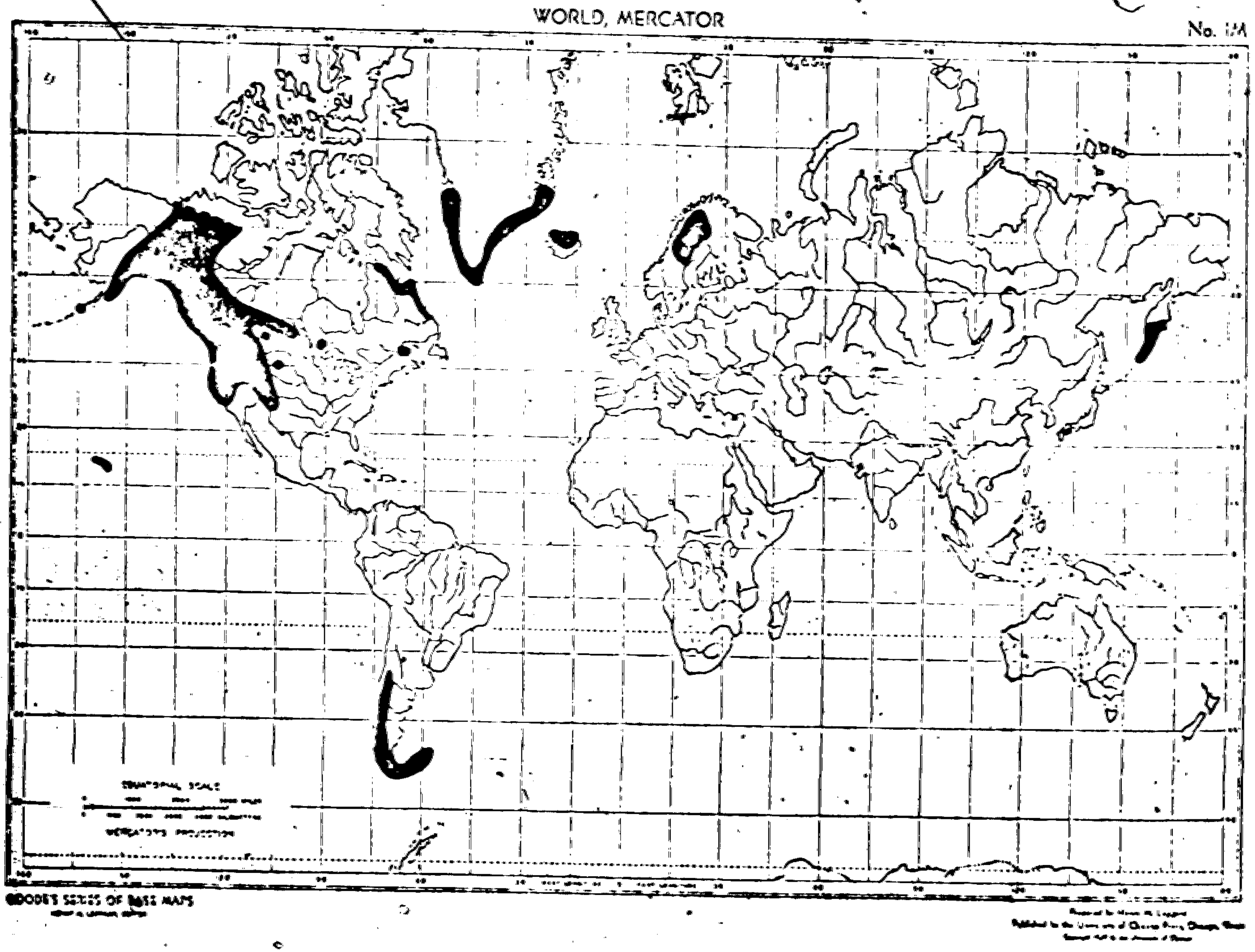
The *Carex macloviana* Aggregate

Carex macloviana sensu lato is one of the larger and more complex aggregates of the section *Ovales*. This complexity is a result of the similarity and overlap in variation among the morphological characters used to delimit the taxa within the group, which in turn has led to the description of many species, subspecies and varieties in North America. Today, it is generally agreed that the aggregate comprises seven species in three groups: an inland, montane to alpine group, comprised of *C. microptera* Mackenzie, *C. festivella* Mack., *C. haydeniana* Olney, and *C. ebenea* Rydberg; a coastal lowland to montane species, *C. pachystachya* Chamisso *ex* Steudel, which shows similarities to other Cascadian and Californian species, which taken collectively, may be best treated as a complex in itself; and a boreal to subarctic, montane to subalpine species, *C. macloviana* D'Urville (Cronquist, 1969, 1977).

All but two members of the *Carex macloviana* aggregate are restricted to western North America. *Carex pachystachya* grows also in thermophilous habitats on the Kamtchatka Peninsula of Sibera (Hultén, 1927, 1942; Krechetovich, 1935). *Carex macloviana* has long been known as a bipolar disjunct,occurring in western North America, the eastern Canadian Arctic, Greenland, Iceland, northern Fenoscandia, South America in the Andes from 32° S latitude to Tierra del Feugo, and in the Falkland Islands (Mackenzie, 1931-35; Moore and Chater, 1971). A map of the generalized distribution of the *C. macloviana* aggregate is shown in Figure 1.

Carex macloviana was described in 1826 by Dumont-D'Urville from specimens he had collected in the Falkland Islands while on the Antarctic expedition of the *La Coquille*. Ten years later, Dewey (1836) described some specimens of *Carex* which Dr. Richardson had collected at Great Bear Lake on the second Franklin Polar Sea Expedition, as *C. festiva*. Since the *Carex macloviana* aggregate is best developed in western North America, all the taxa which were described from

Figure 1. World distribution of the *Carex macloviana* aggregate, based on data from Hultén (1958), Moore and Chater (1991), Porsild and Cody (1980) and herbarium specimens.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specimens collected in that area were allied to *C. festiva*, while the Europeans had allied their material to *C. macloviana*. This situation remained for seventy years, although some caricologist noted the similarity between the two species (see Holm, 1903). In 1909, Kükenthal placed all of the North American material of *C. festiva* under *C. macloviana*. Kükenthal recognized five varieties, and two forms, as well as typical *C. macloviana* for the North American continent (Table 1). This interpretation of the group represents one taxonomic extreme, where all previously recognizable taxa are combined under one species. In the years following Kükenthal's work, a number of species were segregated from the 'Festivae' group, by the American caricologist, K. K. Mackenzie. Between 1909 and 1916, Mackenzie proposed ten species which showed simil[illegible]s to *C. macloviana sensu lato*, five from California. In his monograph of North American carices, Mackenzie listed 23 species in his 'Festivae' subdivision, 13 of which showed morphological similarities to *C. macloviana*, and five of which remain as members of the aggregate today (Table 1). Mackenzie's treatment represents the other taxonomic extreme, one which recognized every deviating type as a species, and it the procedure followed in may modern treatments. More recently, a few species of the 'Festivae' assemblage have been combined while Hermann (1945, 1956, 1968, 1971) has added four species and two new varieties, and Kelso (1953) a new variety. Cronquist (1969, 1977) synonymized *C. preslii* Steud., *C. platylepis* Mack. and *C. pachystachya*. However, Hudson (1977) has discussed the differences between *C. pachystachya* and *C. preslii* and concluded the two are quite distinct. The status of *Carex preslii* and *C. platylepis* are discussed in subsequent chapters. Looman and Best(1979)

Table 1. Comparison of Kükenthal's (1909) and Mackenzie's (1931-35) treatment of the *Carex macloviana* aggregate for North America.

Kükenthal (1909)	Mackenzie (1931-35)
C. macloviana	*C. macloviana*
var. *subfusca*	*C. subfusca*
var. *stricta*	*C. subfusca*
f. *viridis*	*C. microptera*
f. *decumbens*	*C. haydeniana*
var. *haydeniana*	*C. haydeniana*
var. *pachystachya*	*C. pachystachya*
var. *gracilis*	var. *gracilis*

included *C. limnophila* F. J. Hermann with those species that have been distinguished as members of the *Carex macloviana* aggregate. Table 2 is a listing of all the species which were initially examined in this study.

Work on the aggregate so far has been morphological, especially by authors of floristic studies who have tried to deal with those members of the aggregate which occurred in a particular area (see Hultén, 1968; Cronquist, 1969, 1977; Hermann, 1970; Hudson, 1977: and Boivin, 1979). Other studies have been concerned mostly with the report of chromosome numbers, and are listed in Table 3. However, two investigations have included material from the aggregate as part of a larger survey. Clausen, Keck and Hiesey (1940), reported that clones of *C. festivella* grew well in all three of their experimental gardens, with the individuals at the Mather station (1400 m) the most vigorous. They concluded that these species preferred the sunny, well drained situation which the Mather station provided. In addition, the karyotype of *C. festivella* was found to be very similar to Swedish material of *C. macloviana*, although the chromosome numbers differed (see Table 3). Moore and Chater (1971) studied amount of morphological divergence between the various population of bipolar carices. The results showed that Northern Hemisphere and Southern Hemisphere populations of *C. macloviana* did not exhibit enough differences to warrant taxonomic recognition.

The present investigation was initiated to study the *Carex macloviana* aggregate in western Canada and Alaska. This excludes the peripheral species of the Cascade Mountains and California, and *C. ebenea* which is distinct except for some intermediates between it and

Table 2. List of taxa initally investigated for the present study.

Carex macloviana D'Urv.

Carex microptera Mack.

Carex festivella Mack.

Carex haydeniana Olney

Carex pachystachya Cham. *ex* Steud.

Carex limnophila Hermann

Carex preslii Steud.

Carex platylepis Mack.

Table 3. Reported chromosome numbers for members of the *Carex macloviana* aggregate.

TAXON	n	2n	REFERENCE
C. ebenea	42		Wahl (1940)
C. festivella	45		Clausen, Keck and Hiesey (1940)
C. macloviana		ca. 82	Böcher (1938)
	43		Heilborn (1939)
		82-86	Clausen, Keck and Hiesey (1940)
		86	Löve and Löve (1956)*
		86	Jörgensen, Sörensen and Westergaard (1958)
		86	Engelskjön and Knaben (1971)*
		86	Engelskjön (1979)
C. microptera	41		Wahl (1940)
C. pachystachya	38		Taylor and Mulligan (1968)

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*As reported in Löve and Löve (1975)

C. haydeniana (Cronquist, 1977). The main research objective was to study the morphological variation in the aggregate as a method to resolve the classificatory difficulties encountered in the past. In addition, cytological and phytogeographical aspects were investigated and used in conjunction with the morphological analysis.

Taxonomic Procedure

In any taxonomic work, the treatment of the taxa and the conclusions reached about them, reflect, in part, the philosophical views the researcher holds in regards to taxonomy. For those who review these works, an understanding of the researcher's concepts add insight as to why certain lines of investigation were followed and how some conclusions were reached. Therefore, I would like to explain some of my views about some philosophical contentions in taxonomy.

First is my species concept. The literature is replete with the philosophical foundations of the various species concepts, and I will not go into the pros and cons of each. Suffice to say that I agree with Cronquist (1978) that a working consensus among plant taxonomists has developed, which in effect states, "if you can't tell the things apart, they belong to the same species, regardless of reproductive or cryptic morphological differences that might exist" (Cronquist, 1978: 14). Cronquist goes on to formulate a definition which reflects this attitude: "Species are the smallest goups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist, 1978: 15). Critically reviewing the definition, smallest groups means the group under study cannot be further divided and still meet the criteria of the definition. Consistent means the features exhibited by any individual fits into the range of variation of the whole group and that the group variation has a discontinuity with variation exhibited by other such groups. Persistent means a reasonable assurance that offspring of members of the group will show the same pattern of variation. And finally, ordinary measn are those commonly used by the investigator to study and delimit species. Therefore, a bacterial taxonomist may ordinarily use an electron microscope to distinguish species while a vascular plant taxonomist uses only a hand lens.

The definition is admittedly one which stresses phenetic discontinuity over all other criteria. However, as Cronquist points out, it is understood that phenetic discontinuity cannot be maintained in the absence of a barrier to interbreeding. Therefore, reproductive isolation is implied by this definition.

If species (or taxa) are defined on a phenetic basis, then the delimitation of taxa should also be based on phenetics. A powerful tool which has been developed to deal with the phenetic relationship among groups of organisms is found in numerical analysis (numerical taxonomy of Sneath and Sokal, 1973). As Reyment (1973) has pointed out, quantitative analysis plays an important role when it is necessary to examine the variation within a group of organisms. Sneath and Sokal (1973) have also shown that quantitative methods can be more discriminating among a number of characters than human neural assessment. As previously discussed, a large part of the confusion in the *Carex macloviana* group results from incomplete understanding of variation in morphological characters used to delimit the taxa. Because the main research objective of the present investigation was to study the morphological variation in the aggregate, a large part of the analysis was carried out using numerical methods.

MATERIALS AND METHODS

Morphology

Herbarium Studies: Morphological and distributional studies were based on herbarium specimens from the following herbaria: University of Alaska (ALA); University of Alberta (ALTA); Liberty Hyde Bailey Hortorium of Cornell University (BH); Brown University (BRU); The Clinton Herbarium of the Buffalo Museum of Science (BUF); National Museums of Canada (CAN); California Academy of Sciences (CAS); Biosystematic Research Institute, Department of Agriculture (DAO); The Gray Herbarium of Harvard University (GH); Lyon University (LY); United States National Arboretum (NA); The New York Botanical Garden (NY); University of Oregon (ORE); Oregon State University (OSC); Rocky Mountain Herbarium of the University of Wyoming (RM); Rancho Santa Ana Botanic Garden (RSA); Swedish Museum of Natural History (S); The W. P. Fraser Herbarium of the University of Saskatchewan (SASK); United States National Herbarium of the Smithsonian Institution (US); The University of British Columbia (UBC); Washington State University (WS); University of Washington (WTU). The abbreviations follow those used by Homlgren and Keuken (1974).

Collections: In addition, collections of the *Carex macloviana* aggregate were made throughout most of western Canada and Alaska, to augment herbarium collections, to obtain live material for cytological studies, and to observe any ecological differences among the taxa. Most collections included pressed specimens, live plants and inflorescences preserved for cytological investigations.

Morphological Analysis: Herbarium specimens from the entire range of the *Carex macloviana* aggregate (see Figure 1) were examined, as well as type specimens and original descriptions. Included were specimens and types of taxonomically peripheral taxa. This was done to gain a concept of each taxon and to erect limits to the aggregate. Once the aggregate was characterized, all specimens from western Canada and Alaska were critically examined[1], separated into groups of more or less recognizable subunits (Table 4), and mapped to seek correlations among the morphological variants and their geographical distribution. The subunits were then examined and specimens picked to sample the morphological variation and geographical range of each subunit. This resulted in selection of 215 specimens (OTU's of Sneath and Sokal, 1973[2])which became the basis of the statistical and numerical analyses.

On the basis of previous authors' treatments of the aggregate (Kükenthal, 1909; Mackenzie, 1931-35; Cronquist, 1969, 1977; Hermann, 1970) and on examination of the taxa within it, a suite of 55 characters was selected for scoring the specimens (Table 5). Each specimen was scored a maximum of three times for each character by examining each specimen sheet and choosing three fertile culms which exhibited most of the variation on that sheet and scoring each culm for the suite of characters. In this way, scoring specimens required, on the average, 45 minutes.

For the statistical and numerical analyses, only those characters which were quantitative were used, resulting in the selection of 7 vegetative, 34 reproductive and 5 ratio characters, of which 1 was vegetative and 4 reproductive (see Table 5). The quantitative characters

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[1] This involved examination of each specimen's inflorescence under a dissecting microscope, followed by an examination of a perigynium and achene.

[2] Operational Taxonomic Unit: lowest ranking taxon employed in a given study (Sneath and Sokal, 1973: 69).

Table 4. Reconizable morphological units (taxa) and subunits in the *Carex macloviana* aggregate for western Canada and Alaska.

- *C. pachystachya*
  - a) typical
  - b) greenish upper perigynia body
  - c) long beaks
  - d) reddish beaks
  - e) small heads
  - f) small perigynia, brown beaks
  - g) small perigynia and heads
  - h) few-flowered, loose heads
  - i) slender heads, red scales
  - j) dark colored perigynia and scales
  - k) macloviana body color
  - l) stramineous perigynia
- 'stubby'
  - a) typical
  - b) coppery perigynia
  - c) reddish perigynia
- *C. macloviana*
  - a) typical
  - b) coppery perigynia
  - c) broad perigynia and heads
  - d) depauperate
- *C. festivella*
  - a) typical
  - b) keyed
- *C. limnophila*
  - a) typical
  - b) + large heads
  - c) large perigynia
- *C. haydeniana*
  - a) short beaks
  - b) long beaks
- *C. microptera*
  - a) typical
  - b) ± widely winged perigynia
  - c) ∓ darkly colored, + widely winged perigynia
  - d) darkly colored perigynia
  - e) large greenish perigynia

Table 5. Suite of characters used in scoring specimens and for the analyses. Characters 1-41 were used for scoring specimens and for the analyses, characters 42-47 were ratios derived from characters 1,2,17,23,26,34,35,39 and 40 and used in the analyses, characters 48-55 were additional characters used to score specimens but excluded from the analyses.

CHARACTER	MODE OF ASSESSMENT
1) Divergence of uppermost blade, height.	cm.
2) Culm height.	cm.
3) Culm width, above point of emergence from uppermost sheath.	mm.
4) Culm width, above first sheath.	mm.
5) Leaf blades, number per culm.	
6) Leaf blade, width.	mm.
7) Leaf blade, length.	cm.
8) Inflorescence type.	1 (loosely aggregate, spikes overlapping, internodes visible), 2 (aggregate, spikes overlapping, internodes hardly visible, spikes distinguishable), 3 (densely aggregate, spikes not easily distinguishable).
9) Inflorescence length.	mm.
10) Inflorescence width.	mm.
11) Inflorescence 1st internode length.	mm.
12) Inflorescence 2nd internode length.	mm.
13) Spikes, number per inflorescence.	
14) Spike length.	mm.
15) Spike width.	mm.
16) Orientation of perigynia tips in spikes.	1 (appressed), 2 (ascending), 3 (spreading), 4 (divergent).
17) Scale length.	mm.
18) Scale width	mm.
19) Scale apex.	1 (acute)-3 (obtuse).
20) Scale margins.	1 (concolorous with scale)-3 (hyaline).
21) Anther length.	mm.
22) Perigynium cross-sectional shape.	1 (flat and distended by achene), 2 (concave-convex), 3 (plano-convex).
23) Perigynium length.	mm.
24) Perigynium width.	mm.
25) Perigynium margin, % serrulate.	1 (0-1/3), 2 (1/3-2/3), 3 (2/3 or greater).
26) Perigynium margin width.	mm.
27) Perigynium base.	1 (acute)-3 (obtuse).

Table 5. (Continued)

CHARACTER	MODE OF ASSESSMENT
28) Perigynium, number of dorsal nerves.	
29) Perigynium, degree of dorsal nerves.	1 (faint)-3 (evident).
30) Perigynium, number of ventral nerves.	
31) Perigynium, degree of ventral nerves.	1 (faint)-3 (evident).
32) Perigynium, extension of ventral nerves.	1 (absent or basally)-3 (entire length of perigynium body).
33) Perigynium, number of ventral folds.	
34) Beak length.	mm.
35) Beak tip length (terete or marginless portion of beak).	mm.
36) Beak tip margins.	1 (same texture as beak)-3 (hyaline).
37) Beak tip (size of teeth).	1 (erose), 2 (0.1 mm), 3 (0.2 mm), 4 (0.4 mm).
38) Spongy filling in base of perigynium.	1 (none)-3 (abundant).
39) Achene length.	mm.
40) Achene width.	mm.
41) Achene stipe length.	mm.
42) Ratio of 1:2 (%of culm leafy).	
43) Ratio of 34:23 (relation of beak length to perigynium length).	
44) Ratio of 35:35 (relation of beak tip length to beak length).	
45) Ratio of 39 X 40 : (23-34) X (24-2(26)) (relation of achene area to perigynium area).	
46) Ratio of 17:23 (relation of scale length to perigynium length).	
47) Ratio of 39 X 40 : 23 X 24 (relation of achene area to perigynium area).	
48) Inflorescence shape.	Standard shapes in Radford et al., 1974:131.
49) Inflorescence color	Green or stramineous, red, red-brown, brown, coppery, red-coppery, coppery-brown, blackish.
50) Scale color.	Same as in character 49.
51) Perigynium shape.	Same as in character 48.
52) Perigynium body color.	Same as in character 49.
53) Perigynium upper body color.	Same as in character 49.
54) Perigynium margin color.	Same as in character 49.
55) Beak tip color.	Same as in character 49.

are readily amendable to statistical treatment. The classed characters were also analyzed statistically since it is arguable that they represent continuous characters, but were classed for ease of recording observations. In addition, it is known that grouping observations into classes has little effect on the statistic unless the class intervals are unevenly spaced or unequal in size (Sneath and Sokal, 1973). A basic data matrix was formed by calculating the arithmetic mean for each of the 46 quantitative characters (see Appendix 2 for all formulae) for each OTU, and treating each character from that point on as a continuous quantitative character.

The statistical treatment consisted of calculating the mean and standard deviation of each of the taxa recognized in the first part of the morphological analysis, using the MIDAS statistical package and the computing facilities of the University of Alberta. From these data, the standard error of the mean and the coefficient of variation were hand calculated for each character. This analysis provided a means of evaluating characters which have been used in the literature and in finding new characters of diagnostic value.

The numerical analysis was an attempt to objectively evaluate the taxa which had been recognized in the first part of the morphological analysis, and to illustrate the phenetic relationships among them. Thus, the numerical analysis was run on two levels: on the individual OTU's for evaluating the validity of the taxa, and on the taxa for evaluating the phenetic relationships. In the individual OTU study, those OTU's which had missing data values were left out. This gave a new data matrix consisting of 191 OTU's with ten type specimens inclusive (Appendix 3). For the taxa analysis, the mean values from the statistical treatment were used, producing a data matrix of seven OTU's (Appendix 4).

All numerical classification programs consist of two parts. The first is calculation of the relative similarity or distance between every pair of OTU's. There are a number of these similarity coefficients, based on structure of the data and on assumptions about relative phenetic relationships. Sneath and Sokal (1973) give a detailed review of the more widely used coefficients of similarity. The second part of a numerical taxonomic program is to find clusters of OTU's, based on their relative similarity or distance. Again, a number of algorithms have been formulated, based on type of similarity coefficient used, and on ideas of how clusters should be formed. These clustering techniques try to mimic the decisions a taxonomist makes in formulating taxa. The most commonly used strategies for biological classification are sequential, agglomerative, hierarchic, non-overlapping clustering methods, or SAHN techniques (after Sneath and Sokal, 1973). The basis of these techniques is that clusters are sequentially built into a hierarchial pattern, and that at any one level of hierarchy, the clusters are mutually exclusive. Again, Sneath and Sokal (1973) give a review of these techniques.

Two different classification programs were usedized for the present analysis, both of which are programs in the public file library of the Univeristy of Alberta computing facilities. The first of these was the TAXMAP classification program developed by J. W. Carmichael of the University of Alberta. The similarity coefficient is based on relative proximity and is the complement of similarity formulated by Carmichael, Julius and Martin (1965) and is similar to the widely used Gower (1971) coefficient (Sneath and Sokal, 1973). This coefficient automatically standardizes the character scores by range normalizing (Gower, 1971) and allows for mixed data types (i.e. qualitative and quantitative). An option in the program, which was utilized, allows for weighing the characters according to their relative information content (see Carmichael, 1980 and Appendix 2). Values range from 0 for identity to 1 for complete dissimilarity.

The clustering procedure starts with the two nearest OTU's (based on relative proximity) forming the nucleus of a cluster. The next nearest OTU is added to this cluster and the average distance of this OTU to the OTU's already in the cluster is calculated. Four criteria are used to terminate clustering (see Carmichael, George, and Julius, 1968, and Carmichael, 1980) which uses elements of single linkage and average linkage clustering methods. The results are illustrated by means of a taxometric map (Carmichael and Sneath, 1969) which is a two-dimensional image of the multidimensional hyperspace the OTU's exist in, with circles representing clusters and lines joining circles the undistorted phenetic distances between clusters. Taxometric maps were drawn with the aid of the Calcomp plotter of the University of Alberta computing facilities.

The second classification program used was the CLUSTAN program developed by D. Wishart of Edinburgh University. CLUSTAN allows the user to choose any of 40 different similarity coefficients and 8 different clustering methods. For the present analysis, the Pearson product-moment correlation coefficient was chosen for the computation of the similarity matrix, with all characters give equal weight. Correlation coefficients are angular functions which measure the proportionality and independence of OTU vectors, and are meaningful with continuous quantitative characters (Cormack, 1971; Sneath and Sokal, 1973). They are widely used in numerical taxonomic studies and "when the interpretation of taxonomic structure is made on the basis of phenograms, correlation coefficients are usually the most suitable measure when the results are evaluated by conventional taxonomists" (Sneath and Sokal, 1973: 140). Because correlation coefficients are angular measures, they are a measure of shape differences between OTU's, as opposed to other similarity coefficients which generally measure size differences between OTU's. Figure 2 is a graphic representation of this difference. Before computing correlations, all character scores were standardized so that they would have a mean of zero and a standard deviation of one. ~~As in~~ ranging, this is done to standardize the variation exhibited by each character. The resulting values ranged from -1 for complete dissimilarity to +1 for identity.

The clustering strategy employed was average linkage or unweighted pair group method using arithmetic averages (UPGMA, following Sneath and Sokal, 1973). Average linkage has widely been used, and gives the least amount of distortion of the original similarity matrix (Rohlf, 1970; Sneath and Sokal, 1973). Average linkage clusters by taking the average distance of an OTU to all members of an extant cluster. Clustering continues at progressively higher and higher levels until all the OTU's are joined into one larger cluster. The results are illustrated in a phenogram, and it is left up to the investigator to decide at which level the clusters make the most biological sense. Phenograms were produced with the aid of the Calcomp plotter.

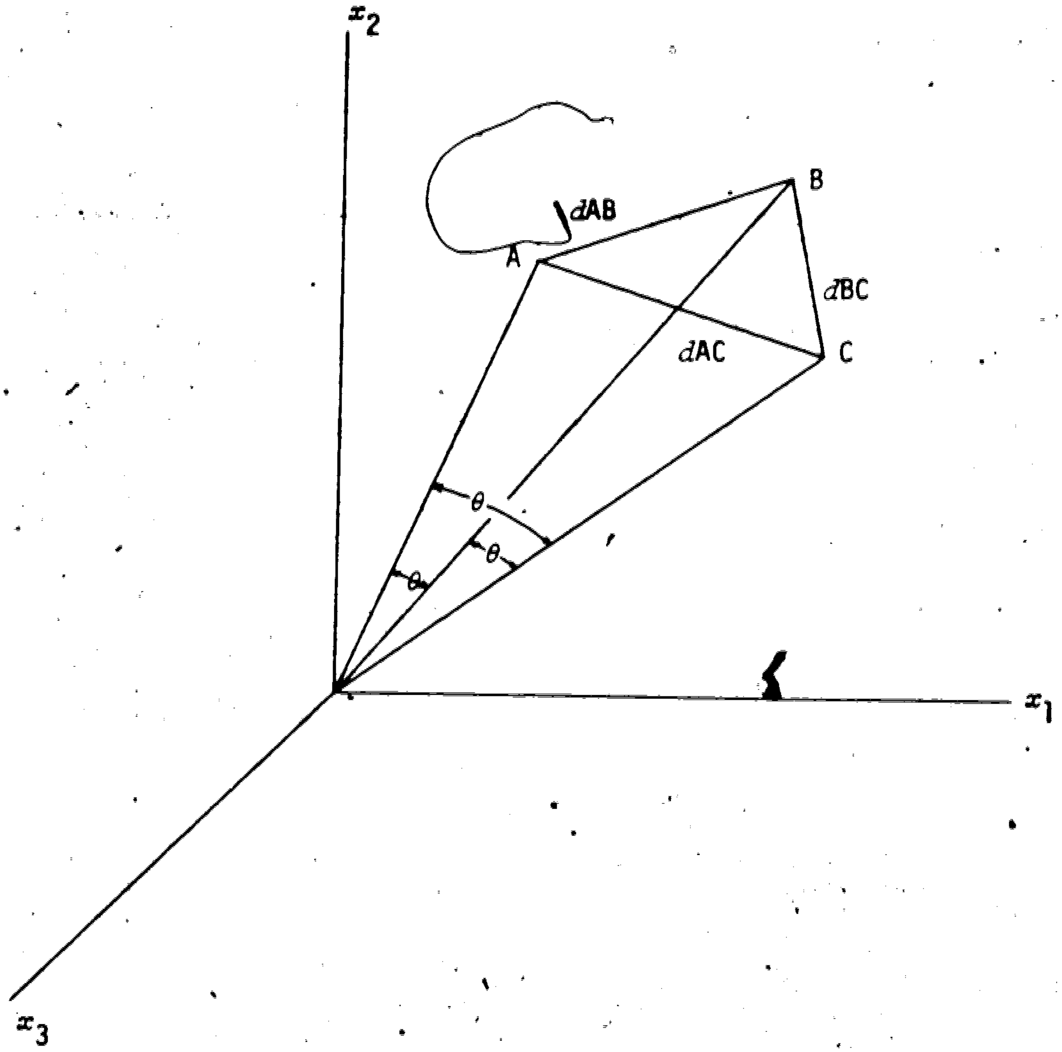


Figure 2. Graphic representation of three OTU's (A,B and C) plotted in a three-dimensional character space. Correlation coefficients measure similarity between OTU's as a function of the angle, θ, between the lines connecting the OTU's to the origin, other similarity coefficients measure similarity between OTU's as a function of distance, d, between OTU's. (Modified from Sneath and Sokal, 1973).

Numerical clustering techniques are known to preserve the smaller phenetic distances (i.e. within cluster distances); however, Rohlf (1970) and Sneath and Sokal (1973) have pointed out that numerical clustering techniques show a tendency to distort the larger phenetic distances (i.e. between cluster distances). Since an aim of the present investigation was to attempt to understand the phenetic relationships among the various taxa, the results of the cluster analysis could not be used to show these. A technique which does faithfully represent the larger phenetic distances is that of ordination. However, since ordinations distort the smaller phenetic distances (Sneath and Sokal, 1973), both an ordination and cluster analysis should be used to produce an overall view of phenetic relationships. A principal componene analysis was performed on the taxa using CLUSTAN. Principal components plots OTU's (in this case, the taxa) into a multidimensional hyperspace, with each character representing an orthogonal axis. New axes are found which represent the variation expressed by the OTU's in as few dimensions as possible. The results are a listing of the OTU's and their coordinates on the new axes (principal components). The taxa were hand plotted onto the first three principal components to illustrate the phenetic relationships among the taxa.

Cultivation

Live plants collected from the field were transplanted into 5 inch pots and grown at the greenhouse facilities of the University of Alberta. The plants were kept outside in beds of moist peat moss and allowed to go through a natural cycle. This was sufficient to induce flowering. During the flowering period, plants were checked periodically (on a daily basis during the peak flowering period) and immature inflorescences collected and preserved in a mixture of methanol, chloroform, and propionic acid (6:3:2) for cytological investigation. It has been the author's experience that inflorescences of *Carex* which are just emergent from the sheath possess the highest meiotic activity, especially in the early morning hours (possibly a phytochrome effect). Squashes of pollen spore mother cells were made in the evening (see below), and if Metaphase I could not be found, inflorescences were recollected the following morning and the procedure repeated.

Cytological Studies

Meiotic chromosome counts were made from pollen spore mother cells, following the procedure of Cooperrider and Morrison (1967). Anthers were dissected from immature inflorescences, placed on a glass slide, and a drop of 2 percent lactic acetic orcein was applied for staining of the chromosomes. A cover slip was applied, the slides inverted on a paper towel, and thumb pressure was applied to squash the material. The slides were then examined under a microscope for Metaphase I plates. Those slides which contained the proper stage were made semi-permanent by ringing the coverslip with nailpolish. Chromosome counts were obtained from Metaphase I plates under the oil immersion objective of an American Optical microscope. Drawings of the Metaphase I plates for the taxa were obtained using the oil immersion objective of a Zeiss microscope and Zeiss camera lucida.

RESULTS

Morphology

Herbarium Studies: Of the eight original taxa examined, six were considered to be within the circumscription of the *Carex maclovianа* aggregate as understood by previous authors for Western Canada and Alaska (Moss, 1959; Cronquist, 1969, 1977; Hudson, 1977; Looman and Best, 1979). The *Carex macloviana* aggregate was recognized as members of the section *Ovales* which possess inconspicuous bracts that are shorter than the inflorescence, or scale-like, dark colored scales which are shorter than the perigynia, terete tipped perigynia beaks, and achenes generally shorter than 1.75 mm. *Carex preslii* was excluded because it possesses large, oblong-quadrate achenes which are 1.7 x 1.3 mm. in size or greater, flattened perigynia beak tips, and scales which are subequal to the perigynia (Mackenzie, 1931-35; Hermann, 1970). The general aspect of the heads and perigynia of *C. preslii* resemble more closely those of *C. multicostata* Mackenzie and *C. straminiformis* Bailey in Mackenzie's 'Festucaceae' group of the *Ovales*. *Carex platylepis* was also excluded since it possesses large achenes (1.75 x 1.0mm.) and scales which are subequal to the perigynia (Hermann, 1970). Some forms of *C. pachystachya* possess scales which are subequal to the perigynia and may be confused with *C. preslii* or *C. platylepis* (see Cronquist, 1969, 1977 for a treatment of this nature). However, *C. pachystachya* does not have perigynia as plump in appearance as *C. preslii*, due to the smaller achenes, and the beak tips of the perigynia of *C. pachystachya* are terete in comparison to the flattened beak tips of *C. preslii*. *Carex platylepis* is quickly distinguished from *C. pachystachya* by the white hyaline margins of scales and perigynia tips. However, the type specimen of *C. platylepis* bears a resemblence to *C. macloviana* in the features just mentioned, and for this reason, it was included in the numerical analyses.

In examining material of *C. macloviana* and *C. pachystachya*, specimens which resembled *C. pachystachya*, but had shorter, darker perigynia were noted. At first it was thought these were misidentified specimens of *C. illota* Bailey, a species in the section *Ovales* which is characterized by its small, dark heads and perigynia. However, the perigynia of *C. illota* lack noticeable wing margins, especially on the beak of the perigynium (Mackenzie, 1931-35; Hermann, 1970; Boivin, 1979), while the specimens under consideration had perigynia with wing margins throughout. Because of their smaller, darker perigynia, these specimens may have represented intermediates between *C. macloviana* and *C. pachystachya*, therefore, they were treated as a separate taxon (designated 'stubby') in the statistical and numerical analyses to further explore the relationships they shared with the rest of the aggregate.

The characters found useful at this point of the study to distinguish the taxa are listed in Table 6, and are the same characters which have been used by previous authors to differentiate the taxa. Of these, four are qualitative which could not be used in the statistical and numerical analyses. In light of the fact that the four qualitative characters in Table 6 were useful in separating the taxa, they were further analyzed to see if certain character states were of diagnostic value. Figure 3 and Figure 4 present the results of the analysis.

Shape of inflorescences throughout the aggregate were ovoid (Figure 4), with the heads of *C. pachystachya* and *C. festivella* exhibiting a tendency to be more elongate. However, this was not absolute as most of the heads of these two taxa were ovoid, and all

Table 6. Characters and their respective states used in separating taxa in the *Carex macloviana* aggregate in the herbarium study.

	TAXA						
CHARACTER	*pachystachya*	'stubby'	*macloviana*	*haydeniana*	*festivella*	*limnophila*	*microptera*
Shape of inflorescence	oblong-ovoid	ovoid	ovoid	triangular-ovoid	oblong-ovoid	ovoid	ovoid
Scale color	lustrous	dark-lustrous	lustrous	dull	dull	dull-lustrous	dull
Scale margins	± hyaline	not hyaline	white hyaline	± hyaline	± hyaline	not hyaline	not hyaline
Perigynium color	lustrous	dark-lustrous	lustrous	dull-lustrous	dull	dull-lustrous	dull
Perigynium shape	ovate	elliptic-ovate	elliptic-ovate	ovate	ovate	ovate	ovate
Perigynium tip	± hyaline	not hyaline	white hyaline	not hyaline	± hyaline	not hyaline	not hyaline
Perigynium length	3.5-5.0 mm	3.0-4.0 mm	3.5-4.5 mm	4.5-6.5 mm	3.5-4.5 mm	3.0-4.5 mm	3.0-4.5 mm
Dorsal suture	not hyaline	not hyaline	white hyaline	not hyaline	not hyaline	not hyaline	not hyaline

Figure 3. Histograms showing the frequency of the various character states for scale color and perigynium color for taxa of the *Carex macloviana* aggregate. For scale color, the character state 1=red, 2=red-brown, 3=brown, 4=red-coppery, 5=coppery, 6=brown-coppery, and 7=blackish. For perigynium color, the character state 1=stramineous, 2=red, 3=red-brown, 4=brown, 5=red-coppery, 6=coppery, 7=brown-coppery, and 8=blackish. The taxa are represented as abbreviations so that *PACHY=C. pachystachya*, *STUB=*'stubby', *FEST=C. festivella*, *LIMNO=C. limnophila*, *HAY=C. haydeniana*, and *MICRO=C. microptera*.

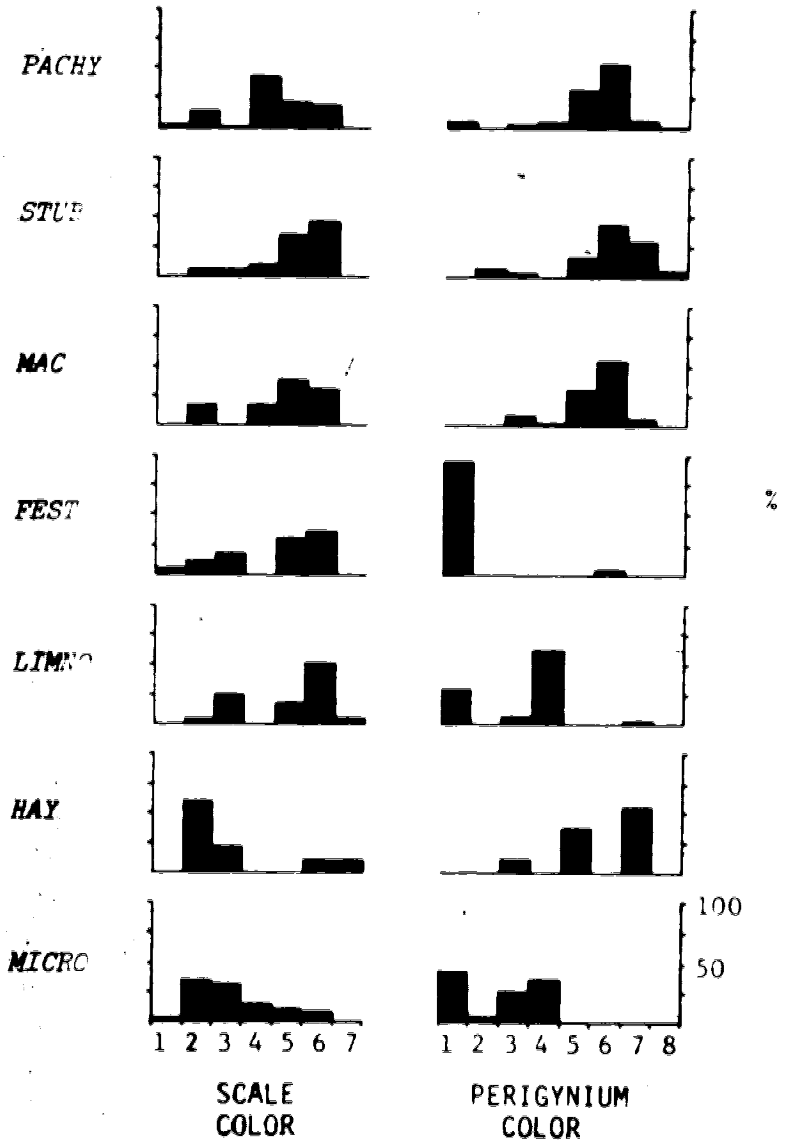
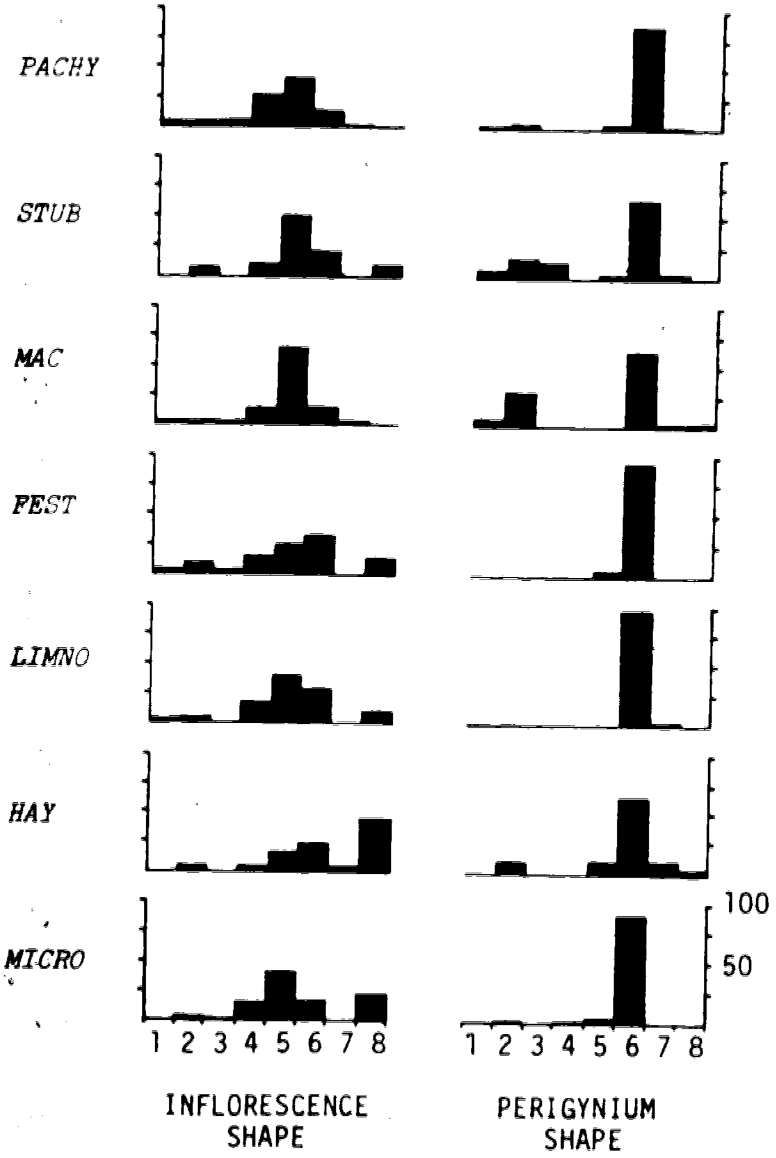

PACHY
STUP
MAC
FEST
LIMNO
HAY
MICRO
%
100
50
1 2 3 4 5 6 7
1 2 3 4 5 6 7 8
SCALE COLOR
PERIGYNIUM COLOR

Figure 4. Histograms showing the frequency of the various character states for inflorescence shape and perigynium shape for taxa of the *Carex macloviana* aggregate. For inflorescence shape, the character state 1=elliptic, 2=elliptic-ovoid, 3=oblong, 4=oblong-ovoid, 5=ovoid, 6=wide-ovoid, 7=obovoid, and 8=triangular-ovoid. For perigynium shape, the character state 1=elliptic, 2=elliptic-ovate, 3=oblong-ovate, 4=lanceolate, 5=narrow-ovate, 6=ovate, 7=wide-ovate, and 8=obovate.


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
%
100
50
1 2 3 4 5 6 7 8
1 2 3 4 5 6 7 8
INFLORESCENCE SHAPE
PERIGYNIUM SHAPE

of the remaining taxa possessed, in low frequencies, oblong- or elliptic-ovoid heads. *Carex haydeniana* showed a marked shift towards triangular-ovoid heads, but this character state was also present in *C. microptera*, *C. limnophila*, *C. festivella* and 'stubby', although to a lesser degree.

The differences between the taxa for perigynia shape was even less pronounced than for inflorescence shape (Figure 4). All members of the aggregate have ovate perigynia, with *C. haydeniana*, *C. macloviana* and 'stubby' exhibiting a tendency toward more elliptic or elongate perigynia.

Unlike the shape characters, the color characters showed a bimodal distribution of states (Figure 3). *Carex macloviana* and *C. pachystachya* have been characterized in the past as possessing coppery colored scales and perigynia. However, actual color is quite variable and it would be more accurate to describe them as possessing a metallic luster. Thus, *Carex pachystachya*, *C. macloviana*, *C. festivella*, *C. limnophila* and 'stubby' have a high frequency of lustrous scales, and *Carex pachystachya*, *C. macloviana*, *C. haydeniana* and 'stubby' were shown to have a high frequency of lustrous perigynia. From these data, two groups of taxa were evident: *Carex pachystachya*, *C. macloviana*, and 'stubby' with lustrous scales and perigynia, and the remaining taxa with one or none of these character states.

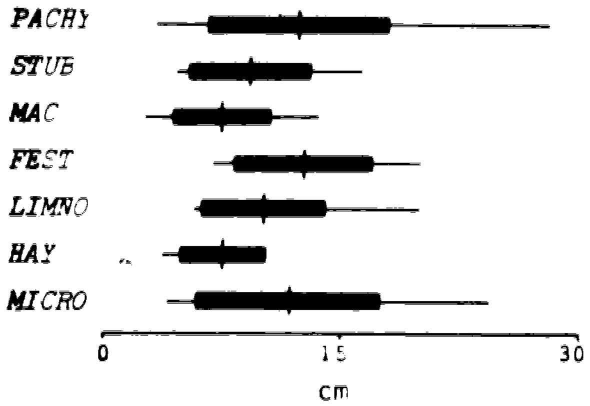
The final aspect of the herbarium study was an attempt to discover additional taxa before commencing with statistical and numerical analyses. The morphological subunits which were recognized for each taxon (Table 4) were mapped to seek geographical correlations with structural features. All subunits, however, were within the geographic range of their taxa's typical subunit, and it was assumed that no new taxa could be recognized.

Statistical Analysis: The sample statistics were calculated to estimate population parameters from which the samples were drawn, since the overall population is of interest (*Carex macloviana* aggregate) and not the samples *per se*. Thus means and standard deviations are unbiased estimates of population parameters. However, size of sample clearly affects how reliable the estimated parameters are: a larger sample will tend to reflect the population parameters more reliably than a small sample (Sokal and Rohlf, 1969). Because the estimated population standard deviation is based on the sample mean, it becomes important to know how reliable an estimate the sample mean is. This was accomplished by calculating the standard error of the mean which is effectively the standard deviation of a number of means calculated from repeated sampling of the same population (Sokal and Rohlf, 1969), or, as Radford *et al.* (1974) put it, it is "the range within which the mean of another random sample from the same population would fall in two cases out of three" (l.c.: 427). Thus, it was expected that *C. haydeniana*, *C. limnophila*, *C. festivella* and 'stubby' would have the larger standard errors because of their small sample sizes. But since sample size was a reflection of variation observed in each taxon, and geographic range of each subunit, those taxa with a greater geographic range and more subunits would have larger sample sizes (i.e. *C. pachystachya*, *C. macloviana* and *C. microptera*). Therefore, the sample statistics with large standard errors are viewed cautiously, but are still considered valid since it is assumed the samples adequately expressed the variation exhibited by their respective taxa. Finally, the coefficient of variation is a statistic which expresses amount of variation exhibited by a sample for a character. It is similar to the standard deviation, but unlike the standard deviation, which cannot be compared between populations which vary appreciably in their means, the coefficient of variation is readily amendable to such comparisons (Sokal and Rohlf, 1969).

Results of the statistical analysis are presented in Figure 5 and Appendix 5. These results provided a grouping of the quantitative characters into three sets (Table 7). The first set consisted of six characters which exhibited enough difference in their variation to be of some diagnostic value for a taxon. All of these were reproductive characters and have been used previously. For character #8 (inflorescence type), *C. haydeniana* showed a noticeable shift towards tightly aggregate inflorescences, although *Carex festivella* and *C. microptera* also included some individuals with tightly aggregate heads. Because the character is a subjective one, it is not, by itself, adequate for distinguishing *Carex haydeniana*. However, taken in conjunction with the taxon's tendency towards triangular-ovoid heads, the combination is useful.

Analysis of character #20 (scale margins), showed that *C. macloviana* possesses a greater frequency of hyaline margined scales. However, the range of variation for the taxon overlaps with that of *C. pachystachya* and *C. festivella*, and some individuals of 'stubby' and *C. limnophila* possess hyaline margined scales. What is not shown by the analysis of this character is that *C. macloviana* has noticeably white hyaline margined scales,while the scales on the other taxa are not as noticeably white hyaline. This distinction,correlated with the white

Figure 5. Results of the statistical analysis of 47 quattitative characters for members of the *Carex macloviana* aggregate for western Canada and Alaska. See Appendix 5 for actual values. Horizontal line indicates range, vertical line indicates mean, and solid bar is plus and minus one standard deviation from the mean.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MAC
FEST
LIMNO
HAY
MICRO
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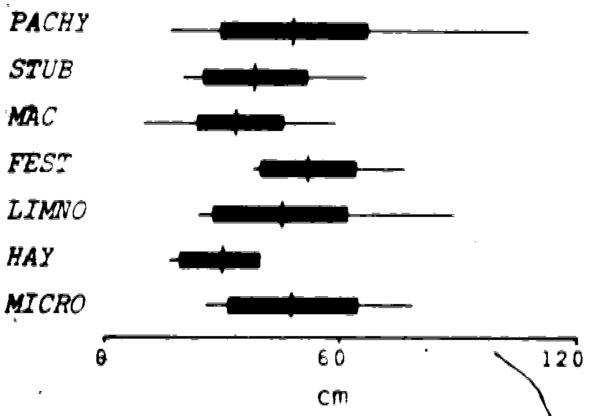
15
30
cm

#1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FEST
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HAY
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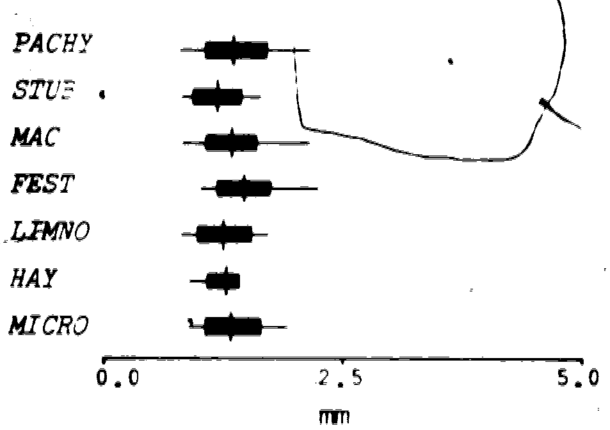
60
120
cm

#2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STUB
MAC
FEST
LIMNO
HAY
MICRO
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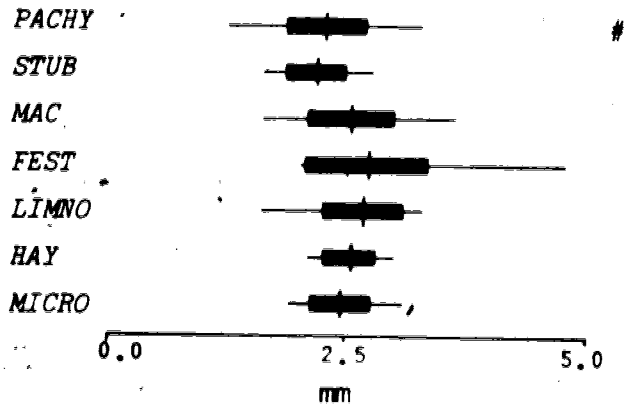
2.5
5.0
mm

#3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STUB
MAC
FEST
LIMNO
HAY
MICRO
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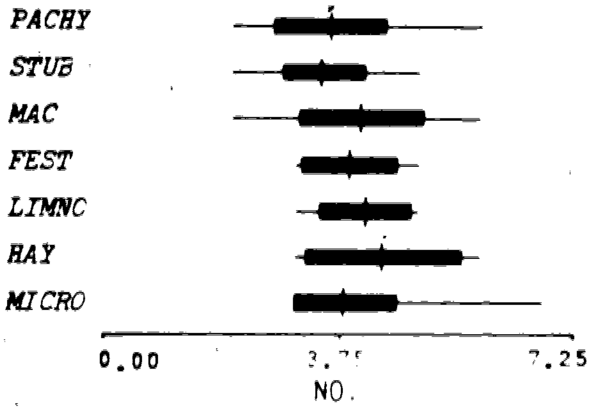
2.5
5.0
mm

#4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MAC
FEST
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HAY
MICRO
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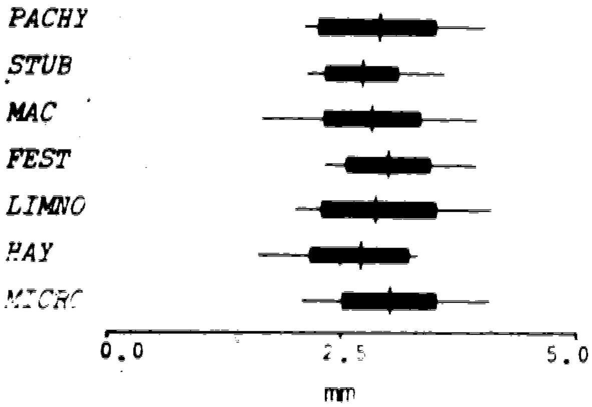
3.75
7.25
NO.

#5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FEST
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HAY
MICRO
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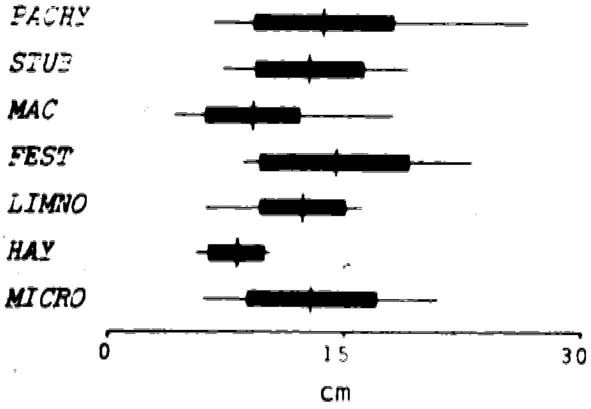
5.0
mm

#6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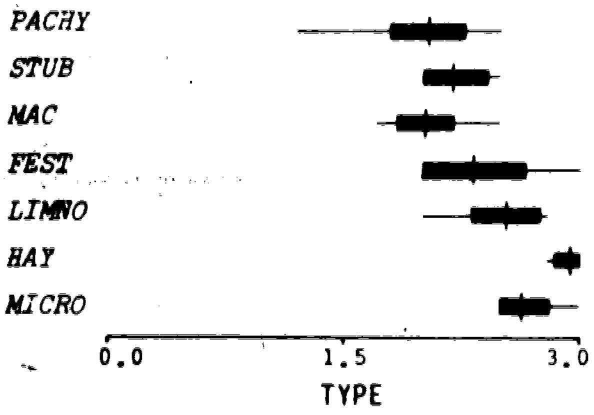
30
cm

#7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FEST
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MICRO
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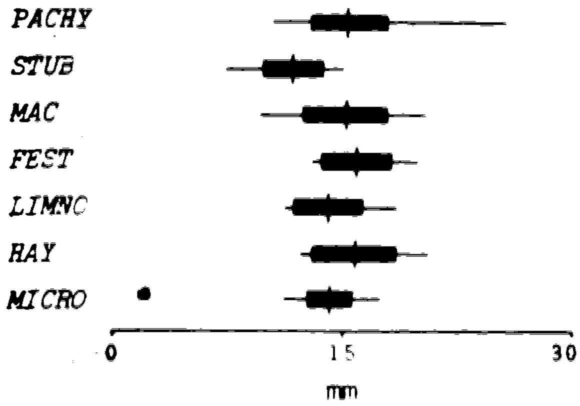
3.0
TYPE

#8

#9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FEST
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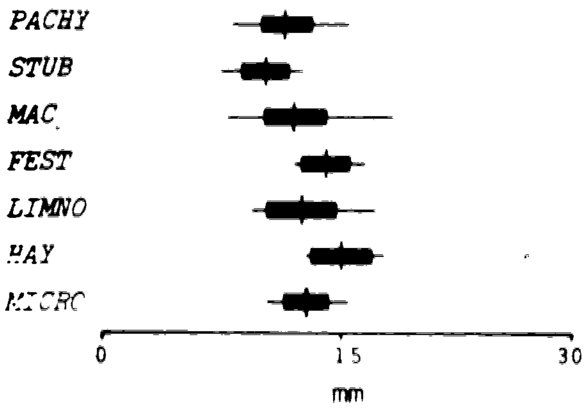
HAY
MICRO
0
15
30
mm

#10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FEST
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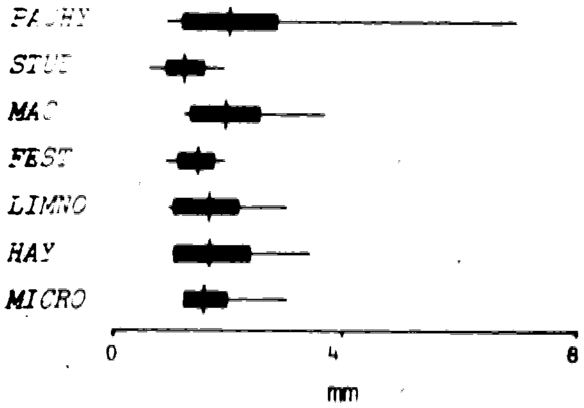
HAY
MICRO
0
15
30
mm

#11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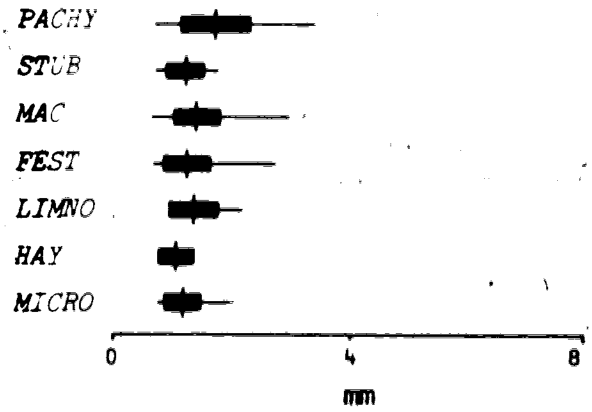
STUB
MAC
FEST
LIMNO
HAY
MICRO
0
4
8
mm

#12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HAY
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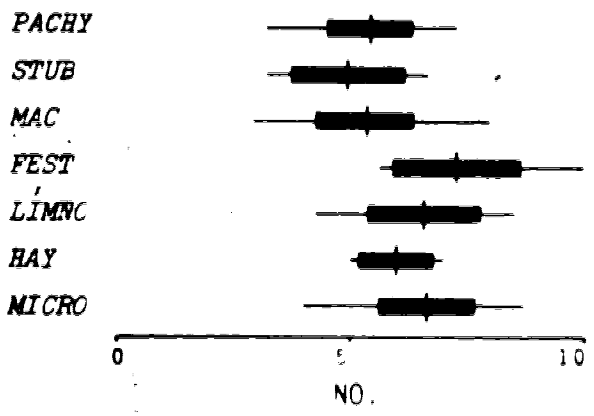
4
8
mm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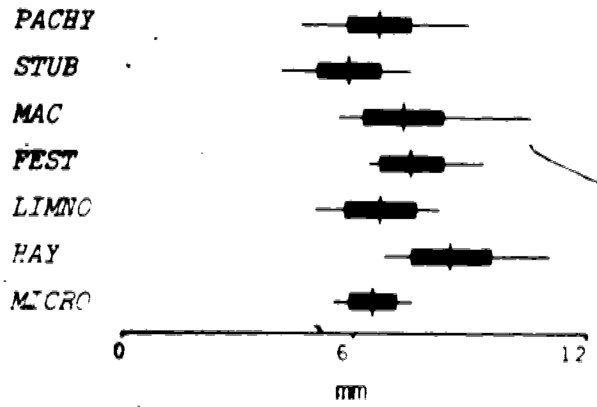
5
10
NO.

#13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FEST
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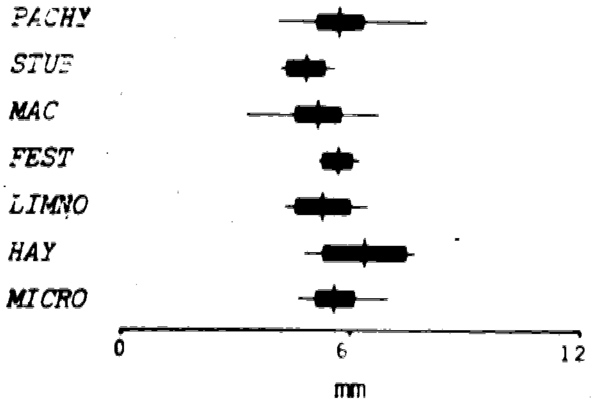
HAY
MICRO
0
6
12
mm

#14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HAY
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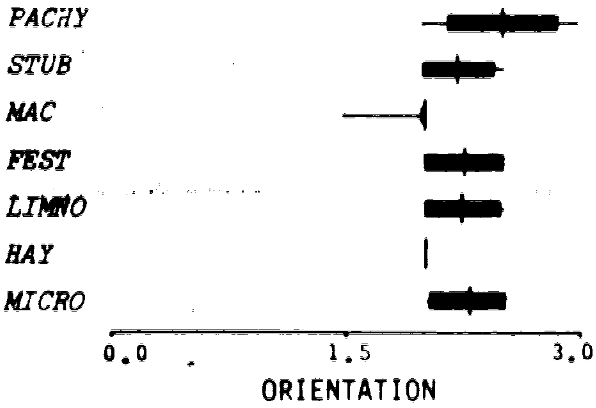
6
12
mm

#15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FEST
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HAY
MICRO
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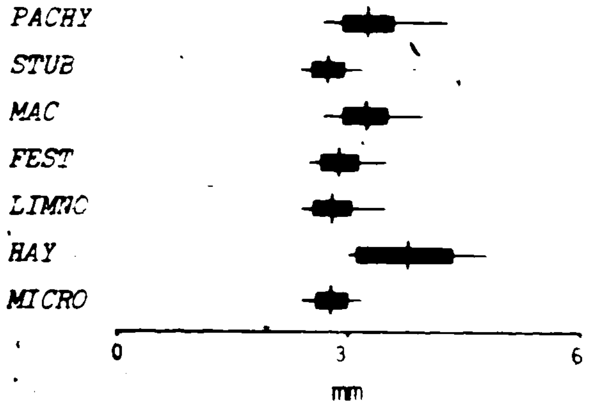
3.0
ORIENTATION

#16


PACHY
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MAC
FEST
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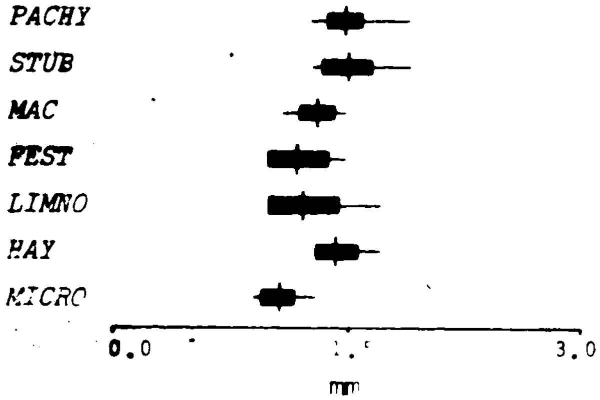
0
3
6
mm

#17


PACHY
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FEST
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HAY
MICRO
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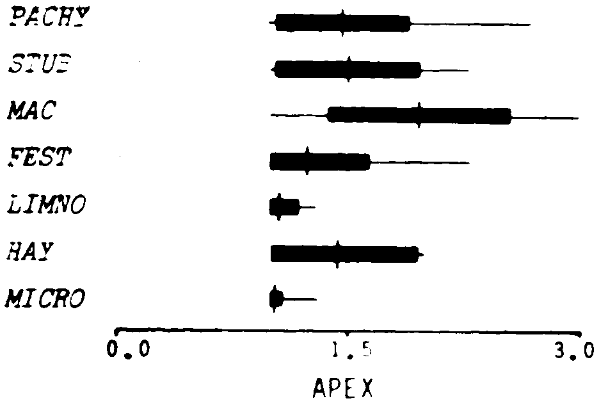
1.5
3.0
mm

#18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FEST
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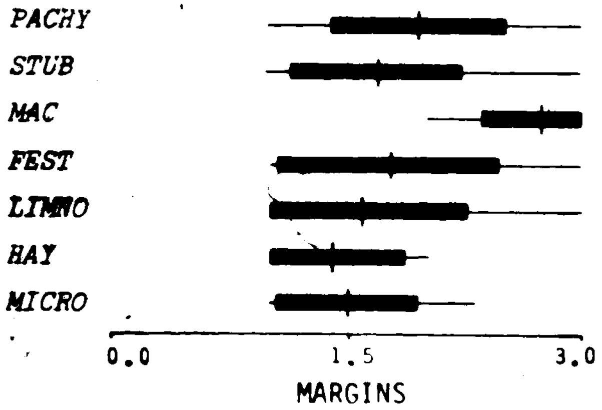
1.5
3.0
APEX

#19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MAC
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MICRO
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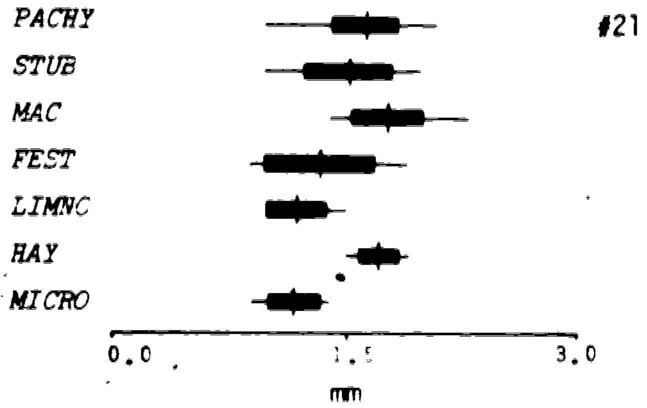
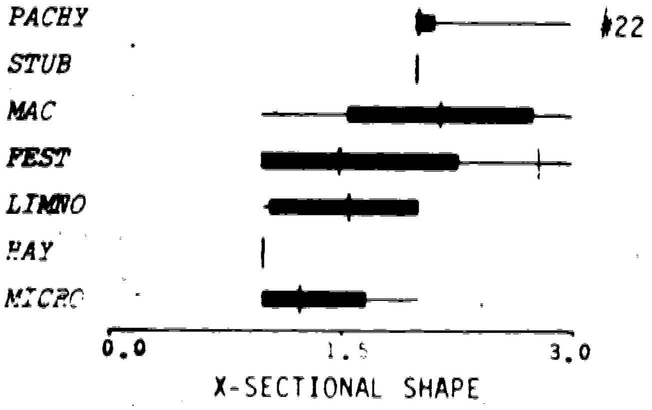
1.5
3.0
MARGINS

#20


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
#21
0.0
1.5
3.0
mm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FEST
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HAY
MICRO
#22
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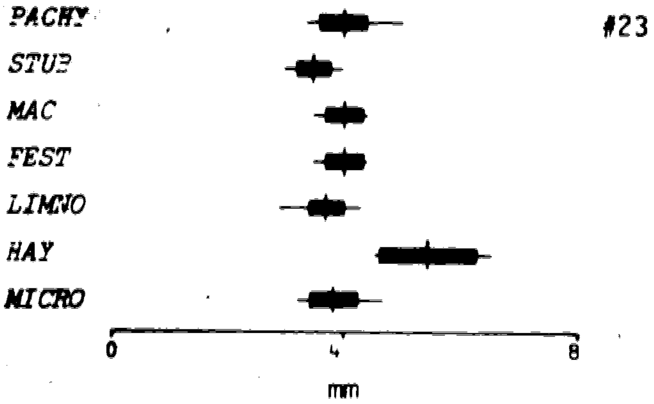
3.0
X-SECTIONAL SHAPE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MAC
FEST
LIMNO
HAY
MICRO
#23
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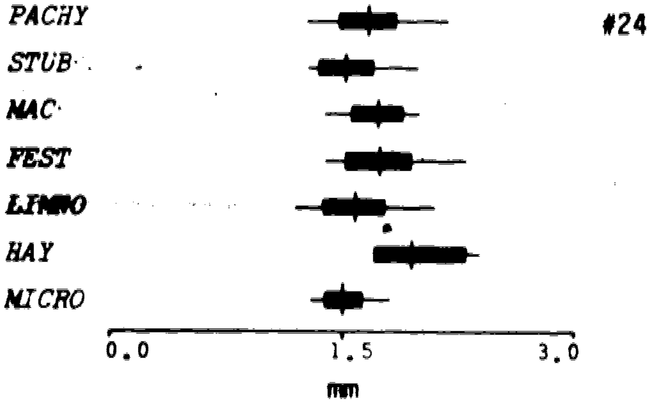
4
8
mm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FEST
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HAY
MICRO
#24
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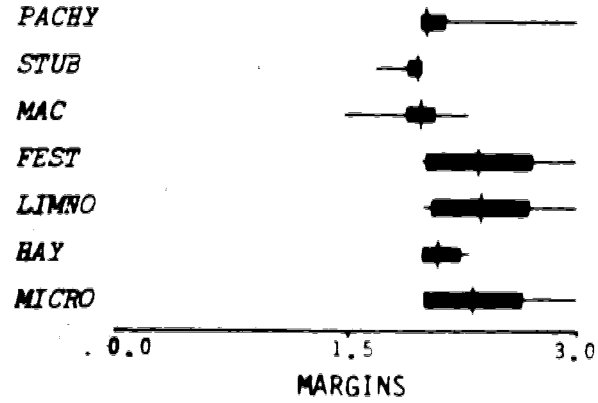
1.5
3.0
mm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FEST
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HAY
MICRO
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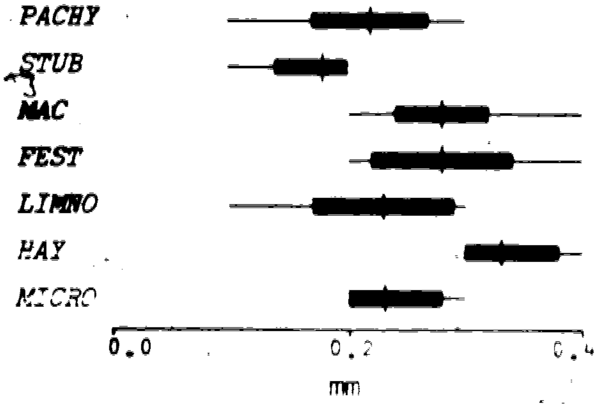
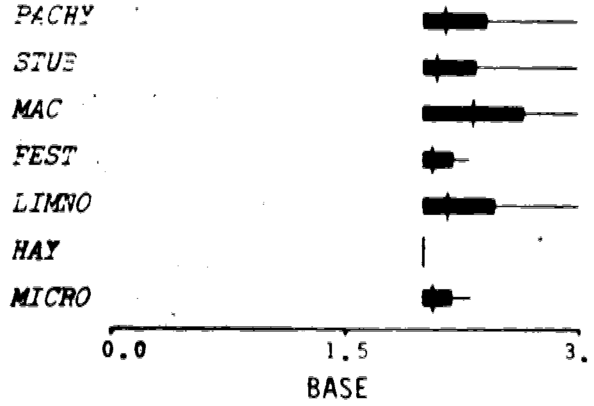
3.0
MARGINS

#25


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.2
0.4
mm

#26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STUB
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FEST
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HAY
MICRO
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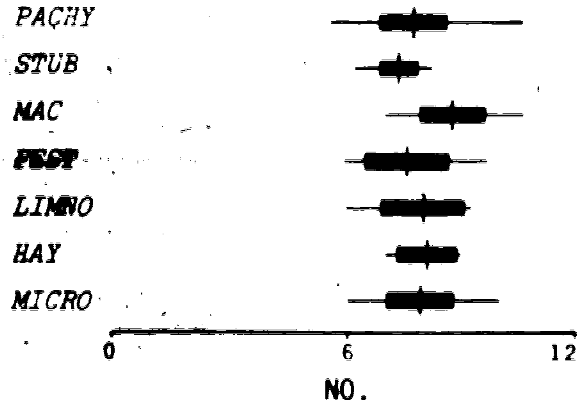
1.5
3.0
BASE

#27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MAC
FEST
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HAY
MICRO
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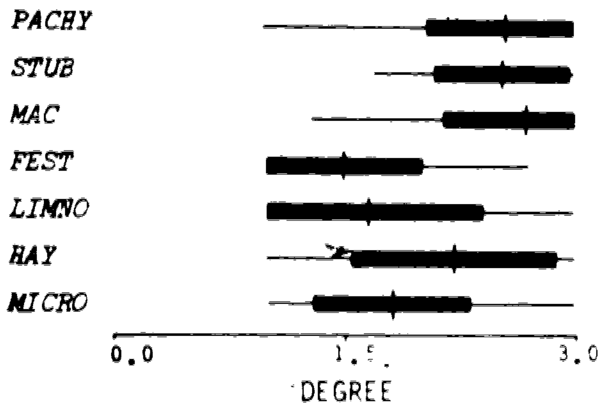
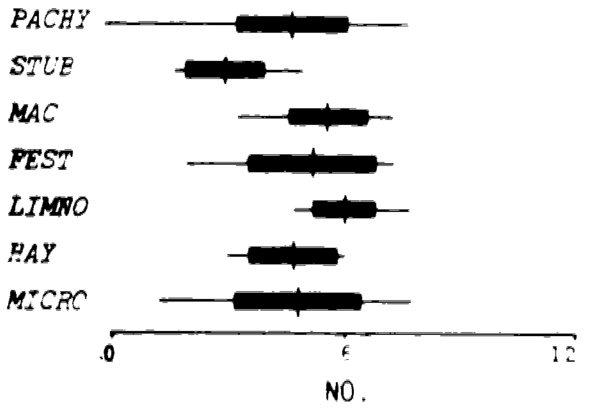
6
12
NO.

#28


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
1.5
3.0
DEGREE

#29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MAC
FEST
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HAY
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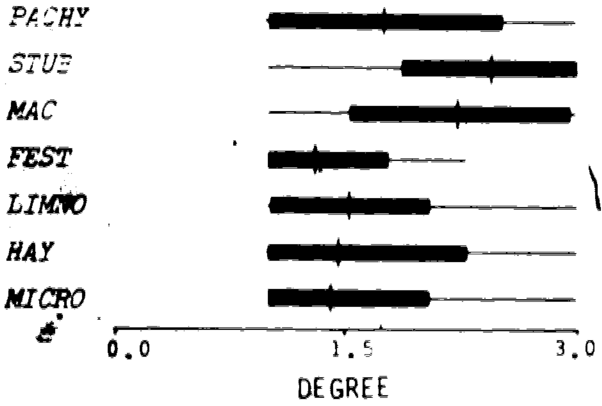
6
12
NO.

#30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FEST
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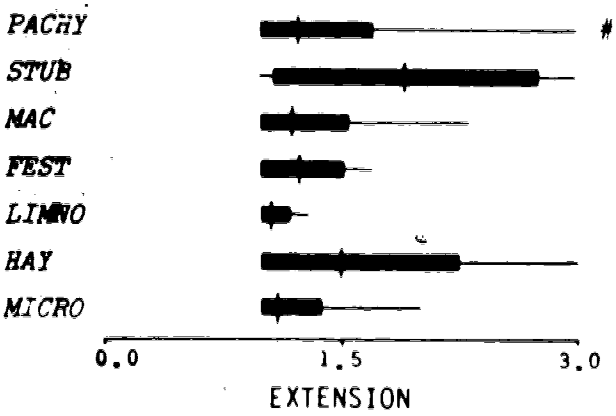
3.0
DEGREE

#31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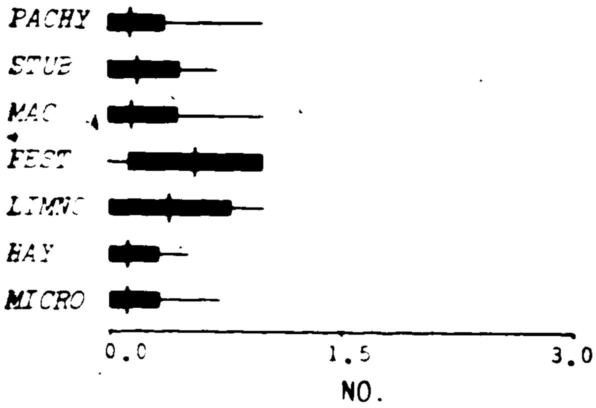
EXTENSION

#32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MAC
FEST
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HAY
MICRO
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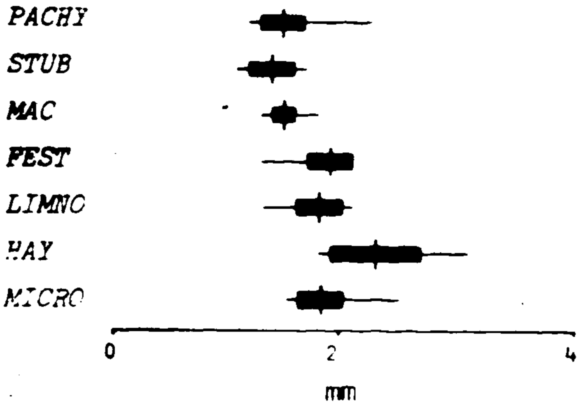
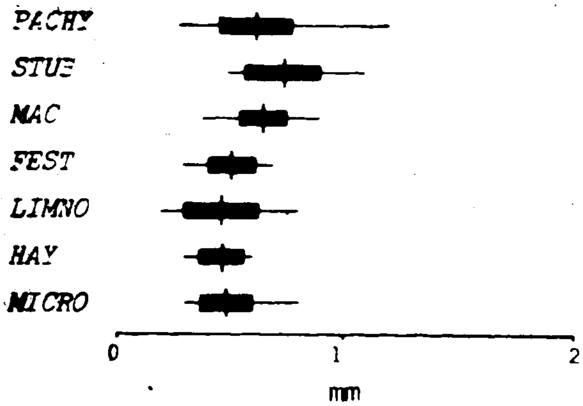
1.5
3.0
NO.

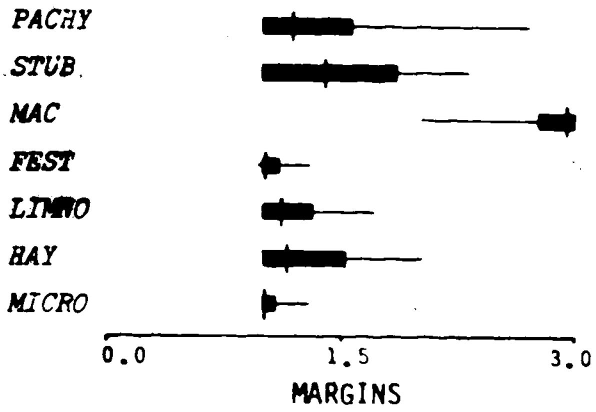
#33


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0
2
4
mm

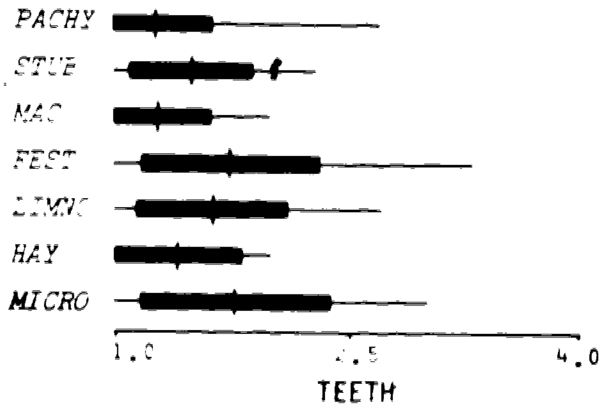
#34


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0
1
2
mm

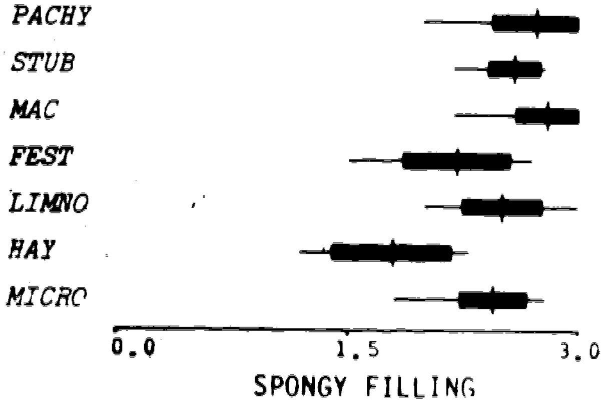
#35


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
1.5
3.0
MARGINS

#36


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
1.0
2.5
4.0
TEETH

#37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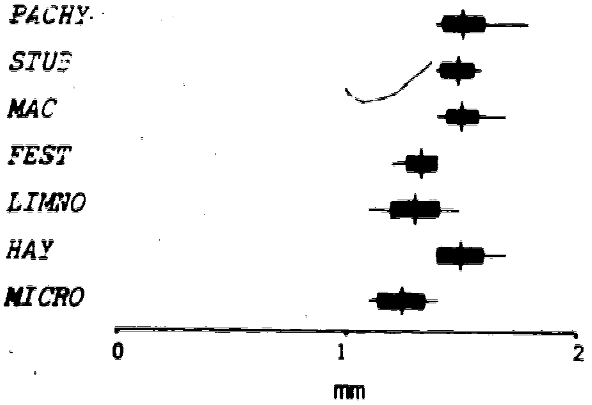
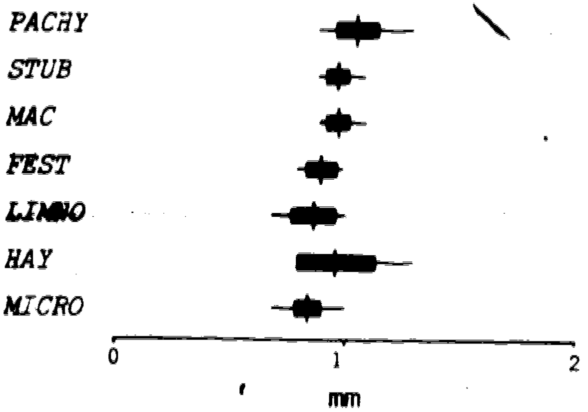
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
1.5
3.0
SPONGY FILLING

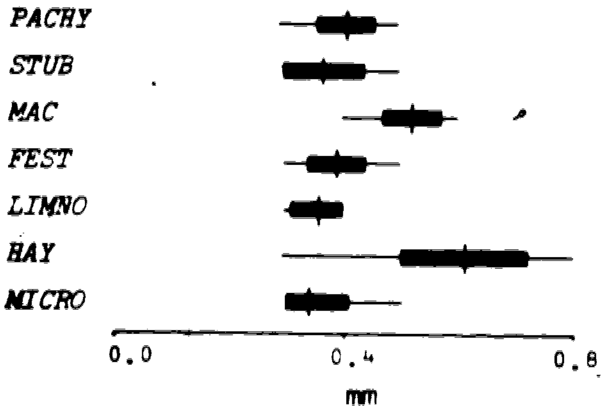
#38


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0
1
2
mm

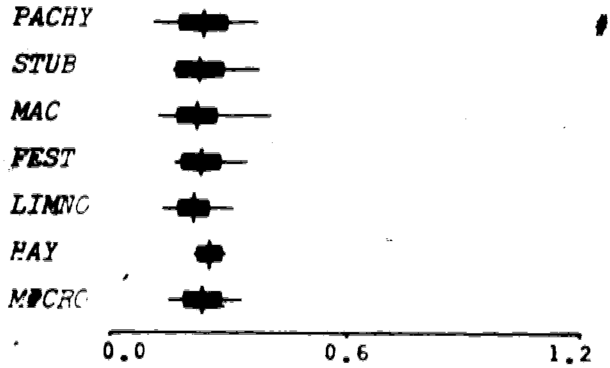
#39


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0
1
2
mm

#40


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.4
0.8
mm

#41


PACHY
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MAC
FEST
LIMNO
HAY
MICRO
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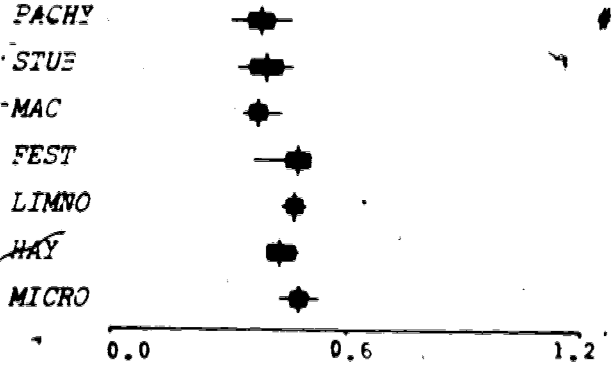
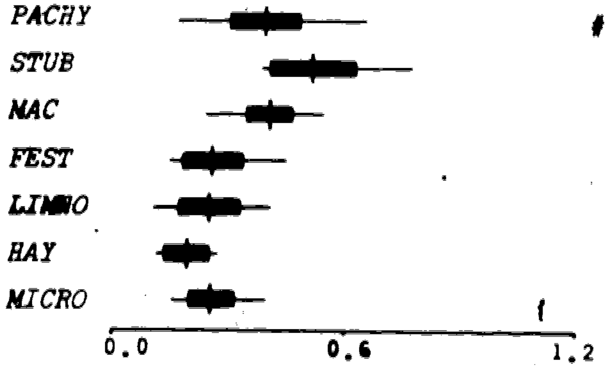
0.6
1.2

#42


PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.6
1.2

#43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STUB
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FEST
LIMNO
HAY
MICRO
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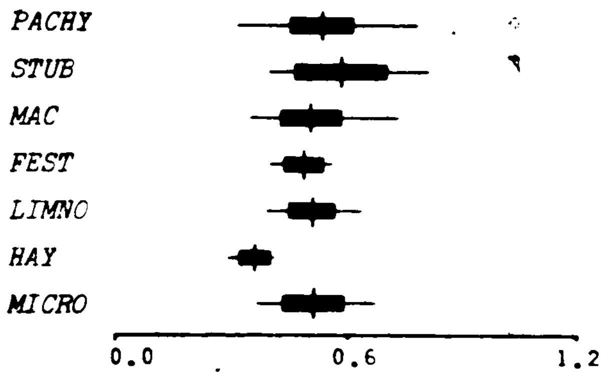
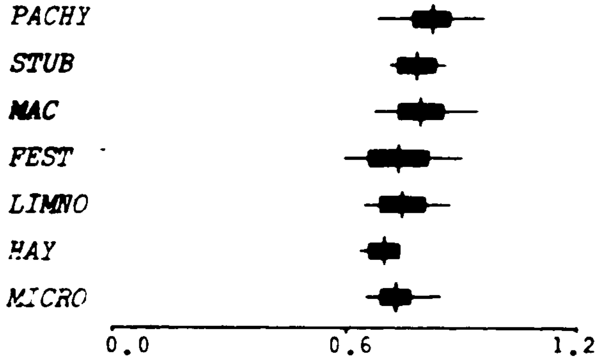
0.6
1.2

#44



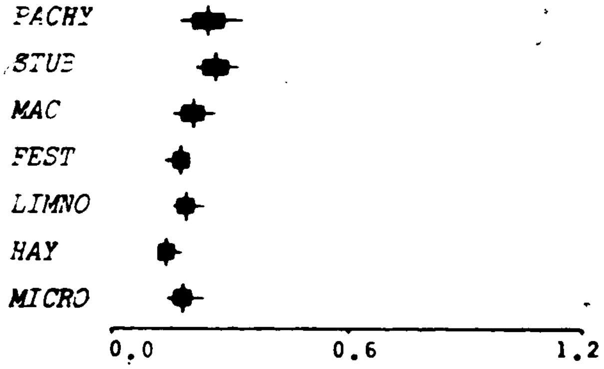
#45

PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.6
1.2



#46

PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.6
1.2



#47

PACHY
STUB
MAC
FEST
LIMNO
HAY
MICRO
0.0
0.6
1.2

Table 7. Grouping of the 47 quantitative characters into three sets evident from the statistical analysis.

Characters which can be used to distinquish a taxon:

#8, 20, 23, 36, 45, 47

Characters which separate taxa into two groups:

#16, 39, 41, 43

Characters too variable or too constant to be of diagnostic value:

#1-7, 9-15, 17-19, 21, 22, 24-35, 37, 38, 40, 42, 44, 46 hyaline perigynium beak tips of *C. macloviana* (character #36), has proven to be a good diagnostic character.

Character #23 (perigynium length) has proven useful in separating *C. haydeniana* from the remaining taxa. Figure 5 shows the perigynia of *C. haydeniana* are larger than the other members of the aggregate, with a mean length greater than 5.0 mm. Although some individuals of *C. pachystachya* have large perigynia, this character correlated well with the cross sectional shape of the perigynia (#22), for which *C. haydeniana* was shown to possess only flattened perigynia, while *C. pachystachya* had only convao- or plano-convex perigynia.

Analysis of character #36 (perigynium beak tip margins), showed that *C. macloviana* possesses a high degree of hyaline tipped beaks. Figure 5 also shows that some individuals of *C. pachystachya* and 'stubby' possess hyaline tipped beaks. However, the beak tips of *C. macloviana* are again, noticeably white hyaline margined while the other taxa are not hyaline tipped to the same degree.

Characters #45 and 47 expressed the relation of area of achene to area of perigynium. Character #47 did this by expressing area of the perigynium as its length and width. Character #45 took into account beak length and perigynium margin width and subtracted these from the perigynium length and width, respectively. Both characters showed that *Carex haydeniana* has smaller values, due to larger perigynia of that taxon. Overlap of range of variation of *Carex haydeniana* with some individuals of *Carex microptera, Carex limnophila, Carex macloviana and C. pachystashya*, indicates this character would best be employed in a relative sense (i. e. achenes small in relation to perigynia). However, in a numerical analysis, redundant characters are inadmissable and, therefore, one of these had to be excluded from further analysis. Since character #47 was dependent on only four other characters, and thus had two fewer sources of error, and exhibited a slightly lower coefficient of variation for all the taxa, it was chosen for the numerical analyses.

The second group of characters which was evident from the analysis, consisted of four which could be used to arrange the taxa in two groups. Again, all were reproductive characters, but only one, #16, had been reported previously. Although a number of authors (Mackenzie, 1931-35; Moss, 1959; Hermann, 1970; Looman and Best, 1979) have used the orientation of the perigynia tips in spikes to distinguish *Carex festivella*, with appressed tips, from *Carex microptera*, with spreading tips, Figure 5 shows that the range of variation for this character was nearly identical for these taxa. Two groups of taxa can be distinguished however, *Carex haydeniana* and *C. macloviana* as one group with ascending perigynia tips within the spikes and the remaining taxa with ascending to spreading perigynia tips. The value of 1.5 for the low end of the range of *C. macloviana* was represented by only a single specimen, while the rest of the specimens measured had a value of 2.

Character #39 (achene length) was shown to distinguish *Carex pachystachya, C. macloviana, C. haydeniana* and 'stubby', with achenes generally more than 1.4 mm long, from *C. limnophila, C. festivella* and *C. microptera* with achenes generally less than 1.4 mm long.

Analysis of character #41 (achene stipe length) showed that *Carex macloviana* and *Carex haydeniana* possess larger stipes than the rest of the taxa, although there is some overlap in the range of variation for these two taxa and the remaining taxa.

Although character #43 (ratio of beak length to perigynium length) showed *C. pachystachya, C. macloviana* and 'stubby' to have relatively short beaks in comparison to the perigynium (2/5 the length), and *C. microptera, C. limnophila* and *C. festivella* have relatively long beaks in comparison to the perigynium (1/2 the length), the low end of the range for the latter group overlapped with the former group to some extent. When the character was tried on a group of specimens, it was not helpful in distinguishing the two groups. Therefore, the character alone is not useful for diagnostic purposes. However, combination of this character with relative size of achene to perigynium (#45 and 47) was useful. The relatively short beak length and large achene size results in the distance from the top of the achene to the perigynium tip one half or less than the overall perigynium length for the taxa *C. pachystachya, C. macloviana* and 'stubby'. For *C. haydeniana, C. festivella, C. limnophila* and *C. microptera*, this distance is one half or greater than the overall perigynium length. This combined character became very useful for diagnostic purposes.

The third group consisted of 37 characters which exhibited too much overlap in their range of variation among all the taxa to be of any diagnostic value. It is interesting to note that seven of these have been used by previous authors to separate taxa within the group, especially characters #22, 30, 31, and 32 which have been used by most major authors who have treated the aggregate (see Mackenzie, 1931-35; Moss, 1959; Cronquist, 1969, 1977; Hermann, 1970; Looman and Best, 1979).

Numerical Analyses: Results of the numerical analyses are presented in two parts, one dealing with the analysis of OTU's and the other with the analysis of taxa. For each program, two analyses were used, one with all 46 characters, and a second with 38 reproductive characters. Reproductive characters were analyzed separately in light of the generally high variability exhibited by the taxa for vegetative characters (see Appendix 5, coefficient of variation), and general utility of reproductive characters in classifying members of the genus.

To distinguish between clusters and taxa, clusters are referred to by either their number or an abbreviated epithet of the most frequent OTU in the cluster.

a) Analysis of OTU's: TAXMAP analyses formed groups of clusters consisting of a primary cluster, and clusters linked to it, or to clusters linked to the primary one (Table 8 and Table 9. See Appendix 6 for cluster membership). Linked clusters would have become part of the clusters to which they were linked had clustering not terminated. Clustering terminated in these instances because the next OTU to be added to the cluster under formation (the linked cluster) was already a member of another cluster (the primary one or one linked to it). Additional clusters were formed which were not linked to the cluster groups, but shared with the cluster groups their next closest OTU. In these instances, clustering terminated because the single linkage criterion of the program was not met. Finally, each analysis had a number of single member clusters which, like the additional clusters, shared their next closest OTU with a preformed cluster. Table 9 shows the clusters these single member clusters were nearest to in the analysis using

Table 8. Tabular results of TAXMAP analysis of OTU's of the *Carex maclovìana* aggregate using all characters, showing cluster groups and single member clusters. Clusters in brackets are subgroups. Clusters with subscripts are linked to the cluster represented by the subscript. Clusters with subscripts in parentheses share their next closest OTU with the cluster represented by the subscript, but are not linked to it. See text for further explanation and Appendix 6 for cluster membership.

PRIMARY CLUSTER	LINKED CLUSTERS	ADDITIONAL CLUSTERS
1 (PACHY)	4, 5, 8_5, (9), (11), 12_{11}, 13_5, 14, 15_5, 17_8, 19, 20_8, 23_{17}, $(26)_{23}$, 28_{15}, 32_{12}, 36_5, 38_{11}, 47, [48]	$6_{(1)}$, $22_{(5)}$, $25_{(15)}$, 30_{25}, $[34]_{(11)}$, 35_6, $39_{(38)}$, $42_{(22)}$, $46_{(19)}$, $49_{(46)}$, $[50]_{34}$
2 (MICRO)	7, 10, 18, 44, [45], [51]	$[27]_{(45)}$, $29_{(2)}$, $31_{(7)}$, $33_{(41)}$, 41_{33}, $43_{(2)}$
3 (MAC)	16, 21, 37	$24_{(3)}$, $40_{(16)}$

SINGLE MEMBER CLUSTERS

52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67

Table 9. Tabular results of TAXMAP analysis of OTU's of the *Carex maclovianа* aggregate using reproductive characters, showing cluster groups and single member clusters. Clusters in brackets are subgroups. Clusters with subscripts are linked to the cluster represented by the subscript. Clusters with subscripts in parentheses share their next closest OTU with the cluster represented by the subscript, but are not linked to it. See text for further explanation and Appendix 6 for cluster membership.

PRIMARY CLUSTER	LINKED CLUSTERS	ADDITIONAL CLUSTERS
1 (PACHY)	[4], 6, 8_6, 10, 15, 16, 17_{15}, 22, 23, 24, $(27)_4$, $[30]_4$, [31], (32)	$(14)_{(1)}$, $25_{(1)}$, $[29]_{(4)}$, $(33)_{(4)}$
2 (MICRO)	3, 5, 7, (9), 11, 12, 13, $(18)_7$, 20, 28	$(19)_{(2)}$, $[21]_{(18)}$, $26_{(2)}$, $[34]_{(2)}$

SINGLE MEMBER CLUSTERS

$35_{(5)}$, $36_{(4)}$, $37_{(2)}$, $38_{(18)}$, $39_{(34)}$, $40_{(2)}$, $41_{(21)}$, $42_{(11)}$, $43_{(2)}$, $44_{(4)}$, $45_{(1)}$, $46_{(1)}$, $47_{(10)}$, $48_{(10)}$, $49_{(1)}$, $50_{(25)}$

reproductive characters. This information for the analysis using all characters was not available because more than 50 clusters were formed in that analysis, and this exceeded the capacity of the program; thus, the mapping aids, from which the information is gathered,were suppressed.

The TAXMAP analysis of all characters produced three cluster groups (Table 8). The most inclusive consisted of OTU's of *Carex pachystachya* and 'stubby' in pure and mixed clusters, and a number of disparate clusters. These consisted of some OTU's of *C. macloviana*, one of *C. limnophila* and two (HAYMIC01 and HAYMIC02) from a population in Waterton Lakes National Park, which were thought to represent hybrids between *C. microptera* and *C. haydeniana*, and were included in the analyses to see where they would be placed. The second cluster group consisted of OTU's of *C. microptera*, *C. festivella* and *C. limnophila* in mixed clusters, and a subgroup of *C. haydeniana* clusters. The third group consisted entirely of *C. macloviana* OTU's. Because more than 50 clusters were formed, the plotting of the TAXMAP was suppressed.

The TAXMAP analysis for the reproductive characters produced two cluster groups (Table 9). The most inclusive consisted of OTU's of *C. pachystachya* and 'stubby' in pure and mixed clusters and a subgroup of *C. macloviana* clusters. Disparate clusters consisted of two mixed clusters of *C. macloviana* and *C. pachystachya* OTU's, and a cluster of one *C. limnophila* and three *C. festivella* OTU's. The second group was comprised of OTU's of *C. microptera*, *C. festivella* and *C. limnophila* in mixed clusters, and a subgroup of *C. haydeniana* clusters. A mixed cluster consisted of HAYMIC OTU's and a *C. microptera* OTU. Figure 6 presents the TAXMAP for the analysis, with clusters represented by circles, the diameter of which represents the distance between the two furthest OTU's

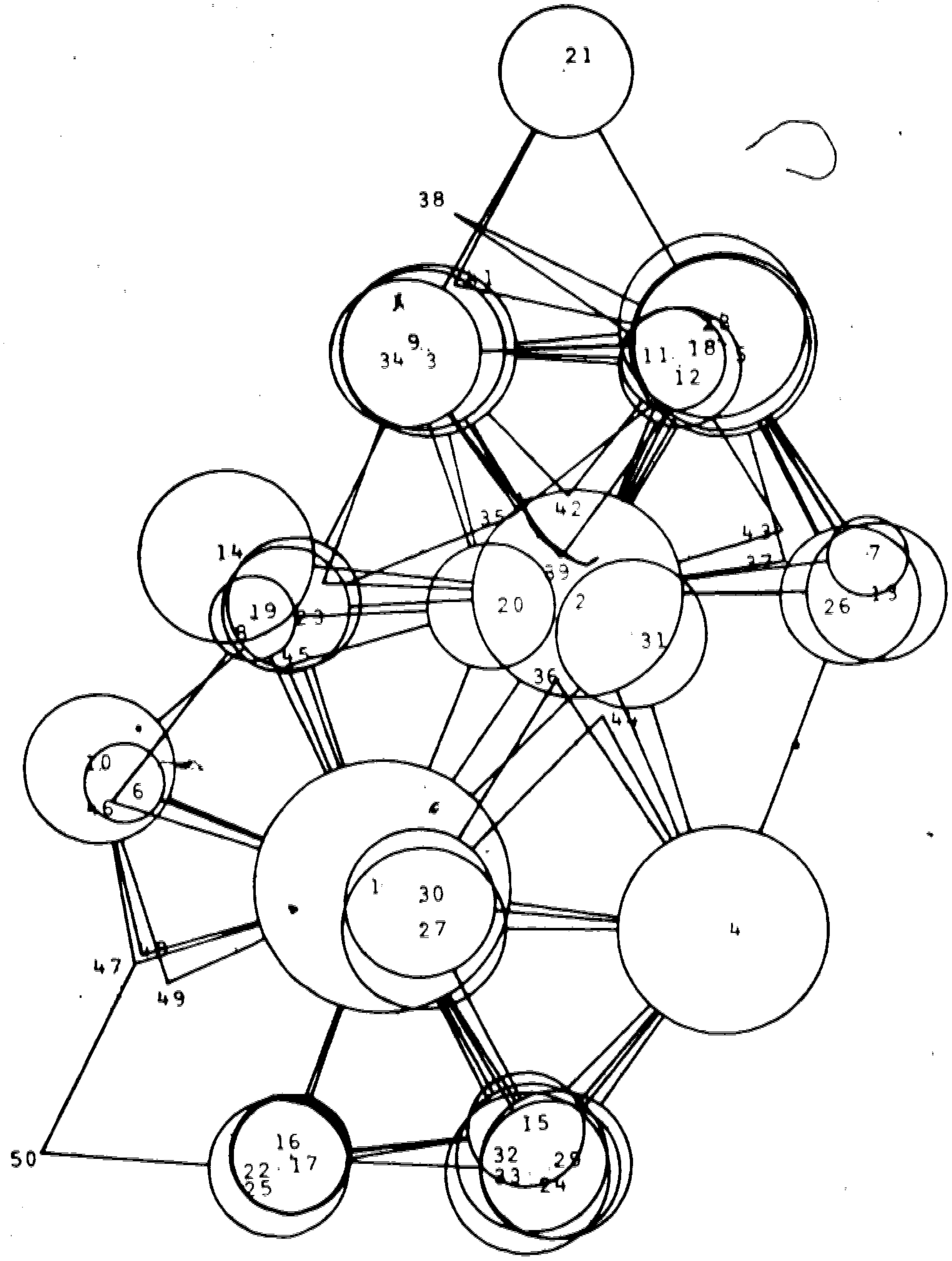


Figure 6. TAXMAP analysis of OTU's of the *Carex macloviana* aggregate using reproductive characters. See Appendix 6 for cluster membership.

in the cluster. Because of the large number of clusters, the TAXMAP was difficult to intrepret, and was redrawn with only the cluster centers plotted and connected by lines with arrows to indicate the nearest neighbor of each cluster (Figure 7). From this figure it was evident that there was a great deal of cohesion within each cluster group or subgroup, with only a few clusters crossing over the boundaries of cluster types.

Results of the CLUSTAN analyses are presented as two phenograms in Figure 8 and Figure 9 (see Appendix 7 for enlarged version with OTU's labelled). The names on the stems indicate the level at which clusters were chosen. The level was picked to approximate the cluster groups produced in the TAXMAP analyses, and to maintain the maxinum homogeneity of each cluster.

The CLUSTAN analysis using all characters produced three large clusters(Figure 8). The PACHY cluster consisted of a mixture of OTU's from *C. pachystachya* and 'stubby',with two *C. macloviana* OTU's. The MAC cluster consisted of only *C. macloviana* OTU's. The MICRO cluster contained OTU's of *C. microptera, C. limnophila* and *C. festivella* freely mixed. Cluster 'X' was a mixed cluster,comprised of the type of *C. soperi* (TYPE03) a synonym for *C. macloviana*,the type of *C. microptera* var. *crassinerva* (TYPE04),the HAYMIC OTU's and an OTU of *C. pachystachya*. Cluster 'Y' was also mixed and consisted of all the *C. haydeniana* OTU's, the type of *C. festivella*(TYPE09), the type of *C. platylepis*(TYPE05), two OTU's of *C. pachystachya*, two of *C. macloviana*, one from *C. limnophila* and three from *C. festivella.*

The CLUSTAN analysis using reproductive characters produced three extensive, relatively homogeneous clusters, and one that was mixed(Figure 9). The PACHY cluster consisted of OTU's of *Carex pachystachya* and of 'stubby', and a single OTU of *Carex macloviana*

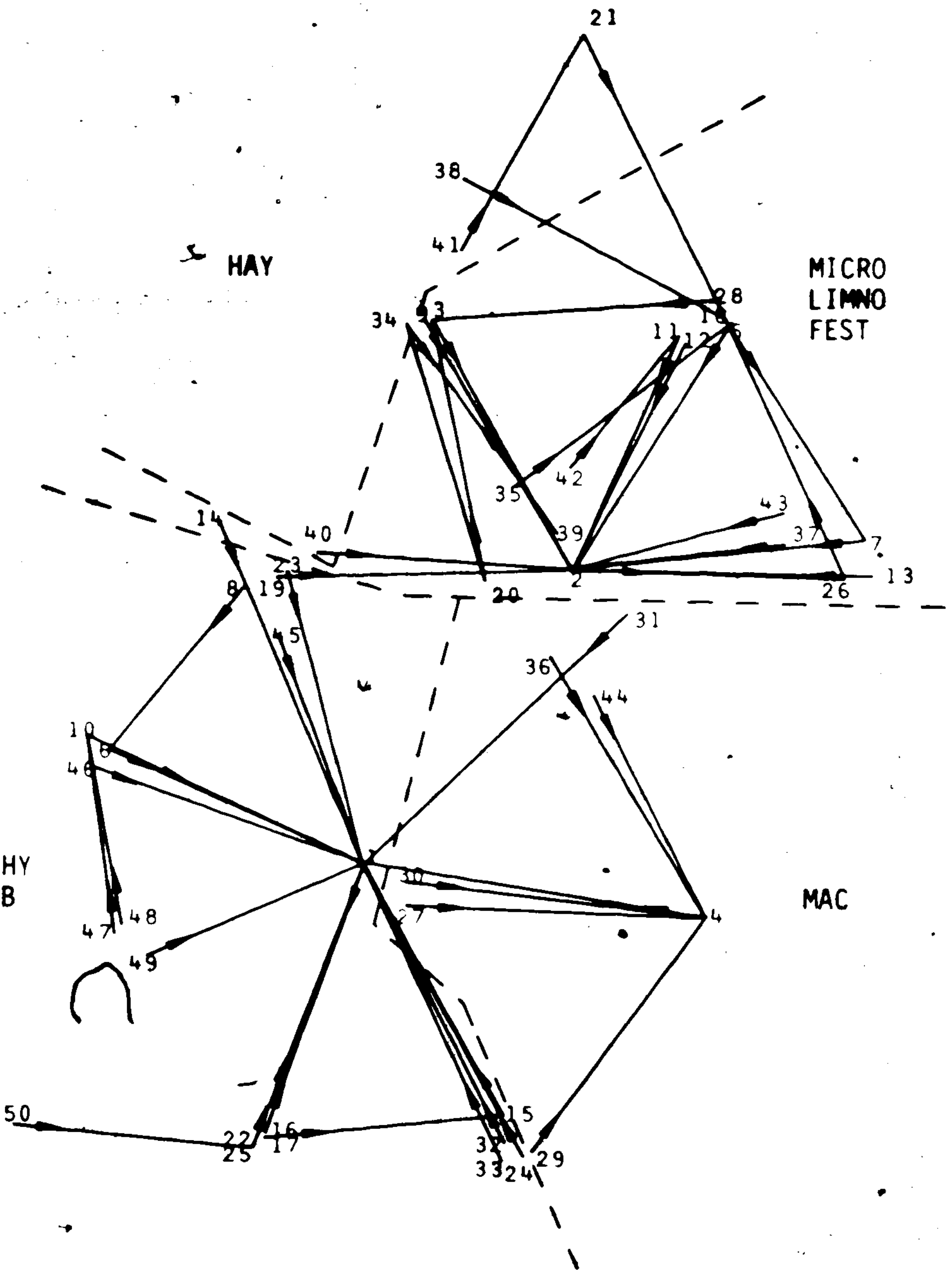


Figure 7. TAXMAP for analysis of OTU's of the *Carex macloviana* aggregate using reproductive characters, redrawn to show only cluster centers and nearest neigbors, indicated by arrows. Dashed lines separate cluster types (i.e. HAY, PACHY and STUB, etc.).

Figure 8. Phenogram produced by CLUSTAN analysis of OTU's using all characters. See Appendix 7 for OTU labels.

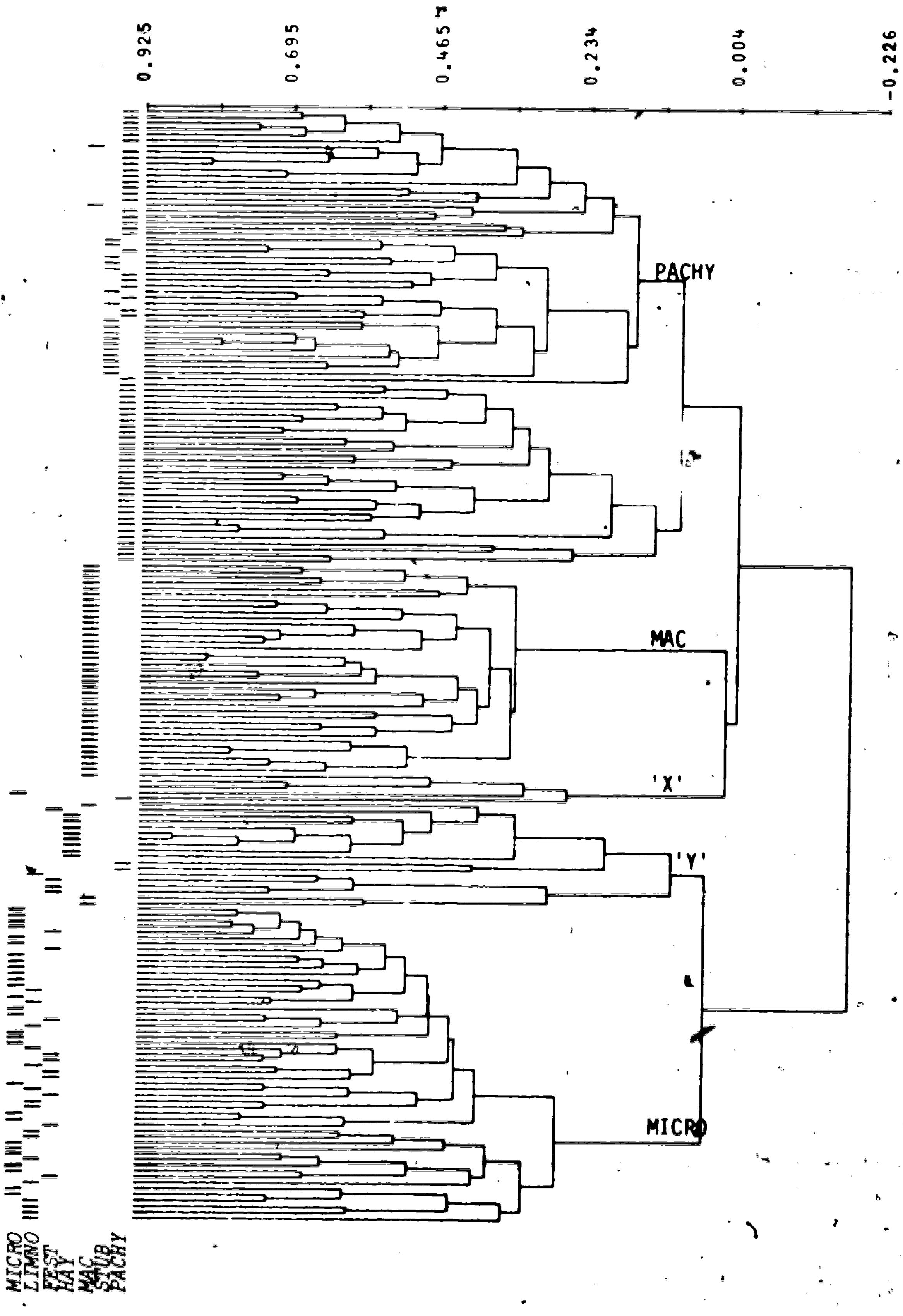
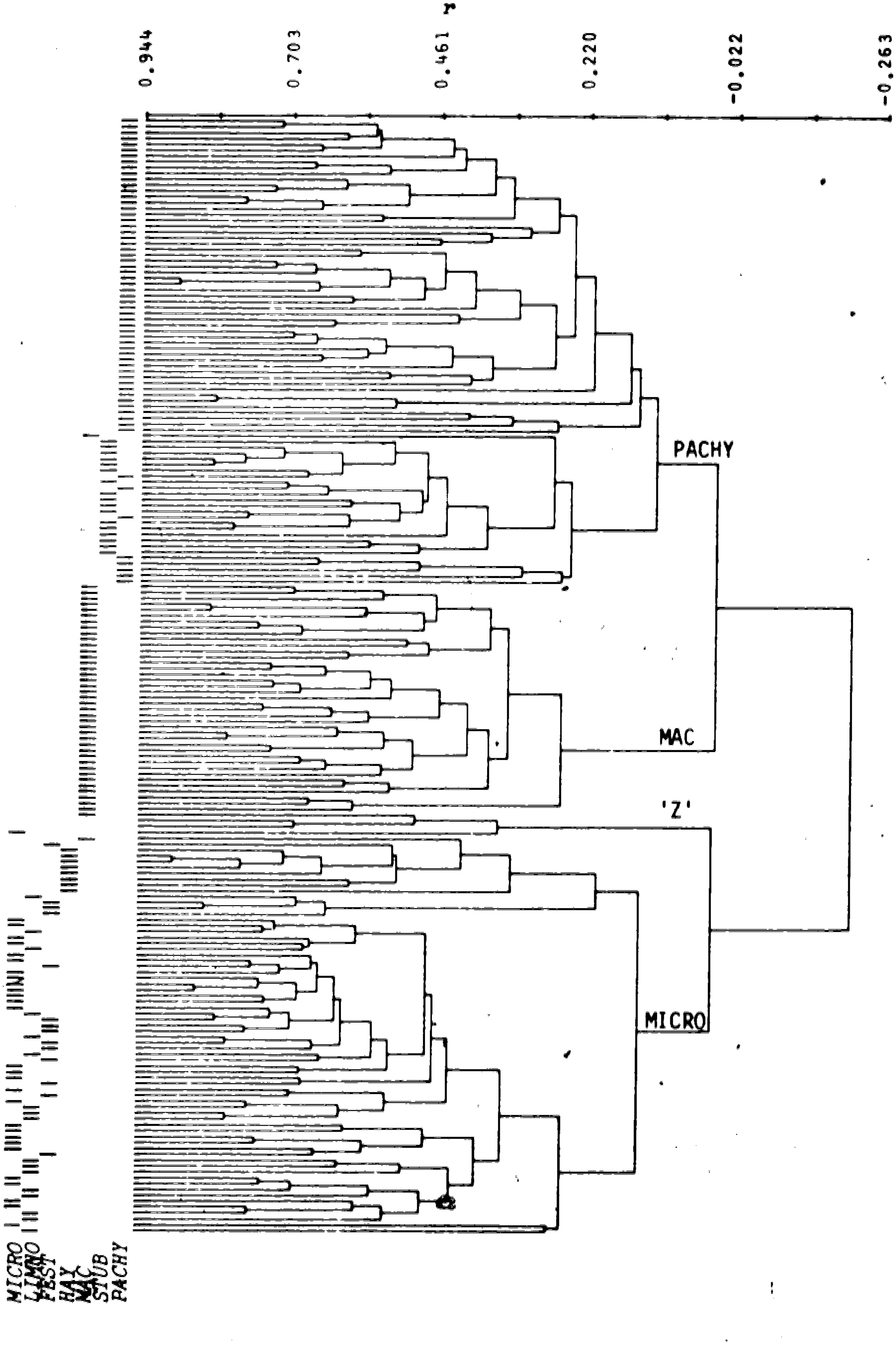

0.925
0.695
0.465
0.234
0.004
-0.226
PACHY
MAC
'X'
'Y'
MICRO
MICRO
LIMNO
FEST
HAY
MAC
SHRUB
PACHY

Figure 9. Phenogram produced by CLUSTAN analysis of OTU's using reproductive characters. See Appendix 7 for OTU labels.


r
0.944
0.703
0.461
0.220
-0.022
-0.263
PACHY
MAC
'Z'
MICRO
MICRO
LIMNO
FEST
HAY
MAC
STUB
PACHY

OTU. The MAC cluster consisted entirely of OTU's of *C. macloviana.* The MICRO cluster was comprised of OTU's of *C. microptera, C. festivella, C. limnophila, C. haydeniana* and the type of *C. platylepis,* all freely intermingled, although the OTU's of *C. haydeniana* remained clustered as a small unit. The mixed cluster 'Z' was comprised of the type of *C. soperi*, the type of *C. microptera* var. *crassinerva* and the two HAYMIC OTU's.

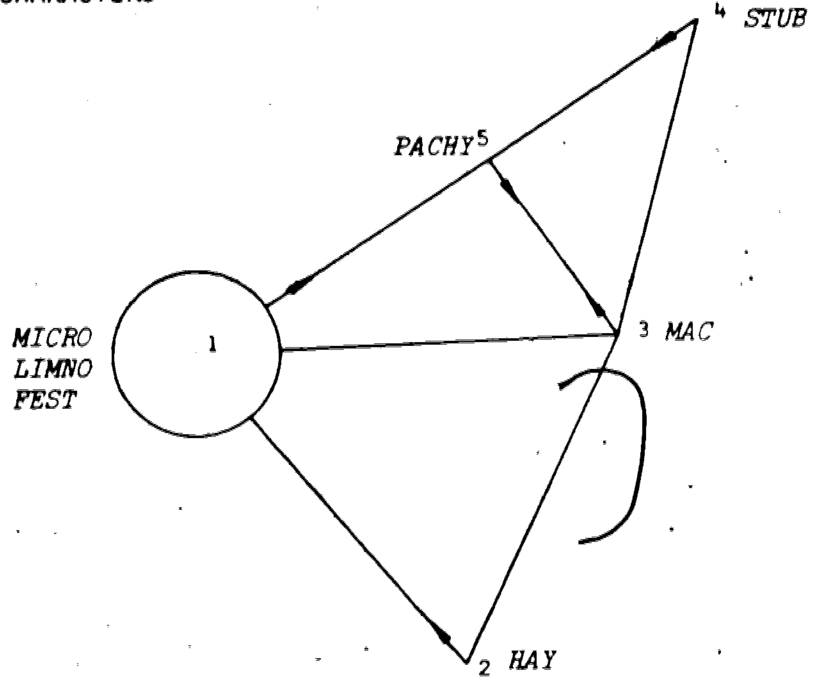
Alteration in technique in a numerical study can lead to different clustering results (see Gower, 1967; Cormack, 1971; and Rohlf, 1970 for a review of techniques, and Ehrlich and Ehrlich, 1967; Sokal and Michner, 1967; Moss, 1968; Schnell, 1970; Baum, 1978; Small, 1978; and McNeill, 1979 for specific examples). This can occur when different character sets, different similarity coefficients and different clustering algorithms are used. To understand if the OTU's which occured in disparate clusters or in single member clusters were due to a function of technique or were truly intermediate or misidentified specimens, this set of OTU's was compared among all four analyses. The OTU's of this set which were shared among three or four analyses were considered significant since their postions were probably not due to technique. It was found that five OTU's (HAYMIC01, HAYMIC02, TYPE04, TYPE05, TYPE09) were placed in disparate clusters in three or four of the analyses. It was not expected that the HAYMIC OTU's would cluster well with other OTU's since cluster membership is based on overall phenetic similarity, and the HAYMIC OTU's were recognized as being morphologically different. Also, it was not expected that the numerical analyses would indicate which clusters the HAYMIC OTU's were intermediate to since previous studies have found the hybrids do not usually lie on a line in phenetic hyperspace that joins two parents (see references in Sneath and Sokal, 1973: 372). Thus, the wandering of the two OTU's throughout the analyses indicated the phenetic distinctiveness of them. Although a detailed study of the population from which the HAYMIC OTU's came from would be interesting, it was not the intent of this investigation to study population systematics, and so the HAYMIC OTU's were disregarded for the remainder of the study. The type for *C. platylepis* (TYPE05) was also not expected to cluster well with other OTU's since it represents a member of a different species. Even though it was included because it shared some features with *C. macloviana*, it was in the MICRO cluster or linked to it at lower coefficient levels in CLUSTAN. The position of the type for *C. festivella* (TYPE09) and the type for *C. microptera* var. *crassinerva* (TYPE04) will be discussed in the next chapter.

b) Taxa Analysis: The results of the cluster analyses on the taxa are presented in Figure 10 and Figure 11. As in the previous analyses, clusters for the phenograms were chosen at a coefficient level which reflected the clustering implied by TAXMAP. The 0.5 coefficient level in the CLUSTAN analyses was found to best approximate the results of TAXMAP.

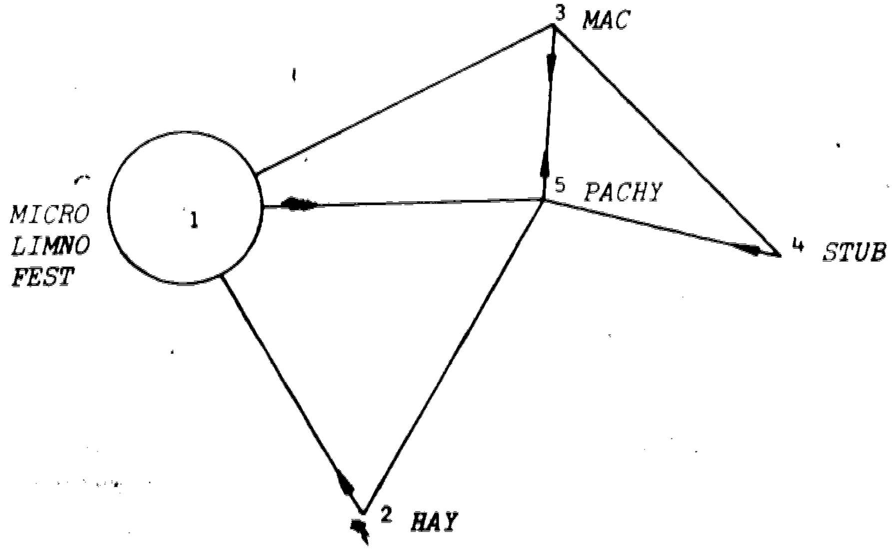
All four analyses showed a cluster of the taxa *Carex microptera*, *C. festivella* and *C. limnophila*, reflecting the clustering of OTU's in the previous analyses, and four single member clusters for the remaining taxa. At lower resolution levels, however, differences did become apparent. *Carex pachystachya* and *C. macloviana* were each other's nearest neighbor in TAXMAP while *C. pachystachya* and 'stubby' were each other's nearest neighbor in CLUSTAN. In TAXMAP, the nearest neighbor to *C. haydeniana* was the cluster which contained *C. microptera*,

Figure 10. TAXMAPs for analyses of taxa of the *Carex macloviana* aggregate.

ALL CHARACTERS



REPRODUCTIVE CHARACTERS



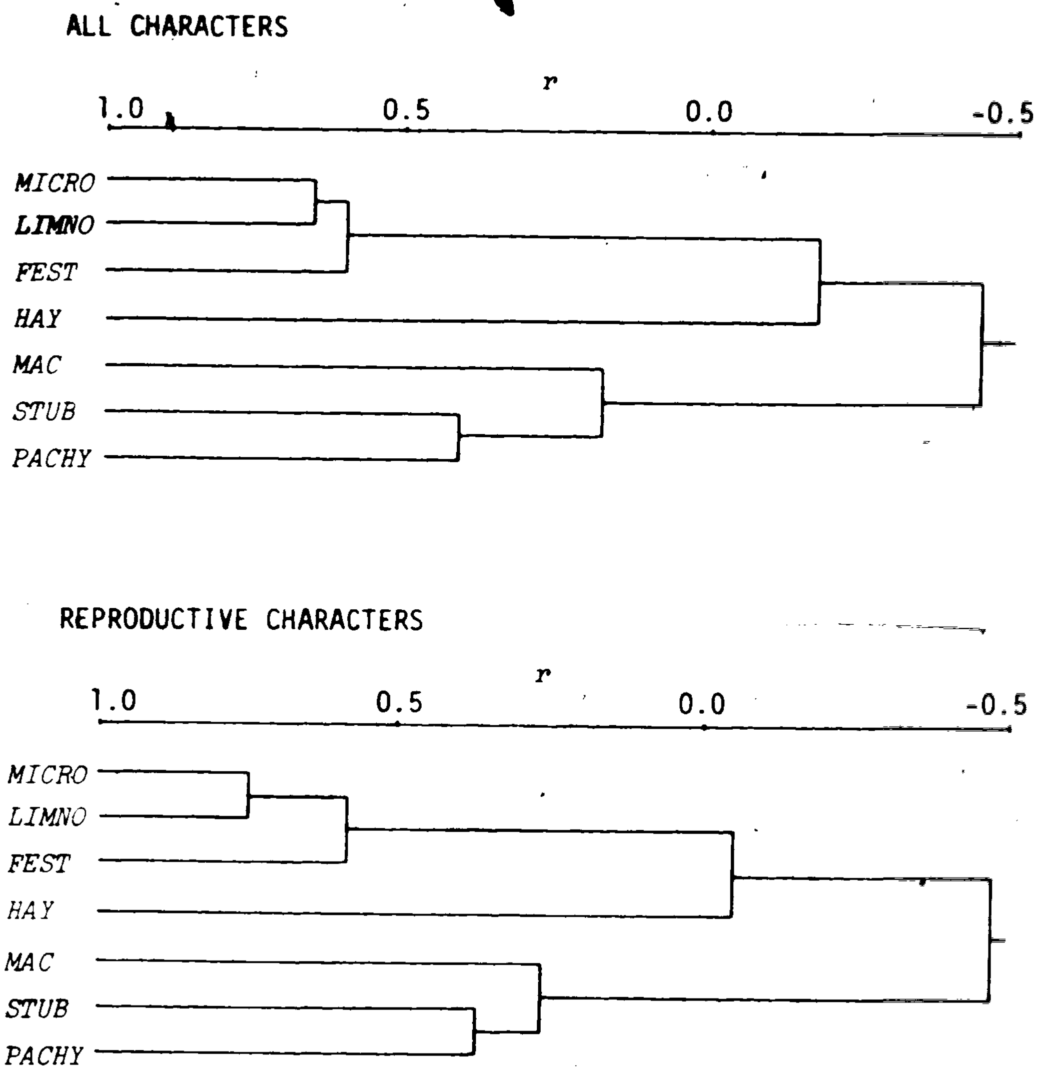


Figure 11. Phenograms produced in the CLUSTAN analyses of taxa of the *Carex macloviana* aggregate using average linkage clustering.

C. festivella and *C. limnophila*, but this cluster would first join with *C. pachystachya* (based on nearest neighbor distances in Table 10), while in CLUSTAN, *C. haydeniana* would first join with the three taxa cluster. These differences may be attributable to the use of different similarity coefficients, or to the distortion of large phenetic relationships which cluster analyses are noted for. Therefore, the principal component analyses, presented in Figure 12 was a more faithful representation of the larger phenetic relationships. Three groups of taxa were evident, a tight group which contained the taxa *C. microptera, C. festivella* and *C. limnophila*, a loose group comprised of *C. pachystachya, C. macloviana* and 'stubby', and an isolated *C. haydeniana.* The implications of these phenetic relationships will be discussed in the next chapter.

Further Analysis of 'Stubby': When the specimens of 'stubby' were first noted, they were thought to represent intermediates between *Carex pachystachya* and *C. macloviana.* This idea was formed on the basis of morphological intermediacy and on labels which showed that the specimens had been identified as either *C. macloviana* or *C. pachystachya.* Published reports of intermediates between the two taxa had not been previously noted. However, Cronquist (1969, 1977) reported that where the geographic ranges of *C. pachystachya* and *C. microptera* overlap, the distinction between the two was not always clear. Therefore, to test if 'stubby' represented an intermediate taxon between *C. pachystachya* and *C. macloviana*, or if it represented the implied intermediates between *C. pachystachya* and *C. microptera*, two further analyses were conducted.

One test for intermediacy is provided by the Andersonian hybrid index. Although this was first developed to check for hybrid individuals

Table 10. Nearest neighbor distances for clusters in TAXMAP analyses of taxa of the *Carex macloviana* aggregate.

ALL CHARACTERS			REPRODUCTIVE CHARACTERS		
CLUSTER	NEAREST NEIGHBOR	DISTANCE X1000	CLUSTER	NEAREST NEIGHBOR	DISTANCE X1000
1 (MICRO)	5	358	1 (MICRO)	5	375
2 (HAY)	1	439	2 (HAY)	1	382
3 (MAC)	5	294	3 (MAC)	5	242
4 (STUB)	5	340	4 (STUB)	5	337
5 (PACHY)	3	294	5 (PACHY)	3	242

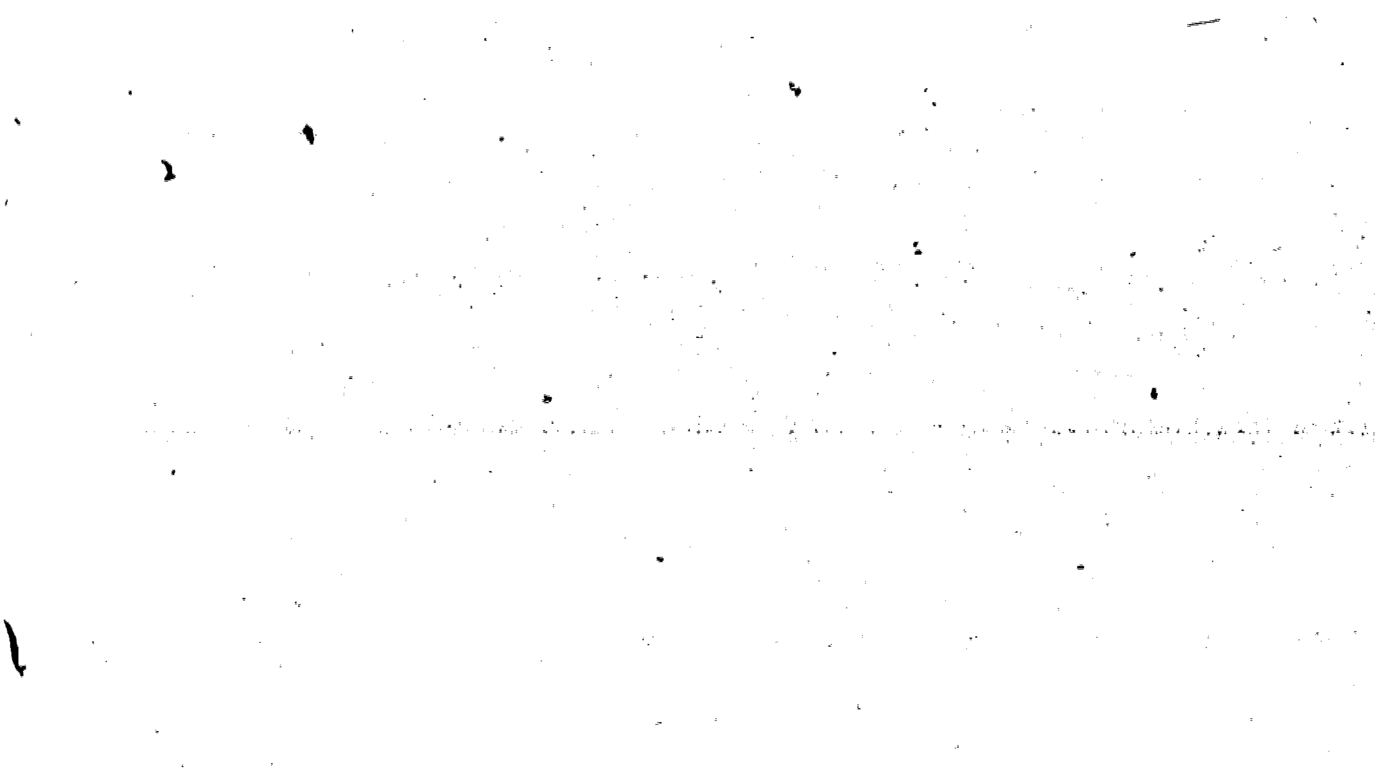
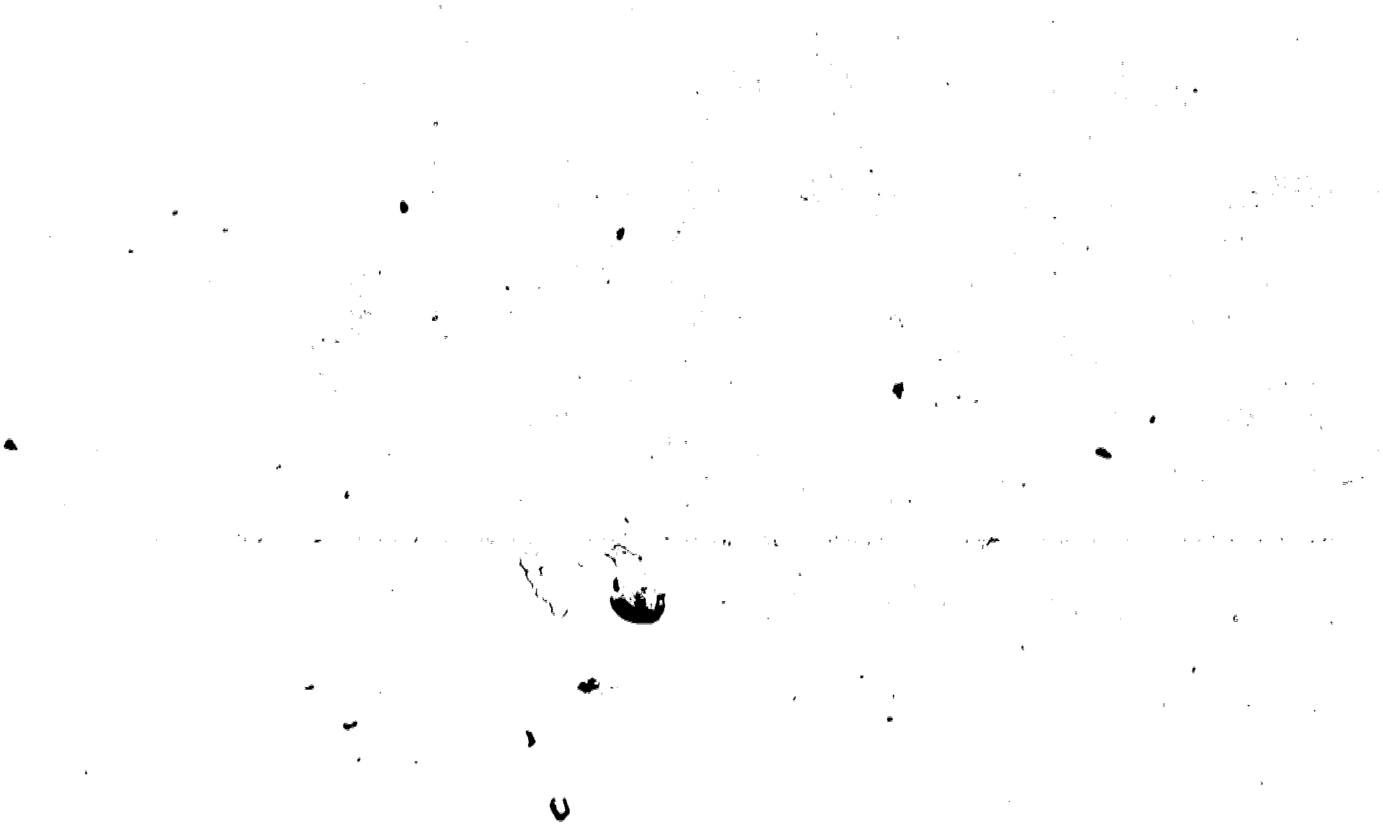
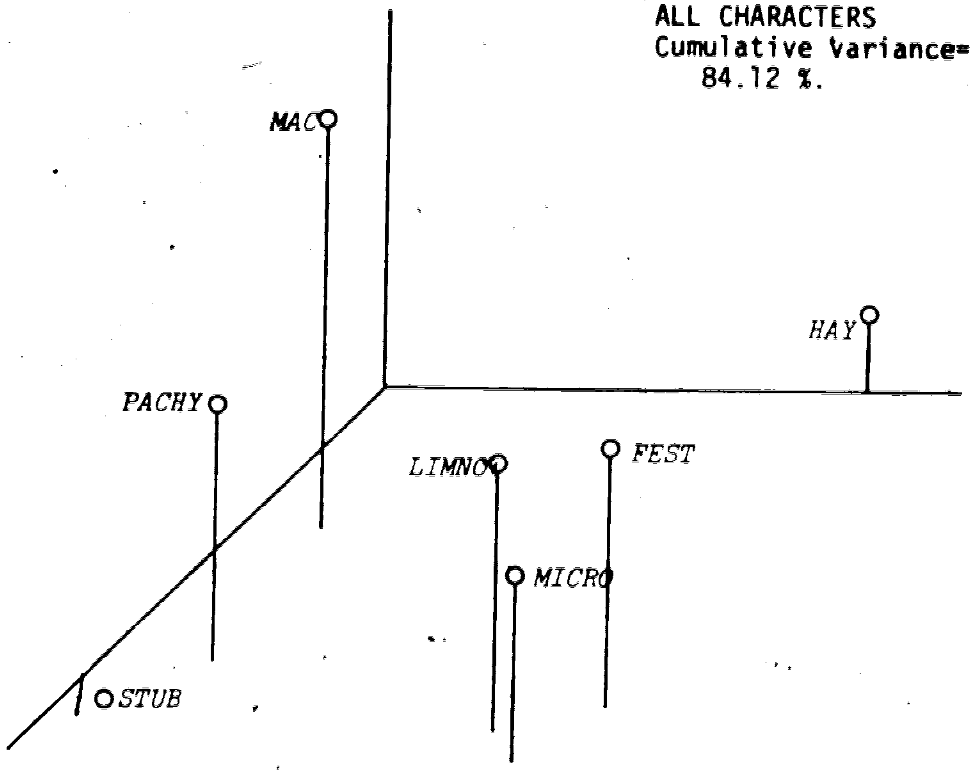
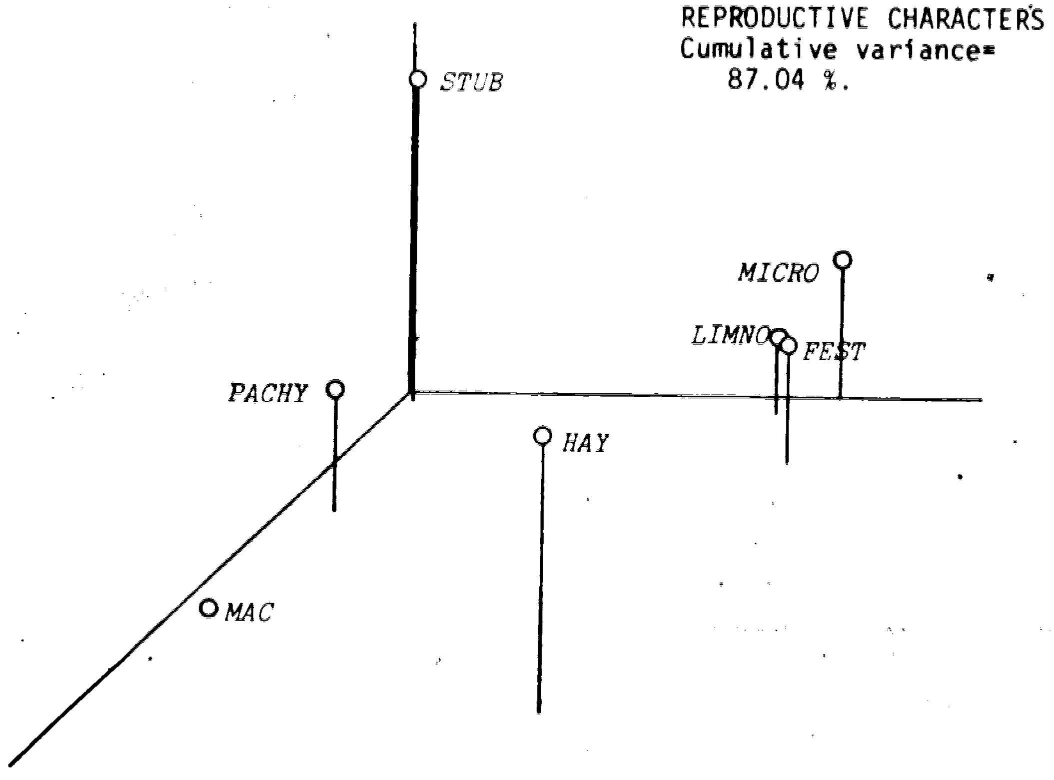


Figure 12. Ordinations produced by CLUSTAN principal components analyses of taxa of the *Carex macloviana* aggregate.





ALL CHARACTERS
Cumulative Variance=
84.12 %.



REPRODUCTIVE CHARACTERS
Cumulative variance=
87.04 %.

within a population, Radford *et al.*, (1974) have shown that it can be used for determining morphologically intermediate taxa. A search for those characters used in the statistical analyses in which the mean value for 'stubby' lay between the mean values of *C. pachystachya* and *C. macloviana*, or *C. pachystachya* and *C. microptera* was conducted. For these characters, the value for *C. pachystachya* was given an index value of 0 and the value for *C. macloviana* or *C. microptera* was given an index value of 1, and the index value for 'stubby' was calculated by interpolation. Table 11 presents the results. It was shown that the mean value of 'stubby' was intermediate between the mean values of *C. pachystachya* and *C. macloviana* in six characters, with the index value of 'stubby' being 2.68. Between *C. pachystachya* and *C. microptera*, 16 characters were shared in which the mean value for 'stubby' was between the means of the two taxa. In this instance, an index value of 7.12 was calculated for 'stubby'. The results are not conclusive, however, since 'stubby' has an intermediate index value in both comparisons. The number of characters for which the index value was calculated is greater for the comparison between *C. pachystachya* and *C. microptera* and may lead to the conclusion that 'stubby' is a hybrid between these two taxa. However, if additional characters which suggest intermediacy (by adjusting the mean values of the characters within the standard error of the mean) are included, then the total number of characters in both comparisons are nearly equal with a total of 21 between *C. pachystachya* and *C. macloviana* and a total of 25 between *C. pachystachya* and *C. microptera*.

If a taxon represents a hybrid between two other taxa, it would be expected that the hybrid would occur most frequently where the geographic ranges of the two putative parent taxa overlapped. The distribution of

Table 11. Morphological index values for 'stubby' and characters for which 'stubby' is intermediate in comparison to *Carex pachystachya* and *C. macloviana*, and to *C. pachystachya* and *C. microptera*.

TAXON	INDEX	CHARACTERS	ADDITIONAL CHARACTERS WHICH SUGGEST INTERMEDIACY	TOTAL
C. pachystachya	0.00	1, 2, 7,	4, 5, 6, 13, 18, 19, 25,	
C. macloviana	6.00	16, 36, 42	27, 29, 31, 33, 39, 40,	21
'stubby'	2.68		43, 46	
C. pachystachya	0.00	8, 12, 20,	4, 5, 6, 7, 16, 17, 18,	
C. microptera	16.00	21, 22, 24,	19, 33	25
'stubby'	7.12	27, 29, 37,		
		38, 39, 40,		
		41, 42, 43,		
		46		

'stubby' was plotted for western Canada and Alaska, along with the geographic ranges of *C. pachystachya*, *C. macloviana* and *C. microptera*. Figure 13 and Figure 14 present the results. In Figure 13, 'stubby' is shown to be located where the ranges of *C. pachystachya* and *C. macloviana* overlap, but is also frequently located outside of the region of sympatry, especially along the coastal regions of British Columbia. Figure 14 shows that 'stubby' again occurs in the region of sympatry between *C. pachystachya* and *C. microptera*, but also outside of this region, especially along coastal British Columbia and Alaska. One observation provided by these maps was that the geographic distribution of 'stubby' is sympatric, for the most part, with the distribution of *C. pachystachya* in western Canada and Alaska.

Cultivation

Plants growing on the greenhouse roof provided an indirect source of evidence of flowering phenology. Whenever inflorescences were collected for cytological study, the date of the collection was noted. These data were plotted and the results, which indicated initiation of pollen meiosis, roughly indicated intiation of flowering in the taxa. The results are shown in Figure 15.

Of the five taxa under cultivation, *Carex macloviana* initiated mother cell (PMC) meiosis the earliest, on April 18. On April 28, a peak period was reached where all the taxa were undergoing PMC meiosis, and this lasted until June 2. Throughout most of June, no flower initiation was observed until June 25. At this point, a second period of flowering began and continued until July 10. After this, all the plants went through a period of maturation, and no further flower initiation was observed for the remainder of the summer. Except for the slightly

Figure 13. Range of *Carex pachystachya* and *C. macloviana*, and distribution of 'stubby' in western Canada and Alaska.

C. pachystachya ▧

C. macloviana ▨

'stubby' ●

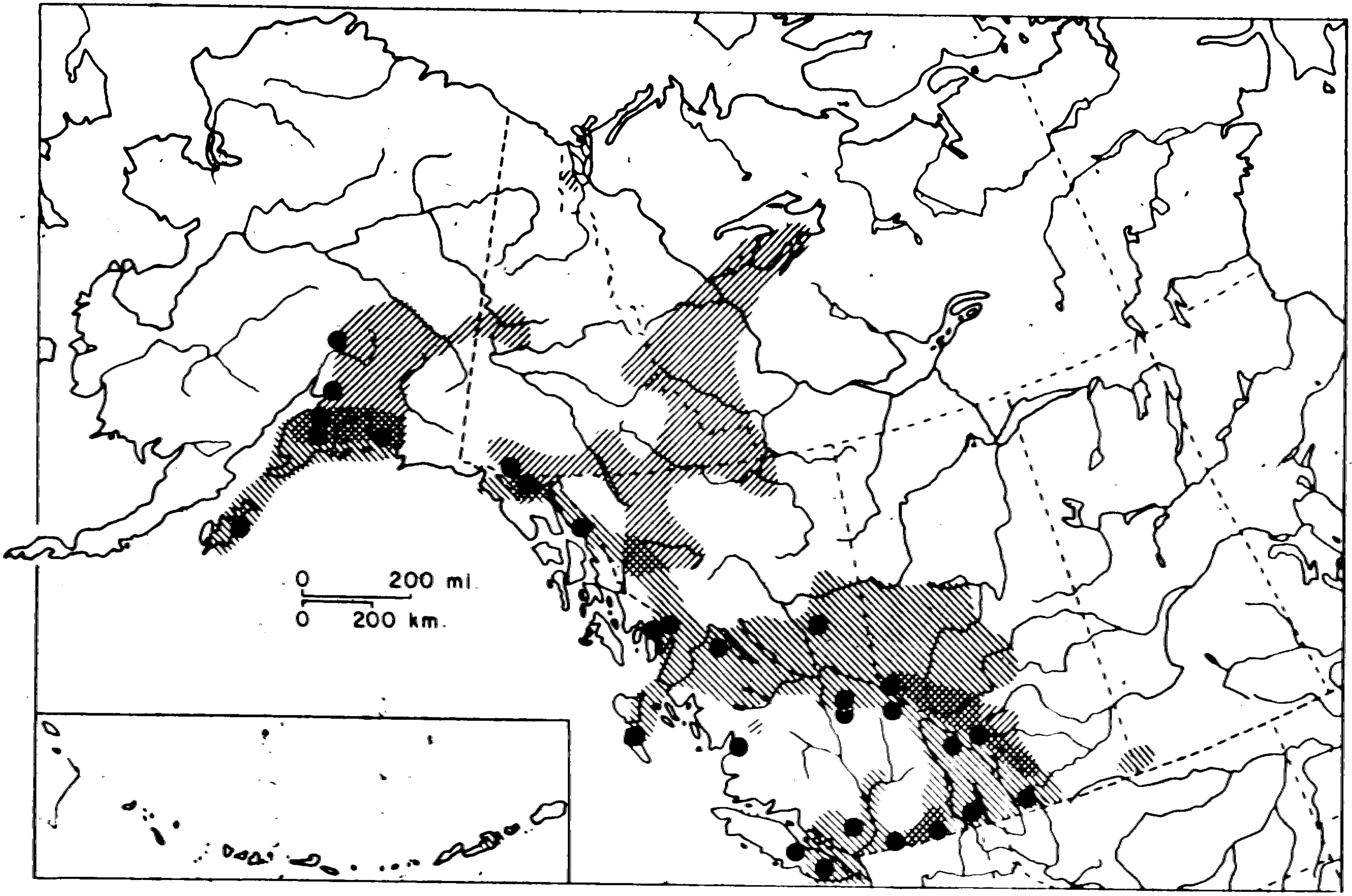

0 200 mi.
0 200 km.

Figure 14. Range of *Carex pachystachya* and *C. microptera*, and distribution of 'stubby' for western Canada and Alaska.

C. pachystachya ▧

C. microptera ▨

'stubby' ●

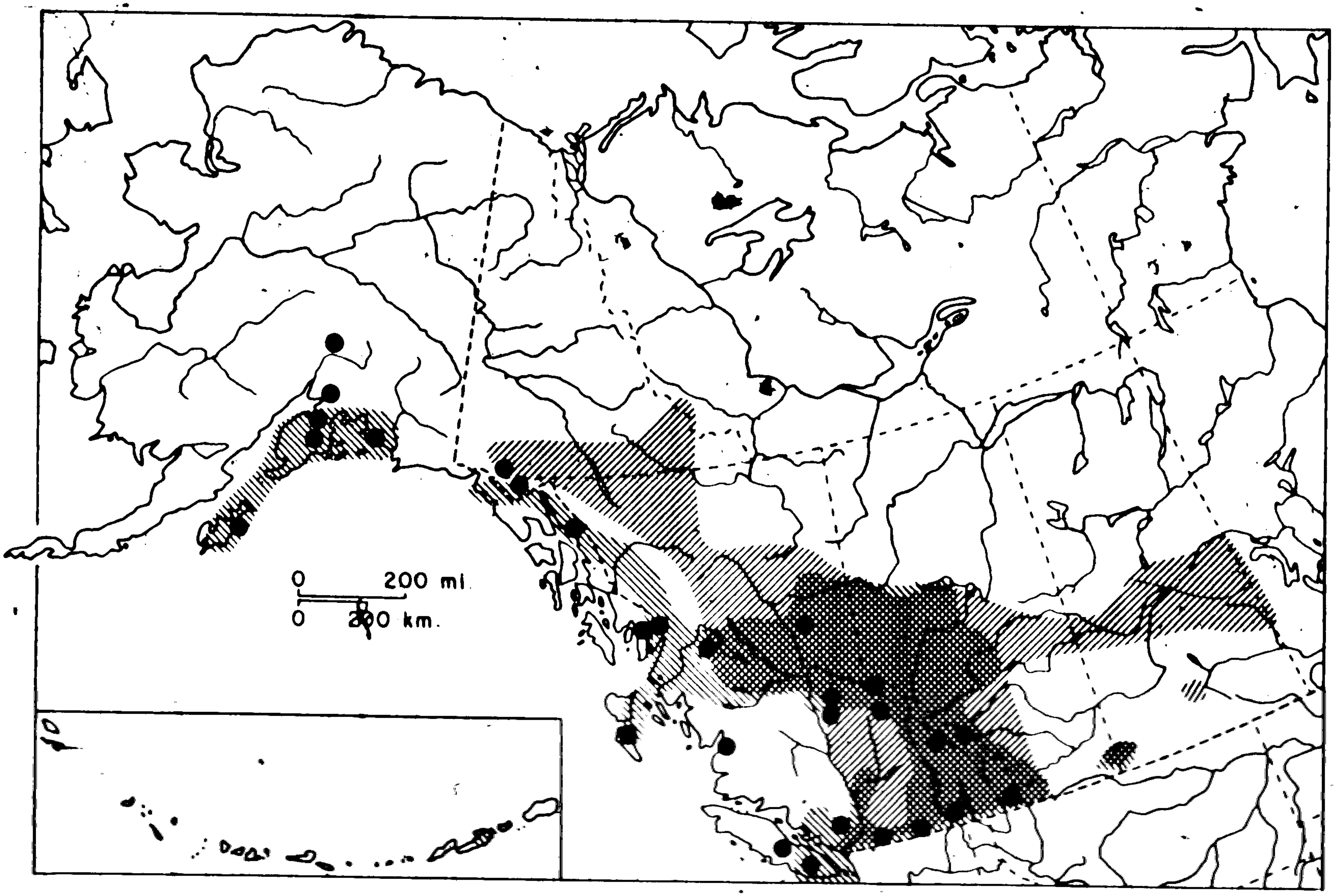
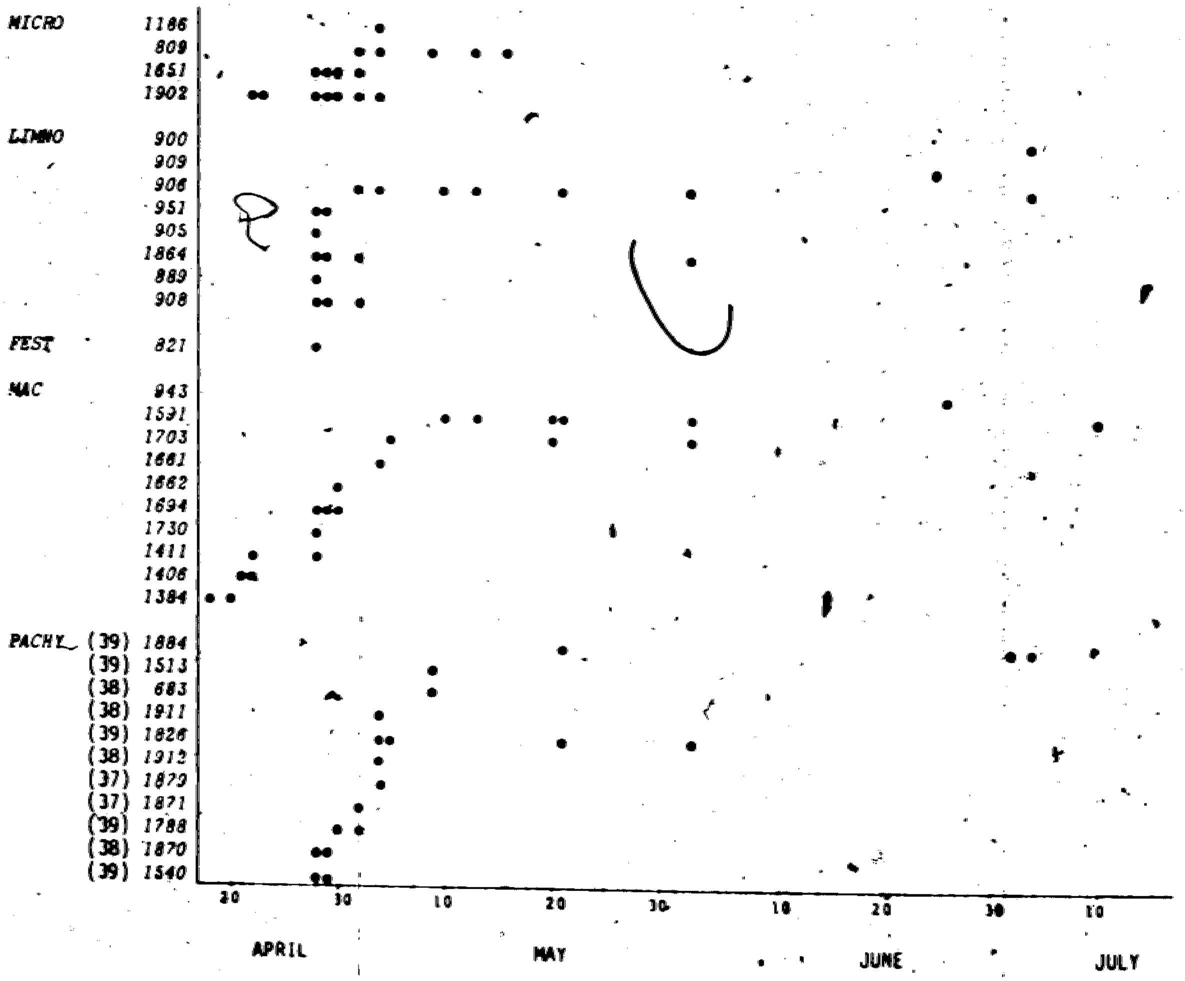

0 200 mi
0 200 km

Figure 15. PMC meiosis phenology observed in specimens of the *Carex macloviana* aggregate for the year 1979. All specimens were collected by the author and kept in cultivation. Numbers in parentheses refer to the cytological races of *C. pachystachya* with each number the haploid number determined for that specimen.


MICRO
1186
809
1651
1902
LIMNO
900
909
906
951
905
1864
889
908
FEST
821
MAC
943
1531
1703
1661
1662
1694
1730
1411
1406
1384
PACHY
(39) 1884
(39) 1513
(38) 683
(38) 1911
(39) 1826
(38) 1913
(37) 1879
(37) 1871
(39) 1788
(38) 1870
(39) 1540
20
30
10
20
30
10
20
30
10
APRIL
MAY
JUNE
JULY

earlier start of *C. macloviana*, it was evident that no significant differences existed for initiation of flowering among the taxa.

Chromosome Numbers

Meiotic chromosome counts were determined for all the taxa, and the results are presented in Table 12. From the data it is evident that an aneuploid series (*sensu lato*) is present in the aggregate. *Carex pachystachya* was found to contain three chromosome races, with n=37, 38, and 39. Mapping of these cytological races and comparison of them with the morphological subunits in *C. pachystachya* did not reveal any strong correlation with distribution or morphology (Figure 16 and Table 13), except two plants which contained the number n=37 were from the Vanderhoof, British Columbia area, and were found in those morphological subunits in which red scales or perigynia beaks were prominent. Examination of Figure 15 shows there is no difference in flowering times for the cytological races. The taxa *C. microptera*, *C. festivella*, and *C. limnophila* all had numbers of n=40. *Carex haydeniana* and 'stubby' had counts of n=41, and *C. macloviana* had the highest number with n=43.

Small size of the chromosomes (1.5 micrometers or less) made karyotypic analysis difficult. However, using the descriptions of chromosome morphology for the genus provided by Wahl (1940) and Faulkner (1972), it was determined that all the taxa exhibited normal pairing, with no univalents present. Figure 17 through Figure 19 shows camera lucida drawings of Metaphase I for all the taxa and chromosome races of the *C. macloviana* aggregate.

Table 12. Meiotic chromosome counts determined for members of the *Carex macloviana* aggregate.

TAXON	n	LOCALITY AND NUMBER*
C. pachystachya	37	58 km E.of Vanderhoof, B. C. 1879.
	37	Vanderhoof, B. C. 1871.
	38	Vanderhoof, B. C. 1870.
	38	Ten Mile Lake Prov. Park, B. C. 683.
	38	28 km S.E.of Dawson Creek, B. C. 1911 & 1912.
	39	75 km N. of Prince George, B. C. 1884.
	39	Skeena Mts. B. C. 1788.
	39	73 km S. of Meziadin Jt., B. C. 1826.
	39	Moose Pass, Kenai Pen., Alaska 1513.
	39	Milepost 38, Seward-Anchorage Hwy. Alaska 1540.
'stubby'	41	76 km S. of Cantwell on Rt. 3, Alaska 1463.
C. macloviana	43	2.4 km S. of Ram falls, Alta. 943.
	43	140 km S. of Haines Jt., B. C. 1694.
	43	74 km S.E. of Teslin, B. C. 1730.
	43	16 km S. of Dease Lake, B. C. 1760.
	43	91 km S. of Haines Jt., Yukon 1661 & 1662.
	43	1.5 km E. of Haines Jt., Yukon 1703.
	43	23 km N. of Paxson, Alaska 1384.
	43	Milepost 21, Denali Hwy., Alaska 1406.
	43	48 km E. of Cantwell, Alaska 1411.
	43	Dry Creek Campground, 5 km N. of jt. of Rts. 1 and 4, Alaska 1591 & 1592.

Table 12. (Continued)

TAXON	n	LOCALITY AND NUMBER
C. haydeniana	41	Plateau Mt., Alta. 1996.
	41	Highwood Pass, Alta. 2006 & 2007.
C. festivella	40	Cypress Hills, Alta. 821.
C. limnophila	40	6.4 km N. of Coleman, Alta. 889.
	40	Lower Kananaskis Lake, Alta. 908 & 909.
	40	57 km N. of Nordegg, Alta. 951.
	40	93 km N. of Nordegg, Alta. 905 & 906.
	40	64 km N. of Coleman, Alta. 900.
	40	1 km S. of Burns Lake, B. C. 1864.
C. microptera	40	Reesor Lake, Cypress Hills, Alta. 809.
	40	87 km N. of McLeod Lake, B. C. 1902.
	40	Whitehorse, Yukon 1186.
	40	25 km S. of Haines Jt., Yukon 1651.

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*All collections were made by the author.

Figure 16. Distribution of cytological races of *Carex pachystachya* for western Canada and Alaska.

▲ n=37

■ n=38

● n=39

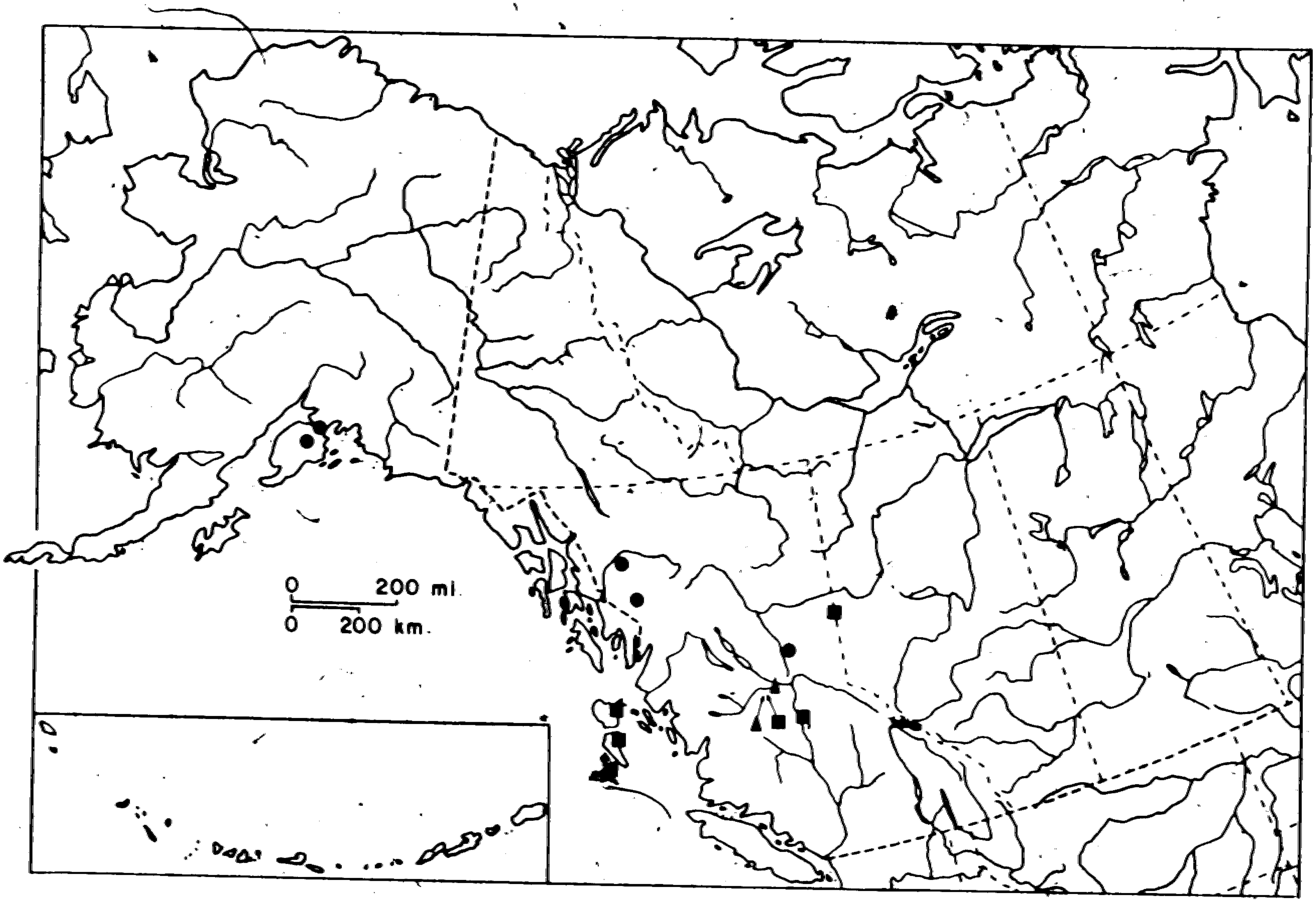

0 200 mi.
0 200 km.

Table 13. Comparison of cytological races of *Carex pachystachya* with morphological subunits recognized for the taxon.

MORPHOLOGICAL SUBUNIT	n	SPECIMEN
Typical	39	*Whitkus 1513*
	39	*Whitkus 1788*
	39	*Whitkus 1826*
	38	*Whitkus 1911*
Small perigynia and heads	39	*Whitkus 1540*
Small heads	38	*Whitkus 683*
	38	*Whitkus 1870*
	38	*Clader and Taylor 35943*
Greenish upper perigynia body	38	*Whitkus 1912*
	38	*Calder and Taylor 35261*
Long beaks	39	*Whitkus 1884*
	38	*Calder, Savile and Taylor 22441*
	38	*Clader, Savile and Taylor 23499*
Reddish beaks	37	*Whitkus 1879*
Slender heads, red scales	37	*Whitkus 1871*

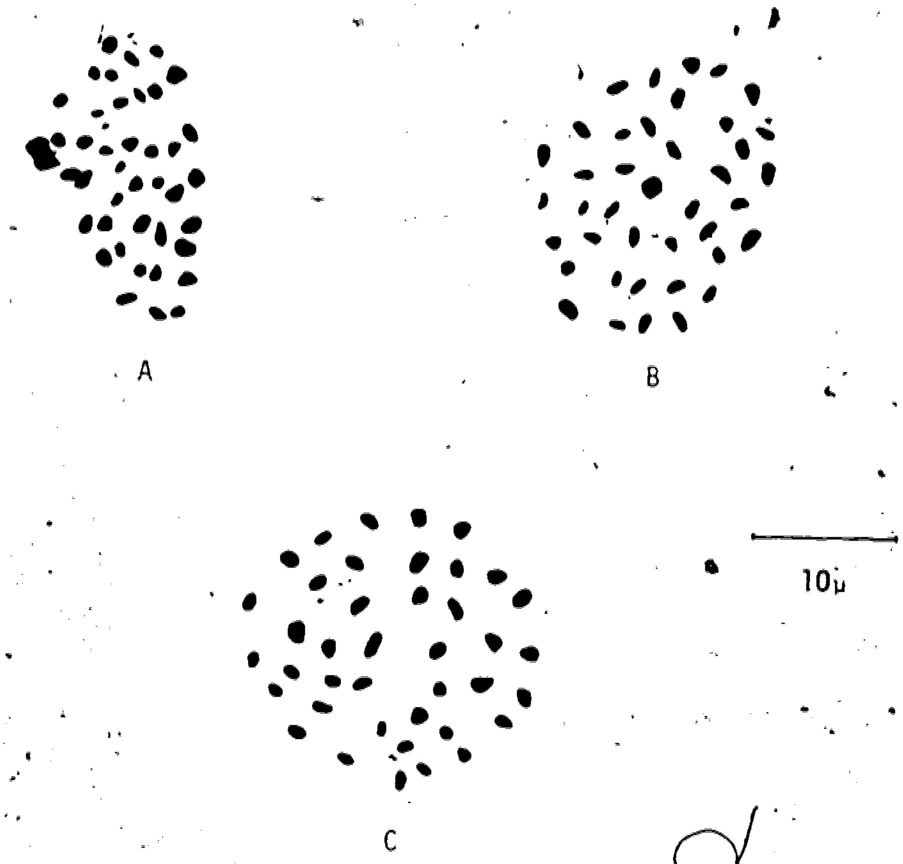


Figure 17. Camera lucida drawings of Metaphase I in pollen spore mother cells of *Carex microptera* (A, n=40), *C. festivella* (B, n=40), and *C. limnophila* (C, n=40).

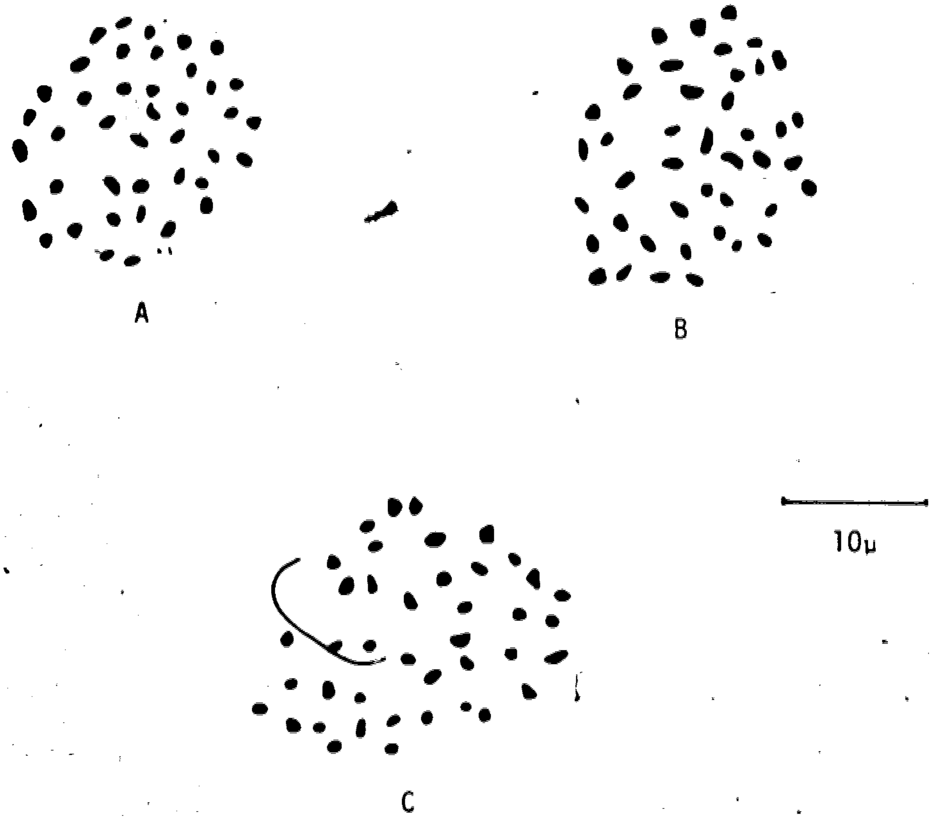


Figure 18. Camera lucida drawings of Metaphase I in pollen spore mother cells of *Carex haydeniana* (A, n=41), *C. macloviana* (B, n=43), and 'stubby' (C, n=41).

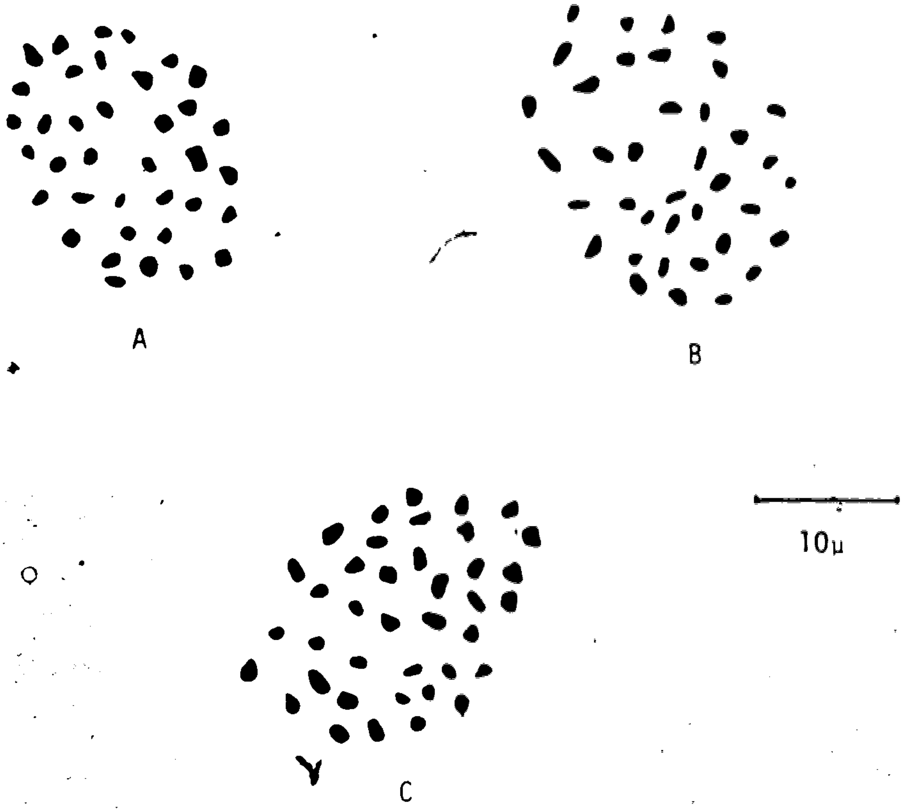


Figure 19. Camera lucida drawings of Metaphase I in pollen spore mother cells of *Carex pachystachya*. A (n=37), B (n=38), C (n=39).

DISCUSSION AND CONCLUSIONS

The results of this investigation indicated that the six taxa which were analyzed, comprise four species: *C. macloviana*, *C. pachystachya* (including 'stubby'), *C. microptera* (including *C. festivella*, and *C. limnophila*), and *C. haydeniana*. The interpretation of the evidence which led to this conclusion is presented in the section on taxonomy, followed by the proposed taxonomic treatment for the aggregate.

Taxonomy

On a phenetic basis, *Carex macloviana* and *C. pachystachya* are very similar to one another. In the numerical analyses of OTU's, this was expressed by *C. macloviana* forming subgroups within the *C. pachystachya* cluster group in TAXMAP, and by the *C. macloviana* cluster joining the *C. pachystachya* cluster at lower coefficient levels in CLUSTAN. In the taxa analyses, the two taxa were each others nearest neighbor in TAXMAP, while *C. macloviana* joined *C. pachystachya* and 'stubby' at lower coefficient levels in CLUSTAN. In addition, both taxa share lustrous scales and perigynia which are generally coppery colored. This phenetic similarity led Hultén (1942) to conclude that *C. pachystachya* is a high-grown race of *C. macloviana*. Based on this conclusion, Hultén included *C. pachystachya* and *C. macloviana* in a single species. However, the distinctiveness of the two taxa has been demonstrated. The integrity of the taxa was maintained in the clustering of OTU's, and they remained distinct in the cluster analyses of taxa and in the ordinations. Cytologically, *C. pachystachya* is variable in chromosome number, but the highest number recorded for *C. pachystachya* (excluding 'stubby') was n=39, and differs significantly from the uniform numbers observed for *C. macloviana* of n=43. Figure 13 shows that *C. pachystachya* is confined to coastal areas in Alaska and northern British Columbia, and extends inland in moist regions of central and southern British Columbia and Alberta, while *C. macloviana* is mainly an inland boreal element in the north and is confined to subalpine or alpine habitats in the Rocky Mountains. It may still be argued that these differences are not enough to overcome the similarities, and that Hultén's concept of these two taxa is still valid. If we take a modern interpretation of a subspecies as:

> ...a considerable segment of a species with a distinct area and more or less distinct morphology, often showing some intergradation... Also extended to cover regional ecotypes, and cases where taxa differ in chromosome number or are partly or incompletely intersterile and exhibit some correlated geographical or ecological differentiation but have an insufficient degree of morphological differentiation to permit satisfactory treatment as separate species. (Davis and Heywood, 1963: 99-100),

then Hultén's concept is valid, but only if we accept his interpretation of the distribution of the taxa. Hultén(1942, 1958: Map 185) envisioned the subspecies *pachystachya* occupying all of western North America, and the typical *C. macloviana* occupying its generally accepted bipolar range minus western North America. Viewed this way, there is a distinct geographic separation of the subspecies, with individuals in the subspecies *pachystachya* exhibiting some morphological intergradation with the subspecies *macloviana*. However, specimens from western Canada and Alaska which not only were shown to be phenetically distinct from *C. pachystachya* but were virtually identical with specimens of *C. macloviana* observed from Scandinavia, Greenland, eastern arctic Canada, South America and the Falkland Islands, indicated the presence of typical *C. macloviana* in western North America, which agrees with the reports of Mackenzie (1931-35), Hermann (1970), and Porsild (1939, 1951). Therefore, Hultén's interpretation must be rejected as an artifical delimitation of the subspecies *pachystachya*. In a more restricted sense, *C. pachystachya* should not be recognized as a subspecies since there are no demonstratable intermediates between the two taxa in areas of sympatry (including 'stubby'), which indicates intersterility, and there does exist sufficient morphological differences indicating separate species (primarily with white hyaline margins of the scales and beak tips, characters #20 and 36, and secondarily with characters #16, 22, and 41). If anything, these distinctions place the two taxa into an aggregate species:

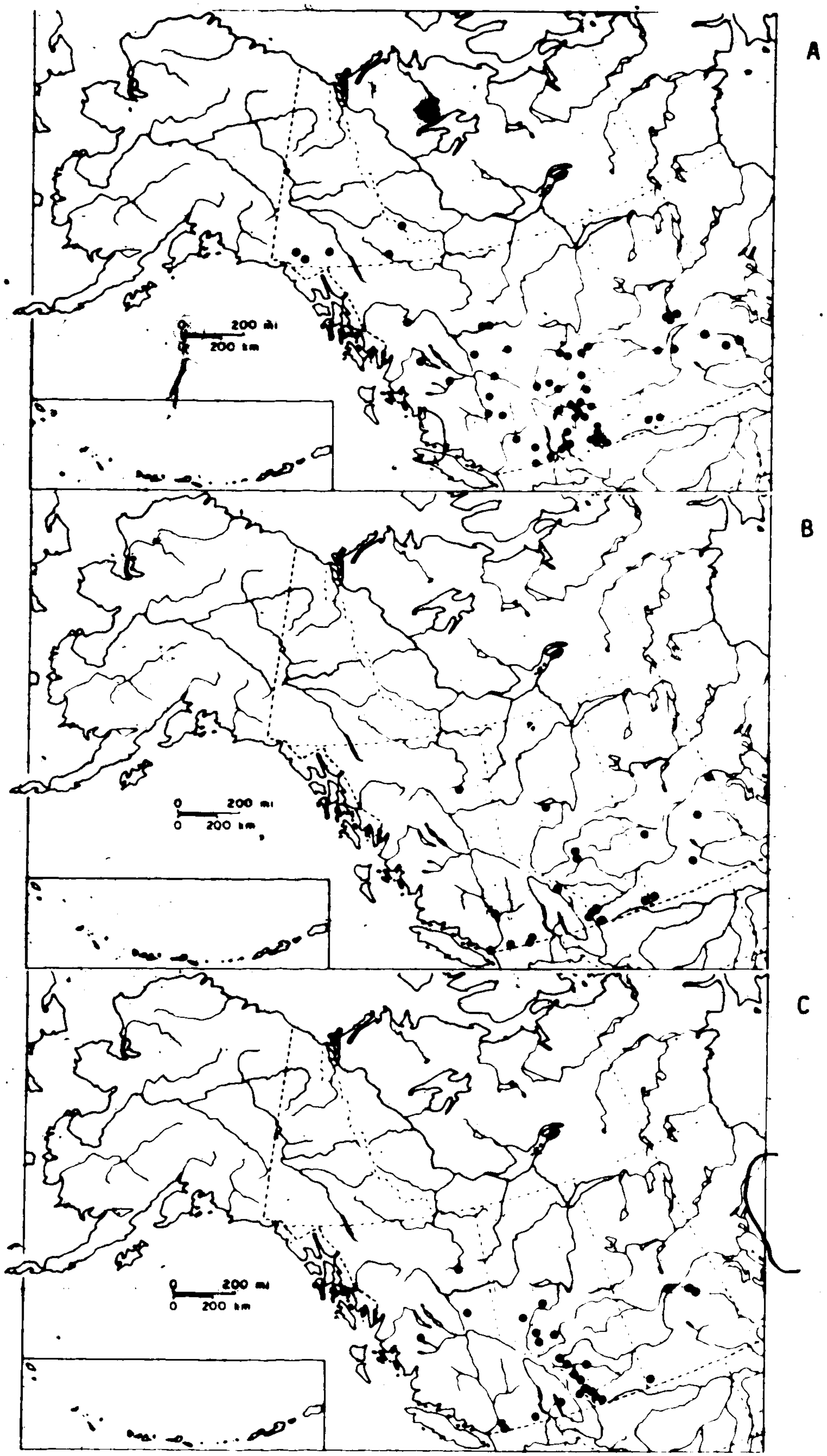
> The aggregate is a device employed to group together, for convenience, a number of species. The component species (binomials) are in taxonomic terms morphologically closely related and difficult to discriminate. The characters distinguishing them, although less pronounced and perhaps fewer in number than those that serve to distinguish between other species within the same genus, are constant and the species appear to be effectively isolated from one another. (Davis and Heywood, 1963: 101).

Thus, the two taxa, though morphologically similar to one another, show indication of isolation by virtue of their distinct chromosome numbers and absence of intermediates. Therefore, the two are maintained as species.

The taxa *C. microptera*, *C. festivella* and *C. limnophila* comprise one species. This was evident in the statistical analysis where the taxa either share the same range of variation, or form a continuum of variation, for all 47 characters. In the cluster analyses of OTU's the three taxa consistently formed mixed clusters, while in the cluster analyses of taxa, they formed a a single cluster, and in the ordinations, the three were in closest proximity to one another. In addition, the taxa share the same chromosome number and the same distribution in western Canada (Figure 20).

A number of recent authors (Cronquist, 1969, 1977; Scoggan, 1978; Boivin, 1979) have proposed that *C. festivella* is conspecific with *C. microptera*. Cronquist (1977: 165) has stated : "the characters by which *C. festivella* is purportedly to be distinguished from *C. microptera* are not well correlated among themselves and do not individually display any obviously bimodal distribution". However, Hermann (1970) has maintained the recognition of the two Mackenziean species, but pointed out that the ubiquitous *C. microptera* is generally confused with the more infrequent *C. festivella*. A comparison of the divergent characters in Mackenzie's original descriptions is presented in Table 14. An examination of these characters, along with comparisons between specimens shows that *C. festivella* is no more than a larger version of *C. microptera*. The types of the two are indeed distinct enough to warrant the separation of the taxa into two species, however, the bewildering array of intermediate forms suggests otherwise. Therefore, *C. microptera* can be interpreted as a variable species which, at the small end of the scale, is represented by Mackenzie's concept of *Carex microptera*, and at the large end of the scale, by *C. festivella*. This variation within the species appears to be clinal, since in the southern part of its range, *C. microptera* is represented by all forms, with the *C. festivella* form frequent. Northwards, the *C. festivella* form becomes less frequent. In the Canadian material studied a typical *C. festivella* group was recognized, but was comprised

Figure 20. Distribution of the taxa *Carex microptera* (A), *C. festivella* (B), and *C. limnophila* (C) for western Canada and Alaska.


A
0 200 mi
0 200 km
B
0 200 mi
0 200 km
C
0 200 mi
0 200 km

Tabel 14. Comparison of divergent characters from original descriptions of *Carex microptera* (Mackenzie, 1909) and *C. festivella* (Mackenzie, 1915).

CHARACTER	*C. microptera*	*C. festivella*
Culms	5-10 dm tall	3-6 dm tall
Leaf blades	2.0-3.5 mm wide 1-3 dm long	2.0-4.0 mm wide 1-2 dm long
Inflorescence	ovoid or suborbicular 12-18 mm long 10-16 mm wide	ovoid or oblong-ovoid 12-25 mm long 10-18 mm wide
Spikes	ovoid 5-8 mm long 4-6 mm wide perigynia tips ascending or somewhat spreading	oblong-ovoid 5-12 mm long 4-8 mm wide perigynia tips erect ascending
Scales	ovate-lanceolate acute brown margins scarcely hyaline	ovate obtuse or acutish dark chestnut to brownish black margins narrow hyaline
Perigynia	lanceolate 3.5-4.0 mm long 1.0-1.5 mm wide plano-convex brownish or straw-colored minutely sharp margined	ovate 3.75-5.0 mm long 1.5-2.0 mm wide flat, distended by achene light green or stramineous strongly thin margined
Achenes	1.25 mm long 1.0 mm wide	1.5 mm long 1.0 mm wide

of mainly large intermediate forms. Only four 'good' *C. festivella* specimens were present in all the Canadian material studied. Two of these were included in the numerical analyses of OTU's (FEST06 and FEST07), in either additional clusters in TAXMAP (cluster 33 in the analysis of all characters and cluster 14 in the analysis of reproductive charaters), or in a mixed cluster in CLUSTAN (cluster 'Y' in the analysis of all characters, and a subgroup in the MICRO cluster which contained OTU's of *C. haydeniana* and the type of *C. festivella,* in the analysis of reproductive characters). The peripheral position of these OTU's, as well as the types of *C. festivella* and *C. microptera* var. *crassinerva* (which is essentially a typical example of *C. festivella*) are due to size differences. However, the overall similarity in morphology (minus the size difference), same chromosome number, similar distribution, and numerous intermediate forms, indicates that *C. festivella* is indeed conspecific with *C. microptera.* Thus, it is preferable to expand the concept of *C. microptera* to include *C. festivella,* than to maintain *C. festivella* as a distinct taxon, arbitrarily delimited on size which does not show any clear discontinuity.

The situation for *C. limnophila* is similar to the one just discussed. Hermann's (1956) description of *C. limnophila* leads one to believe that a distince species exists with small (7-12 mm X 5-10 mm), dark colored heads, lustrous brown scales,and small (2.5-3.25 mm X 1-1.3 mm), brown perigynia. However, examination of the type specimen showed, essentially, a small, darker version of *C. microptera.* The heads are indeed smaller, due to smaller and fewer spikes, and to the fact that most of the perigynia have fallen off. With the perigynia gone, color of inflorescence is derived from the remaining brown glossy scales. The type specimen of *C. microptera* shows the same properties, with the perigynia fallen, off, leaving behind brown scales which give the heads a darker appearence. Scale color in *C. microptera* is by no means restricted to dull brown as shown in the frequency distribution of scale color (Figure 3) and, conversely, not all *C. limnophila* specimens possess lustrous scales. In addition, color of perigynia in *C. microptera* and *C. limnophila* is very similar (Figure 3) and can vary even in a specimen (as it does in the type of *C. limnophila* from brownish-black to stramineous). Perigynia size for the two taxa is similar, as shown in the statistical analysis (character #23 and 24), with *C. limnophila* possessing slightly smaller perigynia. Thus, the continued recognition of *C. limnophila* would be arbitrary, again, based mainly on size, and it is more reasonable to expand the concept of *C. microptera* to include *C. limnophila*, on the basis of similar morphology, same chromosome number, similar distribution, and presence of intermediate forms.

Carex haydeniana was shown to be similar to *C. microptera* on a phenetic basis. In the cluster analyses of OTU's, *C. haydeniana* formed subclusters or subgroups within the MICRO cluster or cluster group, and in the analyses of taxa, *C. microptera* the nearest neighbor to *C. haydeniana*. Although the statistical analysis showed that ten characters separated *C. haydeniana* from members of *C. microptera*(#7,8,17, 21,23,34,41,45 and 47),nine of these were size characters,giving the same situation that was present for *C. microptera, C. festivella* and

C. limnophila. However, there was one important difference in that notable intermediate forms were rare or absent. Of all the Canadian material studied, only one population in Waterton Lakes National Park, Alberta, contained intermediate forms. Also, in the cluster analyses of the taxa, and in the ordinations, *C. haydeniana* consistently formed an isolated cluster; and finally, there is a sharp ecological distinction, with *C. haydeniana* occuring in alpine habitats and *C. microptera* in lowland to montane habitats. Cronquist (1977: 165) noted the similarity between *C. haydeniana* and *C. microptera* and commented: "*Carex microptera, C. haydeniana* and *C. ebenea* form a trio with a complex pattern of relationships. *C. haydeniana* is not sharply distinguished from *C. microptera*, of which it might with some justification be treated as an alpine ecotype". Cronquist then suggested that *C. haydeniana*, along with the other members of the aggregate, might best be treated as infraspecific taxa of *C. macloviana*. Taylor and MacBryde (1978) proposed such a treatment for *C. haydeniana* by ranking it and *C. macloviana* as conspecific subspecies. However, Cronquist, and Taylor and MacBryde did not mention occurrence of frequent intermediates between the two taxa, the presence of which would be needed to reduce *C. haydeniana*. This brings us back to the Davis and Heywood concept of aggregate species, those which are not easy to discriminate, but, nonetheless, appear to be isolated from each other. If there is an absence of isolation between two taxa, it appears to be between *C. haydeniana* and *C. ebenea*, which Cronquist (1977: 165) noted:

> However, toward the southern part of the range of *C. microptera*, the position of *C. haydeniana* as its alpine correlative is largely taken over by *C. ebenea*, which is fairly sharply distinguished from *C. microptera* but intergrades to some extent

> with *C. haydeniana*. Occasional specimens from far north of the range of *C. ebenea*, which apparently represent merely the extreme variation in *C. haydenaian*, would probably pass as *C. ebenea* if they had been collected in Colorado.

A number of Canadian specimens would indeed pass as *C. ebenea* if they were collected further south and the continued recognition of *C. ebenea* and *C. haydeniana* as distinct taxa seems dubious. However, until *C. haydeniana* and *C. microptera* are shown to possess frequent intermediate forms, the status of *C. haydeniana* as a species is maintained.

Status of 'stubby' was more difficult to determine. The morphological index and comparison of distributions did not show 'stubby' to be intermediate between *C. pachystachya* and *C. macloviana*, or between *C. pachystachya* and *C. microptera*. Comparison of distribution of *C. pachystachya* and 'stubby' in western Canada and Alaska, however, did show 'stubby' to be sympatric with that species. Also, a comparison of qualitative and quantitative characters showed 'stubby' was quite similar to *C. pachystachya*, except for the greater frequency of darker scales and perigynia of 'stubby', and its more entire margins (2/3 or less of the margin serrulate for 'stubby' as compared to 2/3 or more for *C. pachystachya*). This suite of differences brings back the similarities first noted between 'stubby' and *C. illota*. Examination of these two taxa shows that they are similar in appearance except for the winged perigynia margins of 'stubby', as compared to the nearly marginless perigynia of *C. illota*, larger perigynia in 'stubby' (3-4 mm measured as compared to the 2.5-3.2 mm reported by Cronquist (1969, 1977) for *C. illota*) and the slightly larger heads of 'stubby' (7.5-15.5 mm measured as compared to the 8-13 mm reported for *C. illota* (l.c.)). However, *C. illota* has only been reported as far north as 53° in Jasper

National Park, Alberta (Scotter and Hudson, 1974), and 'stubby' ranges as far north as Alaska (Figure 13). In addition, Moore and Chalder (1964) reported *C. illota* has a chromosome number of n=32 while 'stubby' has been counted as n=41. Therefore, it is not likely that 'stubby' is an intermediate between *C. pachystachya* and *C. illota*, or an extreme form of *C. illota*. The other choice is to consider 'stubby' as an extreme form of *C. pachystachya*. This is backed by the cluster analyses of OTU's where 'stubby' formed clusters with *C. pachystachya*. However, the failure of 'stubby' to cluster with *C. pachystachya* in the cluster analyses of taxa, the separation of 'stubby' from *C. pachystachya* in the ordinations, and the different chromosome numbers, suggest that 'stubby' should be given some form of recognition. Because 'stubby' did not show clear separation from *C. pachystachya* in morphology, and intermediate forms are frequent, it would probably be considered a variety of *C. pachystachya*. However, in an aggregate species group, the recognition of an infraspecific taxon would prove difficult since the differences on which the taxon would have to be based would be almost as great as the differences which distinguish the species. In light of this, and the fact that 'stubby' cannot be clearly distinguished from *C. pachystachya* (as a survey of the character data shows), it is concluded that 'stubby' should not be give formal taxonomic recognition.

Taxonomic Treatment

The following proposed taxonomic treatment is based upon taxonomic conclusions that are discussed above, which, in turn were based upon available morphological, cytological, distributional and ecological data. It must be reiterated that although this investigation was concerned with the *Carex macloviana* aggregate as it appears in western Canada and Alaska, an understanding of each of the species as they exist throughout their entire geographic range had to first be attained before decisions concerning them could be formulated. Thus, the following treatment may be applied to material outside of the area of this study, but caution must be advised since members of the group which do not occur in Canada or Alaska can cause some confusion, and the descriptions and key are based primarily on Canadian and Alaskan material.

The following is a detailed description of the aggregate as it appears in western [illegible]da and Alaska. It is based on specimens examined in this investigation and is given to delimit the group and to provide descriptions of structural features which are essentially uniform throughout the aggregate.

Carex macloviana sensu lato

Plants perennial, cespitose; rootstocks fibrous; culms stiff to ± lax, erect or ± decumbent, striate, 0.5-10 dm tall, conspicously exceeding the leaves, sharply angled and scabrous above, becoming obtusely angled and smooth below; leaves 3-9 per culm, clustered on lower 1/8 to 2/5 of culm, lowest one or two bladeless soon turning brown, upper ones with well developed blades, straight and ascending or curved, 4-30 cm long, flat, 1.5-4.0 mm wide, margins scabrous, upper portion of blade channeled, grading into attenuate, terete tip, sheaths tight, white hyaline ventrally, short (≤ 2 mm) extended at collar, continuous with ligule, ligule joined to blade, ≤ 3 mm long, acute to obtuse; inflorescence generally captite, usually dark in appearance, ovoid to oblong-ovoid or triangular-ovoid, 7.5-26 mm long, 7.5-18 mm wide, sometimes lowest spike separated from the rest though first internode rarely exceeds 3 mm; spikes 3-10, sessile, gynecandrous, loosely to densely aggregate, ovoid to widely ovoid, 4.0-10.5 mm long, 3-8 mm wide, perigynia tips appressed-ascending to spreading within the spikes; bracts scale-like, membraneous, concolorous with scales, dull to lusterous, reddish to dark brown or coppery, acute to obtuse, margins concolorous with bracts or narrowly to widely white hyaline, midrib differentiated, scabrous, keeled, lower bracts sometimes aristate prolonged, the awn shorter than the inflorescence; scales membraneous, generally dark colored, dull to lusterous, reddish to dark brown or coppery, oblong-lanceolate to ovate, 2.5-5.0 mm long, 0.9-2.0 mm wide, shorter (3/5 to nearly as long) and narrower than the perigynia, exposing the beaks and upper margins, acute to obtuse, margins concolorous with scales to widely white hyaline, especially the lower (male) ones, midrib generally paler or green, somewhat differentiated to scabrous keeled on lower ones, undifferentiated on upper ones; anthers 0.9-2.3 mm long, appiculate scabrous; perigynia membraneous, generally dark colored, dull to lusterous, stramineous or light green to dark brown or coppery, sometimes paler or green on the margins and distal portion of the body of the perigynia, flat and distended by the achenes to plano-convex, generally ovate, 3.0-6.5 mm long, 1.2-2.4 mm wide, margins winged nearly throughout, serrulate scabrate, 0.1-0.4 mm wide, widest towards middle of perigynia, body of perigynia nerved dorsally, nerves 5-11, faint to evident, nerved ventrally, generally towards base but a few extending the length of the body, nerves 0-8, faint to evident, infrequently 1 or 2 ventral folds present, base of perigynia acutish to nearly truncate, spongy filled or spongy filling absent, beak of perigynia gradually contracted from the body, generally darker than the body, 1.0-3.1 mm long, 1/3 to 1/2 the length of the body, serrulate-scabrous and winged in proximal portion, dorsal side with a suture the margins of which are concolorous with the beak or white hyaline, distal portion terete, smooth marginless, darker than the body of the perigynia, 0.3-1.2 mm long, 1/8 to 4/5 the length of the beak, apex concolorous with tip or white hyaline, unevenly angled or bidentulate, the teeth ≤ 2 (2.5) mm long; achenes light to dark brown, dull or shiny, lenticular, ovate to oblong, 1.1-1.8 mm long, 0.7-1.3 mm wide, filling up to 4/5 of the body of the perigynia, stipitate, stipe 0.3-0.8 mm long, apiculate, apicule ≤ 0.6 mm long; styles straight and jointed with the achenes; stigmas 2.

Two factors correlate well with distibution of members of the aggregate: preference for open, seral, or disturbed habitats, and for soils with a generally low organic content. These observations are based on field experience and on herbarium label data, and indicate that members of the group are pioneering or seral species. Further work is needed to test this hypothesis and to quantify the habitat requirements of the species. A third factor which correlates with the distribution of the group, at least in Alaska and Canada, is the occurrence of the aggregate in predominantly calcareous regions. Again, further work is needed to determine how well this relationship holds for the remainder of western North America.

Key to The Species of The *Carex macloviana* Aggregate

In Western Canada and Alaska[1]

Distance from top of achene to perigynium tip one half or less the total length of the perigynium; perigynia reddish to dark coppery-brown.

Scale margins, perigynia tips, and dorsal suture margins noticeably white hyaline; perigynia wings darkened, contrasting with the body of the perigynia.

C. macloviana

Scale margins and perigynia tips not diferentiated or narrow hyaline margined; perigynia wings concolorous with the body of the perigynia, wings at most dark edged.

C. pachystachya

Distance from top of achene to perigynium tip one half or more the total length of the perigynium; perigynia stramineous or light green to dark brown.

Perigynia (4.0) 4.5-6.5 mm long; achenes 1.4-1.7 mm long; achene stipes(0.4) 0.5-0.7 mm long.

C. haydeniana

Perigynia 2.9-4.3 (4.7) mm long; achenes 1.1-1.5 mm long; achene stipes 0.3-0.5 mm long.

C. microptera

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[1] Note on the use of the key: To gain an understanding of the variation exhibited by individual specimens, a number of perigynia should be measured or observed before a decision is reached for each character state. This key, as almost any key for species of *Carex*, is intended for use with mature specimens only. Immature specimens do not contain enough diagnostic characters to allow proper identification with the use of a key; species descriptions, herbarium specimens, or workers familar with the group should be consulted if immature specimens must be identified.

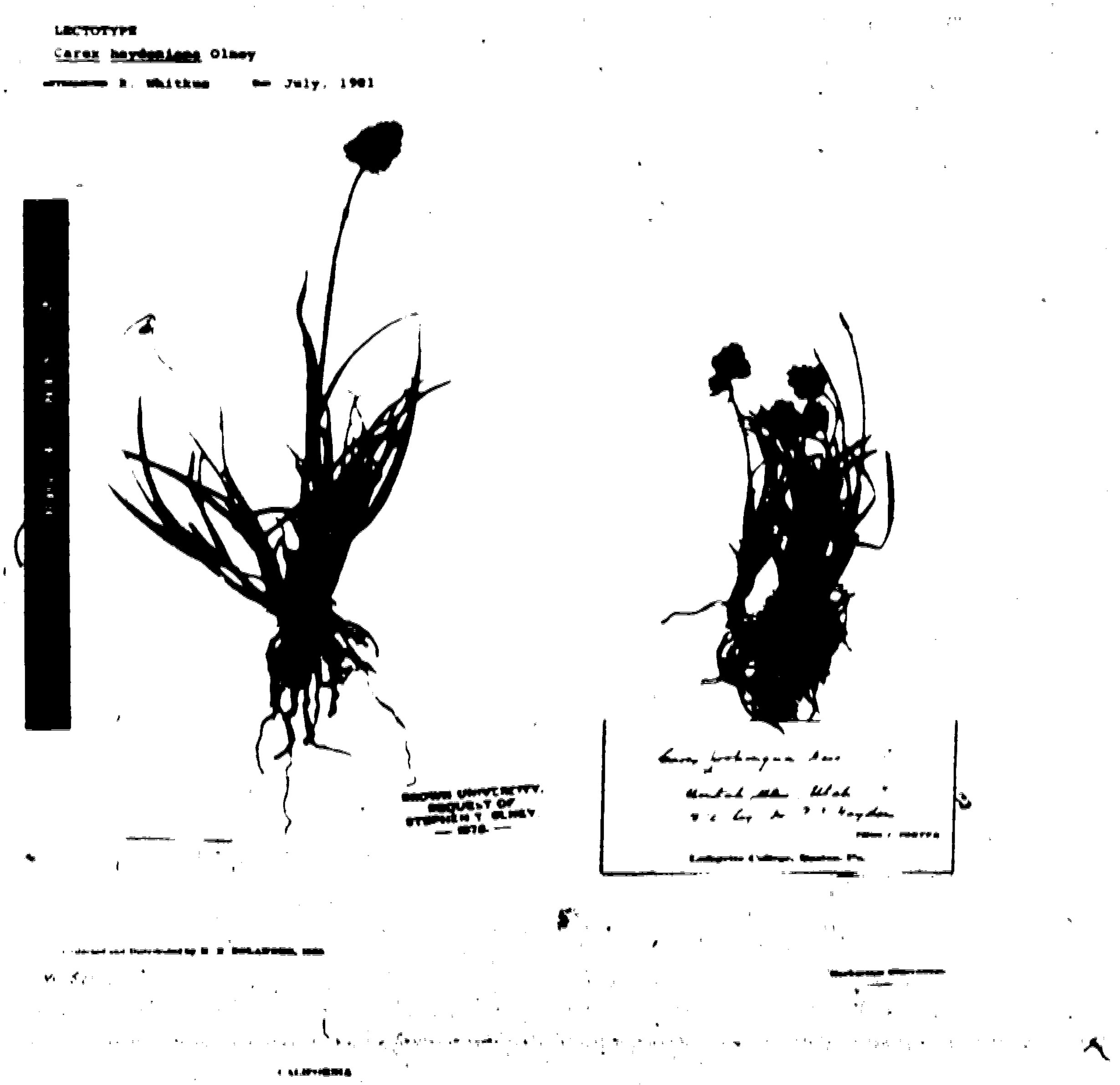
Carex haydeniana Olney

Carex haydeniana Olney in S. Wa[illegible]. King Rep. Geol. Explor. 40th Parallel. 366. 1871.
C. festiva var. *haydeniana* (Olney) W. Boott in S. Wats. Bot. Calif. 2: 234. 1880.
C. macloviana var. *haydeniana* (Olney) Holm, Amer. J. Sci. 160: 266. 1900.
C. macloviana var. *haydeniana* (Olney) Kükenth. in Engl. Pflanzenr. IV. 20 (Heft 38): 196. 1909. *nom. illeg.*
C. macloviana ssp. *haydeniana* (Olney) Taylor and MacBryde, Can. J. Bot. 56: 190. 1978.
Type: Mount Dana, California, *Bolander 5074* (BRU!, lectotype).

Carex festiva var. *decumbens* Holm, Amer. J. Sci. 166: 20, 26. 1903.
C. macloviana var. *stricta* f. *decumbens* (Holm) Kükenth. in Engl. Pflanzenr. IV. 20 (Heft 38): 197. 1909.
C. nubicola Mackenzie, Bull. Torrey Bot. Club 36: 480. 1909.
Type: Pagosa Peak, Colorado, *Baker 232* (NY!, lectotype by Mackenzie, 1931-35; POM!, RM!, isolectotypes).

Cespitose; culms stiff, (1) 1.9-4.0 dm tall, exceeding the leaves; leaves with well developed blades 3-6 per culm, clustered on lower 1/5 to 1/3 of culm, blades stiff, straight to curved, 5.5-10.5 cm long, 1.5-3.3 mm wide; inflorescence triangular-ovoid to ovoid, base usually truncate, (11) [illegible]3-19 (21) mm long, 13-17 (18) mm wide, first internode up to 2.5 (3.4) mm long; spikes 5-7, densely aggregate, 6.5-10 mm long, 4.5-8.0 mm wide, perigynia tips ascending within the spikes; bracts scale-like, concolorous with scales, mostly dull, reddish-brown or occasionally dark coppery-brown, acute to narrowly obtuse, the lowest sometimes short-awned, margins concolorous with bracts to wide white hyaline; scales mostly dull, reddish-brown or occasionally dark coppery-brown, 3.0-4.8 mm long, 1.3-1.7 mm wide, 1/2 to 3/4 the length of the perigynia, acute to narrowly obtuse, margins concolorous with scales to narrow hyaline; anthers 1.5-1.9 mm long; perigynia dull to lusterous, light reddish-brown or tan, occasionally coppery-brown, paler towards the upper margins, sometimes turning purplish-black on the beak and upper medial portion of the body of the perigynia, flat and distended by the achenes, ovate to wide-ovate, occasionally narrow-ovate to elliptic-ovate, (4.0) 4.5-6.5 mm long, 1.7-2.4 mm wide, margins winged to the base, serrulate-scabrate up to 2/3 of their length, 0.3-0.4 mm wide, dorsal nerves 7-9, faint to evident, ventral nerves 3-6, mostly faint and basal, a few extending the length of the body of the perigynia, ventral folds essentially absent, spongy filling in base generally lacking beaks 1.8-2.1 mm long, suture margins concolorous with beaks, beak tips 0.3-0.6 mm long, 1/8 to 1/3 the length of the beaks, distance from the top of the achenes to the apex of the perigynia 1/2 or greater than the overall length of the perigynia, apex concolorous with beaks to narrow hyaline, erose to bidentulate, the teeth up to 0.1 mm long; achenes 1.4-1.7 mm long, 0.8-1.1 (1.3) mm wide, relatively small in relation to the perigynia, filling up to 2/5 of the body of the perigynia, stipes (0.4) 0.5-0.7 (0.8) mm long; n=41. (Figure 21).

Figure 21. Type specimen (left) of *Carex haydeniana* Olney.

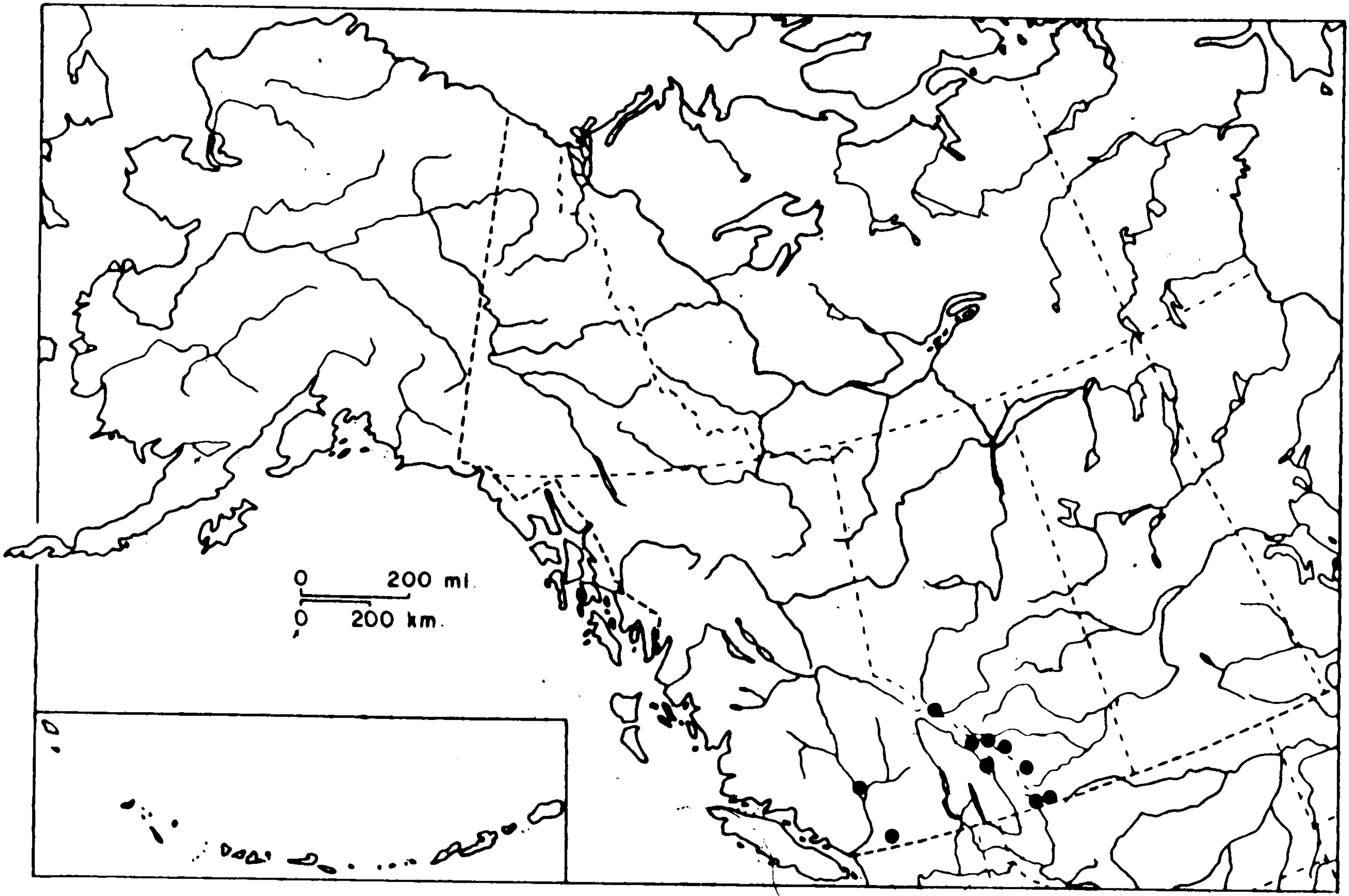

LECTOTYPE
Carex haydeniana Olney
R. Whitkus
July, 1981
BROWN UNIVERSITY, BEQUEST OF STEPHEN T. OLNEY — 1878 —

Distribution: From the Rocky Mountains of Alberta and British Columbia as far north as Sunwapta Pass, Mt. McLean near Lillooet, and the Ashnola Range of British Columbia. Growing in rocky meadows, slopes, and thickets, and on moraines, ledges and stream banks, in subalpine to alpine conditions from 1750 to 2400 meters elevation. Occurring in similar habitats as far south as Colorado in the Rocky Mountains, and in California, east of the crest of the Sierra Nevada to 4300 meters. Reported from Arizona by Hermann (1970) and as being apparently absent from Washington by Cronquist (1969). (Figure 22).

Discussion: Holm (1871) listed two specimens in his description: Bolander's specimen from Mt. Dana in California, and one collected by Dr. F. V. Hayden in 1870 from the Uinta Mountains of eastern Utah. The sheet from Olney's herbarium (BRU) contains both plants mounted side by side, with Bolander's specimen exhibiting the characteristic habit and, to a lesser extent, inflorescence, while Hayden's specimen exhibits the characteristic color in its more mature perigynia, but appears to be depauperate. Olney's description, however, incorporates characteristics of both plants, such as spikes ovate (Bolander) or nearly round (Hayden), perigynia yellowish (Bolander), dark purple at top or finally throughout (Hayden), and culms 4 (Hayden) to 8 (Bolander) inches high. Because Hayden's specimen is depauperate, and most of the description fits Bolander's specimen better than Hayden's, Bolander's specimen is chosen as the lectotype.

The species is distinguished from other members of the aggregate by its large perigynia and densely aggregate, triangular-ovoid heads, and to a lesser extent by its relatively small achenes in comparison to the perigynia. Some forms of *C. pachystachya* have large (5 mm)

Figure 22: Distribution of *Carex haydeniana* for western Canada and Alaska.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perigynia, but are plump and spongy filled in the base while *C. haydeniana* possesses flattened perigynia with little, if any, spongy filling. In addition, the inflorescence of *C. pachystachya* is aggregate to loosely aggregate, with the tips of the perigynia ascending to spreading. The inflorescence of *C. haydeniana*, however, is densely aggregate, and the perigynia tips are ascending in the spikes. In the southern Rocky Mountains, some forms of *C. microptera* (*C. festivella*) possess large (5 mm), flattened perigynia and inflorescences with a truncate base. Cronquist (1977) noted that *C. microptera* and *C. haydeniana* did not appear to be clearly distinguished and was probably reffering to these large perigynia forms of *C. microptera*. However, *C. haydeniana* is further distinguished from *C. microptera* by its larger achenes and achene stipes. The relationship of *C. haydeniana* to *C. ebenea* is in further need of investigation, as well as Cronquist's (1977) idea that *C. haydeniana* is no more than an alpine ecotype of *C. microptera*.

Representative Specimens: CANADA: ALBERTA: 1.3 km. southwest of Lawson Lake, Kananaskis Provincial Park, *Brunton and Paton 1467* (DAO); Bertha Lake, Waterton Lakes National Park, *Kuijt and Blais 2281* (CAN); Highwood Pass, *Moss 10908* (ALTA); 5 miles northwest of Mt. Head, Highwood Pass, *Packer 1969-395* (ALTA); Plateau Mt., *Whitkus 1994* (ALTA).

BRITISH COLUMBIA: West end of Quiniscoe Lake in Ashnola Range, *Calder, Parmelee and Taylor 19595* (RM); Mt. McLean near Lillooet, *Calder, Savile and Ferguson 15558* (RM); Paradise Mine, Windermere, August 28m k844m *Hardy s.n.* (UBC); Yoho Valley, Yoho National Park, *McCalla 7630* (ALTA, UBC); Wall Lake, *Taylor 8970* (UBC).

UNITED STATES OF AMERICA: MONTANA: Goose Lake, Cooke City, *Conard 1914* (RM); Pioneer Range, *Hitchcock and Muhlick 12958* (RM); Mineral Park, Glacier National Park, August 8, 1910, *Jones s.n.* (RM); Logan Pass, Glacier National Park, *Peirson 11970* (ORE).

WYOMING: 1 mile northwest of Beartooth Pass, *Johnson 54* (RM); Above Crater Lake, *Lofgren 115* (RM); Brooklyn Lake, Medicine Bow Range, *Nelson 5188* (RM); La Plata Mines, *Nelson 5190* (RM); Roaring Fork Mountain, Wind River Range, *Scott 323* (RM).

COLORADO: Mt. Kelso, near Gray's Peak, *Holm 465* (S); Arapanoe Park, *Weber 3680* (RM).

IDAHO: Peak east of Castle Park, White Cloud Range, *Hitchcock and Muhlick 10846* (RM).

UTAH: Gunsight Peak, *Maguire, Hobson and Maguire 14560* (CAN); Henrys Forks Basin, *Maguire, Hobson and Maguire 14686* (RM); La Sal Mountains, *Payson and Payson 4049* (RM).

OREGON: Steens Mountain, *Chambers 3354* (OSC); Wallowa Mountains, *Cusick 13311* (ORE); Wallowa Mountains *Cusick 3133* (ORE, RM); 2 miles south of Aneroid Lake, Wallowa Mountains, *Peck 18004* (OSC); North slope of Eagle Cap Peak, Wallowa Mountains, *Sharsmith 3917* (OSC).

Carex macloviana D'Urville

Carex macloviana D'Urville, Mem. Soc. Linn. Paris 4: 599. 1826.
Type: Not seen, presumably at CN.

Carex festiva Dewey, Amer. J. Sci. 29: 246. 1836.
Type: Great Bear Lake, Northwest Territories...."Bear Lake, Dr. Richardson" (NY!, isotype).

Carex soperi Raup, Sagentia 6: 129. 1947.
Type: North of Brintnell Lake, Mackenzie District, Northwest Territories, *Soper and Raup 9534* (CAN!, holotype; ALTA!, isotype)

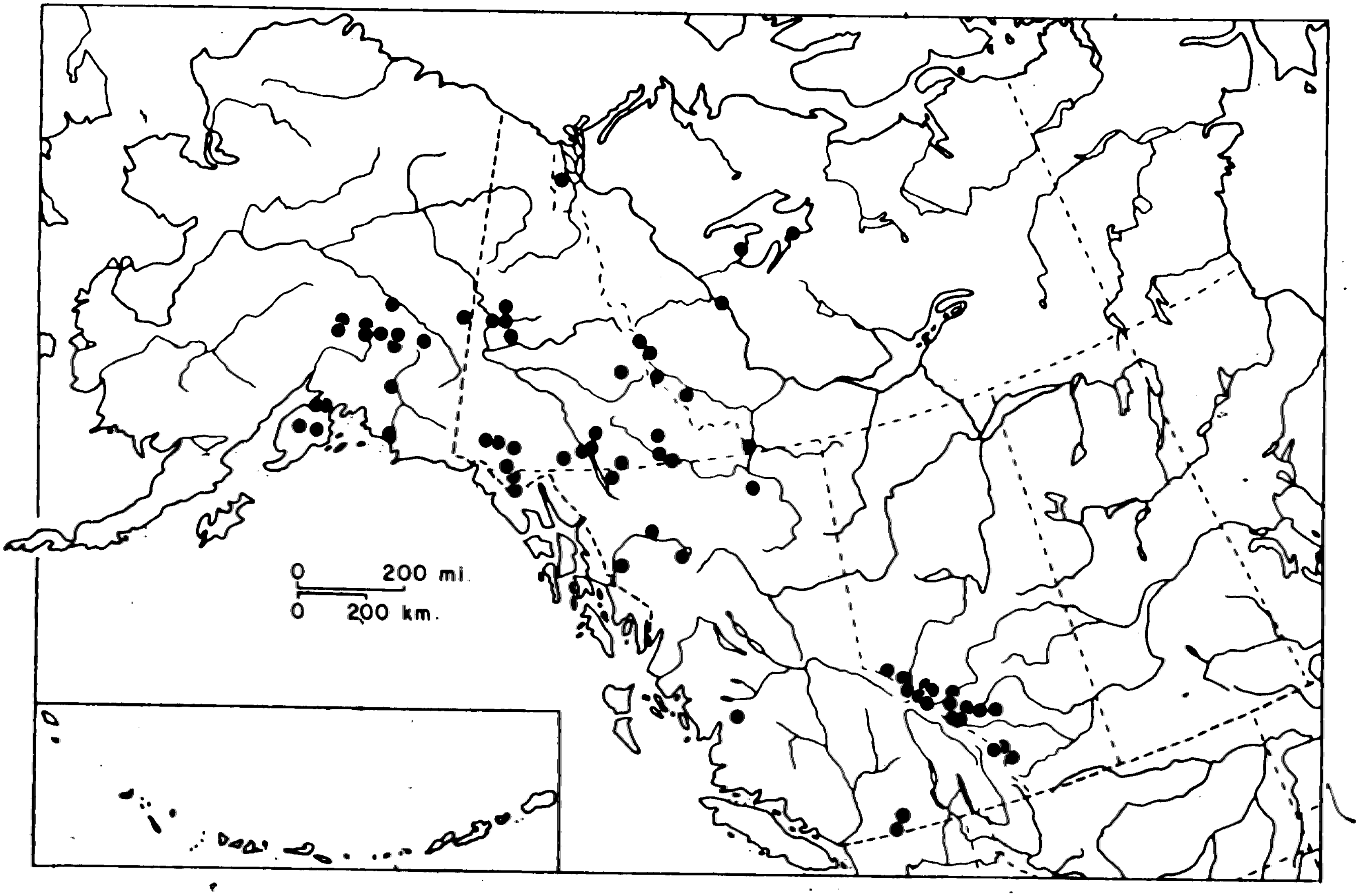
Carex incondita F. J. Hermann, Leafl. W. Bot. 8: 112.
Type: 40 miles south of Nordegg, Alberta, *Hermann 13347* (US, holotype; ALTA!, CAN, CAS, NA, isotypes). 4.5 miles south of Cadomin, Alberta, *Hermann 13444* (ALTA!, CAN, NA, paratypes).

Cespitose; culms stiff, (0.9) 2-4.5 (6.0) dm tall, exceeding the leaves; leaves with well developed blades 2-6 per culm, clustered on lower 1/8 to 2/5 of culm, blades stiff, straight or slightly curved, (4) 6-12 (18) cm long, (1.5) 2-3.5 (4.0) mm wide; inflorescence ovoid to oblong-ovoid or wide-ovoid, (9.5) 12-18 (20.5) mm long, (8.0) 10.5-14.0 (18.5)mm wide, first internode up to 2.5 (3.7) mm long; spikes 3-8, aggregate, 5.5-8.5 (10.5) mm long, (3.0) 4.5-6.0 (7.0) mm wide, perigynia tips appressed-ascending within the spikes; bracts scale-like, concolorous with scales, lusterous, reddish to dark brown or coppery, acute to obtuse, the lowest occasionally short-awned, margins narrow to wide white hyaline; scales lusterous, reddish to dark brown or coppery, (2.7) 3.0-3.5 (4.0) mm long, 1.0-1.5 mm wide, about 3/4 as long as the perigynia, acute to obtuse, margins narrow to wide white hyaline; anthers 1.4-2.0 (2.3) mm long; perigynia lusterous, reddish-brown to coppery-brown, upper portion green to dark green or pale, flat and distended by the achenes to plano-convex, ovate to elliptic-ovate, 3.5-4.5 mm long, 1.4-2.0 mm wide, margins winged to the base, generally darker than the perigynia, serrulate-scabrate up to 2/3 of their length, 0.2-0.3 (0.4) mm wide, dorsal nerves 7-11, faint to evident, ventral nerves 3-8, faint to evident, generally basal, ventral folds 0-1, spongy filling present to abundant in base, beaks 1.3-1.8 mm long, suture margins white hyaline, beak tips (0.4) 0.5-0.8 (0.9) mm long, (1/4) 1/3 to 1/2 the length of the beaks, distance from the top of the achenes to the apex of the perigynia 1/2 of less than the overall length of the perigynia, apex white hyaline, erose to bidentulate, the teeth up to 0.1 mm long; achenes 1.4-1.6 (1.7) mm long, 0.9-1.1 mm wide, relatively large in relation to the perigynia, filling up to 3/5 (3/4) of the body of the perigynia, stipes 0.4-0.6 mm long; n=43.

Distribution: In the Northwest Territiories from Great Bear Lake and Richardson Mountains, south and west to southeastern Alaska and northern British Columbia, discontinuous into the Rocky Mountains of Alberta and British Columbia, and the Itcha Mountains and Ashnola Range of British Columbia. (Figure 23). Growing in clayey, silty, sandy, gravelly soils of lake and river shores and banks, thickets, moist meadows and slopes, moraines, bogs and swales, depressions and openings in poplar, spruce, or pine woods, and disturbed habitats along roads, embankments, ditches, and coal spoils, in boreal-montane to alpine conditions from near sea level to 2400 meters elevation. Also found growing near Ft. Chimo on the Ungava Peninsula, Gaspé Peninsula, and Torngat Mountains of Quebec, among rocky crevices of the Labrador coast, meadows and fjords of Greenland, meadows and openings in the woods of northern Fennoscandia, meadosw, slopes and dwarf *Nothofagus* woods in the mountains of southern Chile to Tierra del Fuego and Falkland Islands. Reported from the Medicine Bow Mountains of Wyoming by Hermann (1970), and from Iceland by DuReitz (1940) and Hultén (1958).

Discussion: Although the type was not seen, the description provided by Kükenthal (1909), who presumably saw the type (under his list of specimens examined: "Falkland Inseln (*D'Urville*)"), as well as material examined in this study from the Falkland Islands and South America, matches the material present in North America, Greenland and Europe. D'Urville provided only a short diagnosis which could fit almost any member of the aggregate, but apparently was sufficient for describing

Figure 23. Distribution of *Carex macloviana* for western Canada and Alaska.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his new species, since it is the only member of the *Ovales* that reaches the Falkland Islands. An additional taxon has been recognized from South American material by Kükenthal (1909) as variety *pseudoleporina*, distinguished by its approximate spikes and lighter colored sclaes. Material of this variety has been seen and it appears that the problem of closely related taxa which are not clearly distinguished on a morphological basis, may be present in South America as well.

The species is distinguished from other members of the aggregate by its very dark colored inflorescence, lustrous scales and perigynia which are generally coppery colored, and noticeable white hyaline scale margins, perigynia tips and perigynia dorsal suture margins. It is further distinguished from *C. pachystachya*, with which it shares some of these features, by noticeably darkened perigynia wing margins contrasting with lighter color of the body of the perigynia, and paler or green upper portion of the perigynia body. *Carex pachystachya* has either dark edged wing margins or is uniformly colored throughout. Also, the perigynia tips of *C. macloviana* are ascending in the spikes, while those of *C. pachystachya* are ascending to spreading.

The chromosome number of this species has not been previously recorded for North America. Counts of n=43 determined in this study agrees with those reported for Greenland and European material. The report of Böcher (1938) of 2n=ca. 82 is apparently erroneous.

Representative Specimens: CANADA: ALBERTA: Saskatchewan Glacier, Banff National Park, *Boivin 5077* (DAO); Mercoal, *Malte and Watson 1886* (CAN, RM); Clearwater Trunk Road, south of Sundre, *McCalla 12272* (ALTA, UBC); Mt. Shunda, north of Nordegg, *A.E. Porsild 20694a* (CAN); Plateau Mt., *Whitkus 1975* (ALTA).

BRITISH COLUMBIA: Along trail to Ashnola Range, *Calder, Parmelee and Taylor 19820* (DAO); Itcha Mts., 26 miles northeast of Anahim Lake, *Clader, Parmelee and Taylor 20220* (ALA); Mountains 10 miles south of Telegraph Creek, *McCabe 8835* (DAO); Apex Mt., 15 miles northeast of Keremeos, *Senn, Frankton and Gillett 5779* (DAO); 72 km. southeast of

Teslin on Alaska Highway, *Whitkus 1730* (ALTA).

NORTHWEST TERRITORIES: East slope of Richardson Mts., *A. E. Porsild 6759* (CAN, S); MacMillan Pass, Canol Road, *A. E. Porsild and Breitung 11211* (CAN, S); Hole-In-The-Wall Lake, Mackenzie Mts., *Scotte 17431* (DAO); Sawmill Bay, Leith Peninsula, Great Bear Lake, *Shacklette 3068* (CAN).

YUKON TERRITORY: 24 miles east of Little Atlin Lake, *Raup and Raup 11372* (ALA, CAN, S, UBC); 1 mile east of Haines Junction, *Raup and Raup 11956* (CAN, S, UBC); Mile 36, Canol Road, *Porsild and Bretiung 10763* (CAN, S); Mile 1022, Alaska Highway, *Schofield and Crum 7642* (CAN, UBC); 70 km. north of Klondike River Lodge on Dempster Highway, *Whitkus 1211* (ALTA).

QUEBEC: Fort Chimo, *Calder 2357* (DAO); Wakeham Bay, Ungava Peninsula, *Duman 2623* (CAN); Fort Chimo, *Dutilly and LePage 14726* (CAN, DAO, S); Mt. AuClair, Tabletop Mts., Gaspé Peninsula, *Fernald and Smith 25521* (ALA, CAN); Mt. AuClair, Tabletop Mts., Gaspé Peninsula, *Raymond, Kucyniak and Rune 1900* (DAO, S).

LABRADOR: Cape Mugford, *Porsild 174* (CAN); Torngat Mts., *Rousseau 1023* (S); Rama, *Stecker 372* (RM).

UNITED STATES OF AMERICA: ALASKA: Savage River Camp, Mt. McKinley National Park, *Henderson 14792* (ORE); 4 miles north of Paxson, *Pegau 131-70* (ALA); Mile 196, Richardson Highway, *Smith 2160* (ALA, CAN, S); McKinley Park R.R. Station, Mt. McKinley National Park, *Viereck 1739* (S); 30 miles east of Cantwell on Rt. 8, *Whitkus 1412* (ALTA).

GREENLAND: Scoresby Land, *Einarsson 31* (ALA, CAN); Igdlorssuit, Prince Charles Sound, *Gravesen and Hansen 66-1844* (ALA); Anivia, *Hansen 66-1045* (CAN, DAO); Majut, *Hansen, Hansen and Petersen 145* (ALA, CAN, DAO); Kong Oscars Fjord, *Raup and Raup 794* (CAN).

NORWAY: Fredheim, Øvergygd, August 2, 1955, *Gjaervoll s.n.* (ALA); Sivertskardet Pass, Mälselv, July 9, 1949, *Norrman s.n.* (DAO); Rundhaug, July 14, 1949, *Norrman s.n.* (DAO).

SWEDEN: Mt. Nuolja, Jukkasjorvi Parish, *Alm 1899* (DAO); Salmijärvi, Jundsuando Parish, *Alm 2783* (DAO); Erkheikki, Pajala Parish, *Alm 2614* (DAO); Albisko, *Clausen 1389* (DAO); Tornetrask, Jukkasjärvi Parish, *Samuelsson 349* (ALA, DAO).

FINLAND: Kilpisjärvi, *Alava, Alho and Kause 4388* (DAO); Kolari, Sieppijarvi, August 4, 1935, *Auer s.n.* (DAO); Muonio, Kemensis Parish, July 17, 1916, *Montell s.n.* (DAO); Kilpisjärvi, August 16, 1958, *Roivainen s.n.* (DAO); Kaaresuanto, Sakkara, July 11, 1939, *Segerman s.n.* (ALTA, DAO).

CHILE: Punta Arenas, *Barros 6015* (DAO); Between Morro Chico and Carpa Manzana, *Kalela 2142* (S); "Magallanes", *Kalela 1987* (S); O'Higgins, *Looser 4606* (DAO); "Magallanes", *Valentin 269* (S).

ARGENTINA: 20 km. east-northeast of Ushuaia, Tierra del Fuego, *Santesson 472* (S); Mendora, *Wall 69* (S).

FALKLAND ISLANDS: *Skottsberg 117* (LY, S).

9

Carex microptera Mackenzie

Carex festiva var. *viridis* L. H. Bailey, Mem. Torrey Bot. Club 1: 51. 1889.
C. macloviana var. *stricta* f. *viridis* (Bailey) Kükenth. in Engl. Pflanzenr. IV. 20 (Heft 38): 197. 1909.
Type: Park County, Montana, *Tweedy s. n.* (BH!, lectotype).

Carex microptera Mackenzie, Muhlenbergia 5: 56. 1909.
C. macloviana var. *microptera* (Mack.) Boivin, Naturaliste Can. 94: 523. 1967.
Type: Deeth, Elko County, Nevada, *Heller 9067* (NY!, holotype; CAS!, isotype).

Carex festivella Mackenzie, Bull. Torrey Bot. Club 42: 609. 1915.
Type: Laramie, Albany County, Wyoming, *A. Nelson 3275* (NY!, holotype; NA!, isotype).

Carex limnophila F. J. Hermann, Leafl. W. Bot. 8:28. 1956.
Type: 7 miles northeast of Pinedale, Sublette County, Wyoming, *Hermann 12252* (US!, holotype).

Cespitose; culms stiff, 2.0-6.5 (9) dm tall, exceeding the leaves; leaves with well developed blades 3-7 per culm, clustered on lower 1/7 to 1/3 of culm, blades stiff to lax, straight to ± curved, (6) 8-19 (23) cm long, 2.0-4.1 mm wide; inflorescence variable, from elliptic-ovoid to trangular-ovoid, the base frequently truncate, (11) 12-19 (20)mm long, 9.5-16 (17.5) mm wide, first internode up to 2.5 (3.0) mm long; spikes 4-10, aggregate to densely aggregate, 5-9 mm long, (4.3) 4.5-6.5 (7.0) mm wide, perigynia tips ascending to ascending-spreading within the spikes; bracts scale-like, concolorous with the scales, dull to lusterous, generally brown, but also reddish-brown to coppery-brown, acute, the lowest occasionally short-awned, margins concolorous with bract to hyaline; anthers 0.9-1.7 (1.9) mm long; scales dull to lusterous, generally brown, but also reddish-brown to coppery-brown, acute, 2.4-3.5 mm long, 1.0-1.5 (1.7) mm wide, 3/5 to 4/5 the length of the perigynia; perigynia mostly dull, stramineous or light green to dark brown, medial portion and beak generally darker, flat and distended by the achenes to low plano-convex, mostly ovate, occasionally narrow-ovate or wide-ovate, (2.9) 3.4-4.3 (4.7) mm long, (1.2) 1.4-2.0 (2.3) mm wide, margins winged to the base, though frequently becoming obsolete towards the base, serrulate-scabrous for up to 2/3 or more of their length,0.1-0.4 mm wide, dorsal nerves 6-10, faint to evident, ventral nerves 1-8, faint to evident, mostly basal, ventral folds 0-1, spongy filling present to abundant in base, beaks (1.3) 1.5-2.1 (2.5) mm long, suture margins concolorous with beaks tips 0.2-0.6 (0.8) mm long, (1/8) 1/6 to 1/3 the length of the beaks, distance from the top of the achenes to the apex of the perigynia 1/2 or greater than the overall length of the perigynia, apex concolorous with beaks, erose to bidentualte, the teeth up to 0.2 mm long; achenes 1.1-1.4 (1.5) mm long, 0.7-1.0 mm wide, relatively small in relation to the perigynia, filling up to 3/5 (2/3) of the body of the perigynia, stipes 0.3-0.5 mm long; n=40,41,45. (Figure 24).

Figure 24. Type specimen of *Carex microptera* Mack.

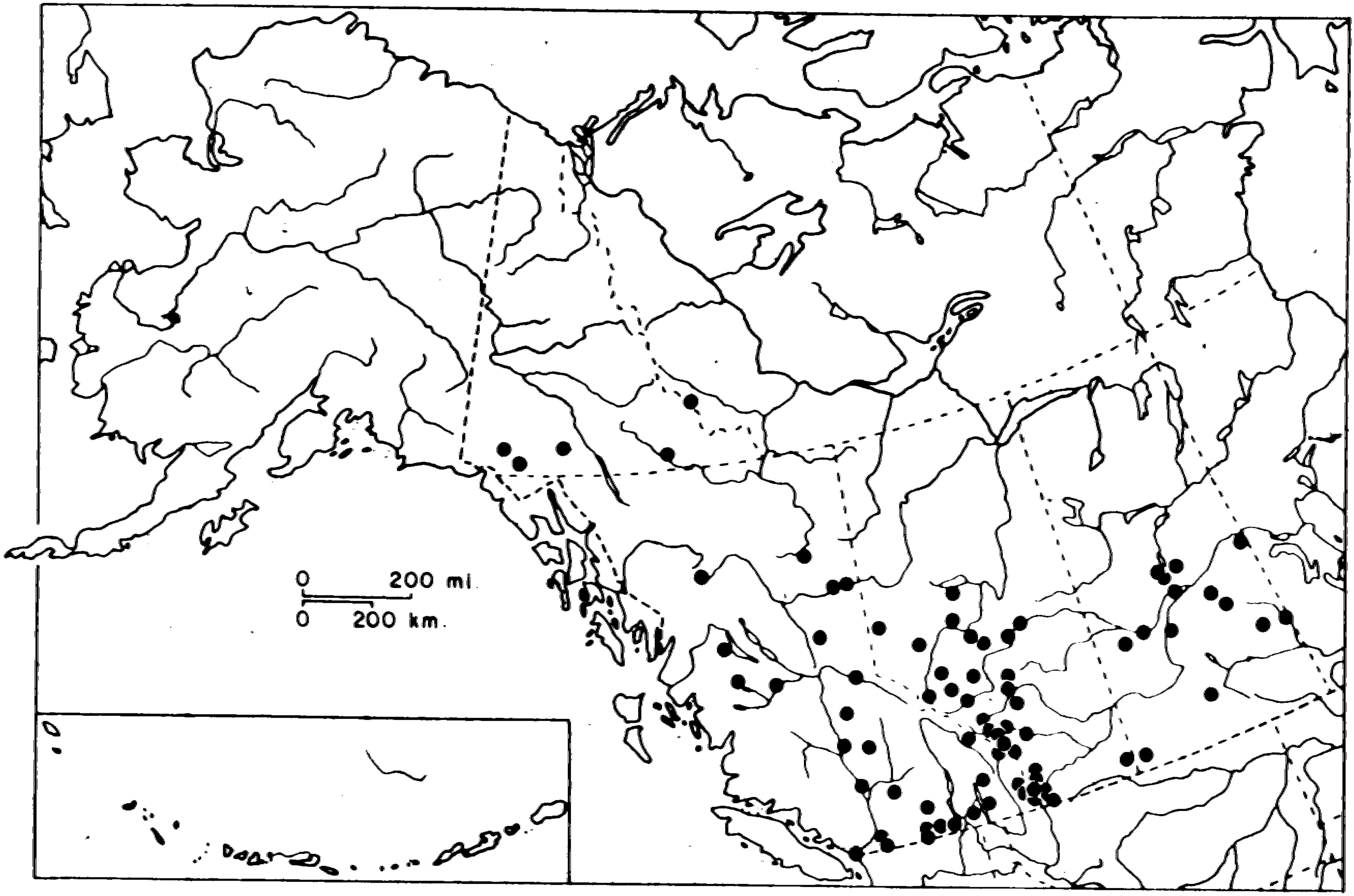
A. A. Heller, Collector

Distribution: In the southern Yukon and Mackenzie Mountains of the Northwest Territories, through interior British Columbia, the mountains of British Columbia and Alberta, the aspen parkland of Alberta through Saskatchewan and into Manitoba, disjunct in the Cypress Hills and in favorable habitats in the prairies (Figure 25). Growing in generally local, moist, open conditions, in clayey, silty, or gravelly soil of river and lake shores and banks, moist meadows and slopes, thickets, edges of bogs and swamps, depressions or disturbances in poplar, spruce or pine woods, and in disturbed habitats such as embankments, ditches, roadsides, and coal spoils, generally in montane conditions, but also from near sea level to 1800 meters elevation. The species is also bound in simialr habitats south of the 49th parallel, up to 3000 meters elevation, as far south as California and Arizona. Reported from New Mexico and the Black Hills of South Dakota by Hermann (1970)and Cronquist (1977).

Discussion: Bailey listed two specimens after his description of *C. festiva* var. *viridis*: *Scribner 315* from 16 Mile Creek, Montana, and *Tweedy s.n.* from Park County, Montana. The sheets from Bailey's herbarium (BH) show that the two specimens are similar to one another, and match the original description equally. However, Scribner's specimen is incomplete, consisting of two loose culms, while Tweedy's specimen consists of a tuft of culms attached to the rootstock. Because it is more complete, Tweedy's specimen is chosen as the lectotype.

The species is distinguished from others in the aggregate by the smaller achenes, and to a lesser extent, by the generally smaller, lighter colored, dull perigynia. The large forms of *C. microptera* which resemble *C. haydeniana* are distinguished by features discussed

Figure 25. Distribution of *Carex microptera* (including *C. festivella* and *C. limnophila*) for western Canada and Alaska.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in the section dealing with taxonomy of the aggregate.

The published reports of the chromosome number of *C. microptera* do not agree with those determined in this study. Wahl's (1940) count of n=41 was from Colorado material and suggests a link between this species and *C. haydeniana*. Another alternative is that the specimen was actually *C. haydeniana,* however, since the voucher was not seen, this can not be concluded. The count of n=45 by Clausen, Keck and Hiesey (1940) seems too high, but in light of the cytological condition in *Carex*, it is plausible.[2]

Representative Specimens: CANADA: MANITOBA: Road to Audey Lake, Riding Mountain National Park, *Lovaas 60-4033* (DAO); Mouth of AuAppelle River, *Macoun and Herriot 66629* (CAN); Wellman Lake, *Parker 2895* (CAN); Edward Creek, Riding Mountain National Park, *Scoggan 11338* (CAN).

SASKATCHEWAN: Candle Lake, *Boivin and Breitung 6243* (DAO); Farewell Creek, Cypress Hills, *Macoun 10743* (CAN); McKaque, *Breitung 15* (SASK); Mortlach, *Hudson 1680* (DAO); Cypress Hills Park, *Russell, Budd and Bolton 32* (SASK).

ALBERTA: 1 mile east of Waterton River Bridge, Waterton Lakes National Park, *Breitung 16528* (DAO); Porcupine Hills, August 18, 1915, *Malte s.n.* (CAN, DAO); Widewater, Lesser Slave Lake, *Moss 8267* (ALTA, DAO); Ma-Me-O Beach, *Turner 7833* (NA); Burnt Timber Creek Campground, Rt. 940, *Whitkus 2065* (ALTA).

BRITISH COLUMBIA: Lizard Creek, Fernie, *Bell and Davidson 7* (UBC); Okanagan, *Copley 8* (UBC); Above Gray Creek, *McCalla 8319* (ALTA, UBC); Vicinity of Buckinghorse River, Alaska Highway, *Raup and Correll 11597* (ALA, S, SASK, UBC); 87 km. northeast of McLeod Lake, Rt. 97, *Whitkus 1906* (ALTA).

YUKON TERRITORY: Fish Lake, 7 or 8 miles east of Whitehorse, *Calder 4663* (DAO); RCAF Station at Whitehorse, *Mitchell 128* (DAO, NA, S); Pine Creek, *Nowosad 142* (DAO); Vicinity of Pine Creek, Alaska Highway near Mile 1019, *Raup, Drury and Raup 13278* (ALA, CAN, S); Road to Fish Lake, 3.7 km. from Alaska Highway, by McIntyre Creek, Whitehorse, *Whitkus 1185* (ALTA).

UNITED STATES OF AMERICA: MONTANA: Rat Lake, 5 miles southeast of Squaw Creek Ranger Station, *Hitchcock and Muhlick 15243* (WTU); Ninemile Bridge, Rimrock Ridge, Little Belt Mts., *Hitchcock and Muhlick 12271* (RM); 15 miles north of Gibbons Pass, *Hitchcock, Rethke and van Raadshooven 3667* (RM).

WYOMING: Jenny Lake, Grand Teton National Park, *Bailey and Bailey 4243* (RM); Jackson Hole Wildlife Park, *Beetle 1628* (RM); Towner Lake, at

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[2] The vouchers for these two counts are not avaiable at this time but have been requested to check their identification.

Beaver House, 9 miles west of Centennial, *Hermann 17785* (RM); North Fork Road, 10 miles north-west of Centennial, *Porter and Porter 9205* (RM, SASK); 20 miles west of Big Piney, *Payson and Payson 2614* (RM).

COLORADO: Gunnison, *Baker 589* (RM); Lake Eldora, *Clokey 3219* (CAN, RM); Tolland, *Clokey 3682* (CAN, ORE, OSC, RM, S); Small lake one-quarter mile below Tolland, *Rameley and Robbins 6710* (RM); Headwaters of Pass Creek, *Rydberg and Vreeland 6453* (RM).

IDAHO: 25 miles east of Lowman, on Payette River, *Hitchcock and Muhlick 9784* (RM); Twilight Gulch, *MacBride 978* (RM); Mackay, *Nelson and Macbride 1541* (RM, S); Palisade National Forest, *Ryder 54* (RM).

UTAH: Marysvale, *Jones 5387* (RM); 2 miles north-west of Tony Grove Lake, near trail to Mt. Naomi, *Maguire 16096* (CAN); Lake Martha, 2 miles south of Brighton, *Maguire 17415* (CAN); Inlet, Tony Grove Lake, *Maguire, Hobson and Maguire 14239* (CAN); La Sal Mts., *Walker 262* (RM); Dixie Forest, head of Mill Caynon, *Woodbury 22* (RM).

NEVADA: Little Falls, Charleston Mts., *Clokey 5414* (RM); Rainbow Falls, Charleston Mts., *Clokey and Clokey 7035* (CAN, OSC, RM); Snake Range, Humboldt National Forest, *Holmgren and Reveal 1614* (OSC); Uintah and Ouray Indian Reservation, Florence Creek, *Holmgren, Reveal and La France 2324* (UBC).

ARIZONA: Black River, White Mts., *Gooding 582* (RM).

WASHINGTON: Chumstick Lookout, *Thompson 14963* (CAN).

Carex pachystachya Chamisso *ex* Steudel

Carex pachystachya Chamisso *ex* Steudel, Syn. Pl. Glum. 2 (Syn. Pl. Cyp.): 197. 1885.
C. festiva var. *pachystachya* (Cham. *ex* Steud.) Bailey, Mem. Torrey Bot. Club 1:51. 1889.
C. macloviana var. *pachystachya* (Cham. *ex* Steud.) Kükenth. in Engl. Pflanzenr. IV. 20 (Heft 38): 197. 1909
C. macloviana ssp. *pachystachya* (Cham. *ex* Steud.) Hultén, Fl. Alaska and Yukon 2: 138. 1942.
Type: Unalaska, Aleutian Islands, Alaska, *Chamisso s. n.* (LE?, holotype; GH!, isotype).

Carex festiva var. *gracilis* Olney *ex* W. Boott, in S. Wats. Bot. Calif. 2: 234. 1880.
C. multimoda L. H. Bailey, Bot. Gaz. 21: 5. 1896.
C. macloviana var. *gracilis* (Olney *ex* W. Boott) Kükenth. in Engl. Pflanzenr. IV. 20 (Heft 38): 197. 1909.
C. pachystachya var. *gracilis* (Olney *ex* W. Boott) Mackenzie, N. Amer. Fl. 18: 136. 1931.
Type: Oregon, 1871, *Hall 589* (BUF!, presumably an isotype).

Carex pyrophila Gandoger, Bull. Soc. Bot. France 60: 420. 1913.
Type: Kamtschatka Peninsula, Siberia, *Komarov 3286* (LE, holtype; photo, ALTA!; LY!, isotype).

Cespitose; culms stiff to ± lax, (1.5) 2.5-7.0 (11) dm tall, exceeding the leaves; leaves with well developed blades 2-6 per culm, clustered on lower 1/8 to 2/5 of culm, blades ± stiff to lax, straight or curved, (6.5) 9.0-18 (26.5) cm long, (1.5) 2.0-3.5 (4.1) mm wide; inflorescence ovoid to elliptic-ovoid, oblong-ovoid or wide-ovoid, (7.5) 10-19 (26) mm long, (7.5) 9-14 (16) mm wide, first internode up to 3 (7) mm long; spikes 3-8, loosely aggregate to aggregate, (4.0) 5.0-7.5 (9.0) mm long, 4.0-6.5 (8.0) mm wide, perigynia tips ascending to spreading within the spikes; bracts scale-like, concolorous with scales, lusterous, reddish to dark brown or coppery, acute to obtuse, the lowest ocassionally awned, the awn shorter than the inflorescence, margins concolorous with bract to narrow hyaline; scales lusterous, reddish to dark brown or coppery, 2.4-3.6 (4.3) mm long, 1.3-1.7 (1.9) mm wide, nearly as long as the perigynia, acute to obtuse, margins concolorous with scales to narrow white hyaline; anthers 1.0-2.0 mm long; perigynia lusterous, reddish to coppery-brown or nearly black, margins sometimes lighter or green, concavo-convex to plano-convex, ovate to elliptic-ovate, 3.0-4.5 (5.0) mm long, 1.3-1.9 (2.2) mm wide, margins winged to the base, often dark edged, serrulate-scabrous up to 2/3 of their length or more, 0.1-0.3 mm wide, dorsal nerves 5-11, faint to evident, ventral nerves 0-8, faint to evident, basal or some extending the length of the body of the perigynia, ventral folds 0-1, spongy filling present to abundant in base, beaks 1.1-1.8 (2.3) mm long, suture margins concolorous with beaks to narrow hyaline, beak tips (0.3) 0.5-0.9 (12) mm long, 1/3 to 3/5 (4/5) the length of the beaks, distance from the top of the achenes to the apex of the perigynia 1/2 or less than the overall length of the perigynia, apex concolorous with beaks or narrow hyaline, erose to bidentulate, the teeth up to 0.1 (0.2) mm long; achenes 1.4-1.6 (1.8) mm long, 0.9-1.3 mm wide, relatively large in comparison to the perigynia, filling up to 3/4 (4/5) of the body of the perigynia, stipes 0.3-0.5 mm long; n=37,38,39,41. (Figure 26).

Distribution: Occurring in Alaska on Unalaska Island, Kodiak Island, and the southeastern portion of the state, especially along the coast, although extending as far inland as the Alaska Range, in southwestern Yukon, northwestern British Columbia, and the Alaskan panhandle, the Queen Charlotte Islands and Vancouver Island, central and southern British Columbia, excluding most of the Fraser River drainage basin, east to the aspen parkland and foothills of Alberta, and disjunct in the Cypress Hills of Alberta and Saskatchewan. Growing in almost any moist or wet, open area, on clayey to gravelly soils, in meadows, marshy areas, depressions in open woods, on open slopes, lake and river banks and shores, or disturbed habitats such as talus slopes, ditches, roadsides, embankments, trails, clearings, logged areas, and gravel pits, in coastal

Figure 26. Type specimen of *Carex pachystachya* Cham. *ex* Steud.


ISO TYPE

to subalpine conditions from sea level to 1800 meters elevation (Figure 27). Found in similar habitats in the contiguous United States, from Idaho and Wyoming west to Washington, Oregon and California, up to 2700 meters elevation. Reported from Colorado by Hermann (1970), and from western Montana and Nevada by Cronquist (1977). Also found on the Kamtchatka Peninsula, commonly around hot springs (*C. pyrophila*) (cf. Hulten, 1927).

Discussion: The problems encountered with trying to recognize 'stubby' as a variety were also found in dealing with the variety *gracilis*. The variety was first proposed by Olney in 1872 under *C. festiva* (as a *nomen nudum*) and validly published by W. Boott in 1880. It was distinguished by its slender habit and oblong inflorescence. Bailey (1896) elevated the variety to specific status under the name *C. multimoda*, but this did not meet with much success, probably because of Bailey's vague description, and more likely because it could not be clearly distinguished from typical *C. pachystachya*. Mackenzie (1931-35) recognized the relationship between Olney's variety and *C. pachystachya* and placed it as a variety under that species. However, Mackenzie stated the following in his short note on the variety: "it (var. *gracilis*) is often well marked and distinct in appearance, but it is connected with the higher mountain plant (typical *C. pachystachya*) by a perplexing series of intermediate plants, and I have so far found no constant differences' (l.c.: 136; parentheses mine). Thus, Mackenzie ran into the same dilemma as I did with 'stubby'. For the same reasons, therefore, the variety *gracilis* has not been considered taxonomically distinct from *C. pachystachya*.

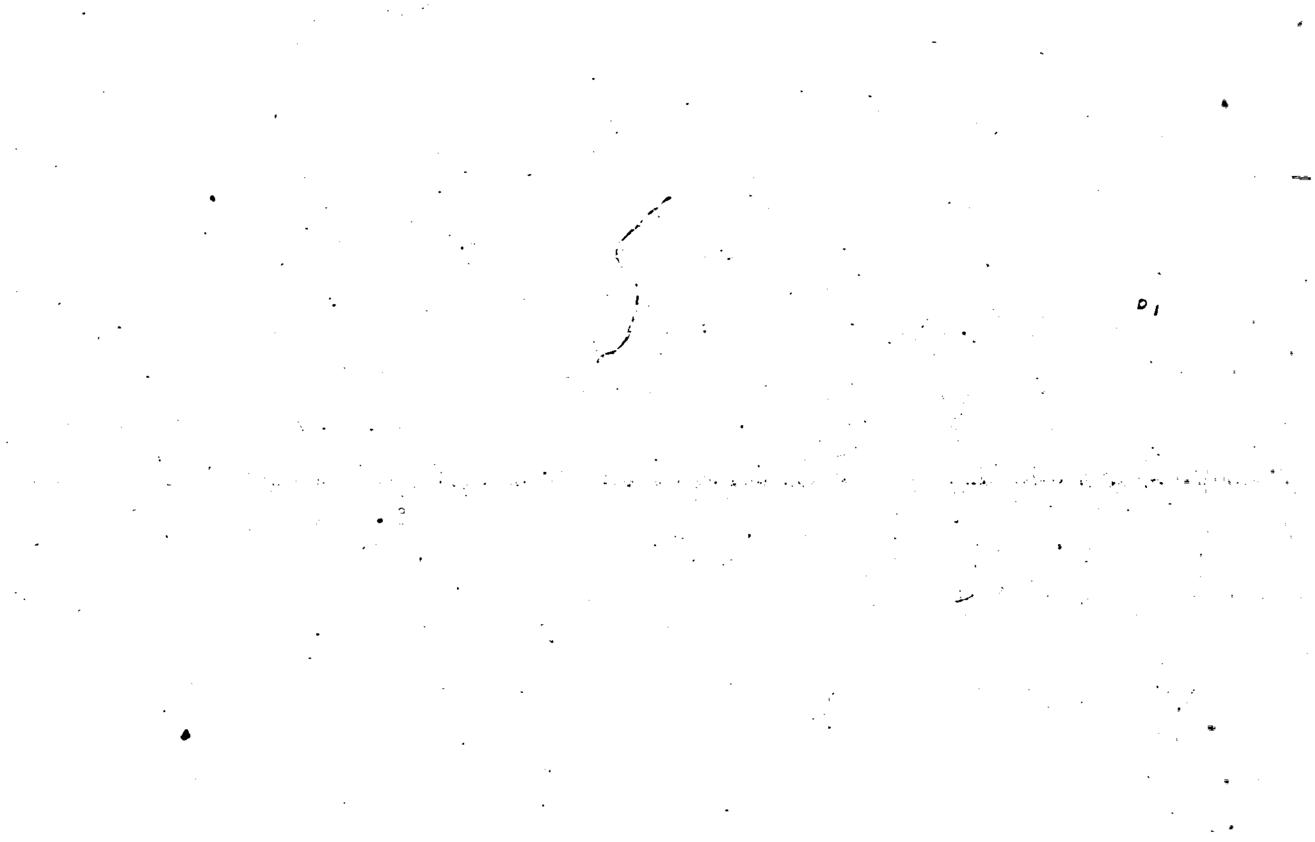
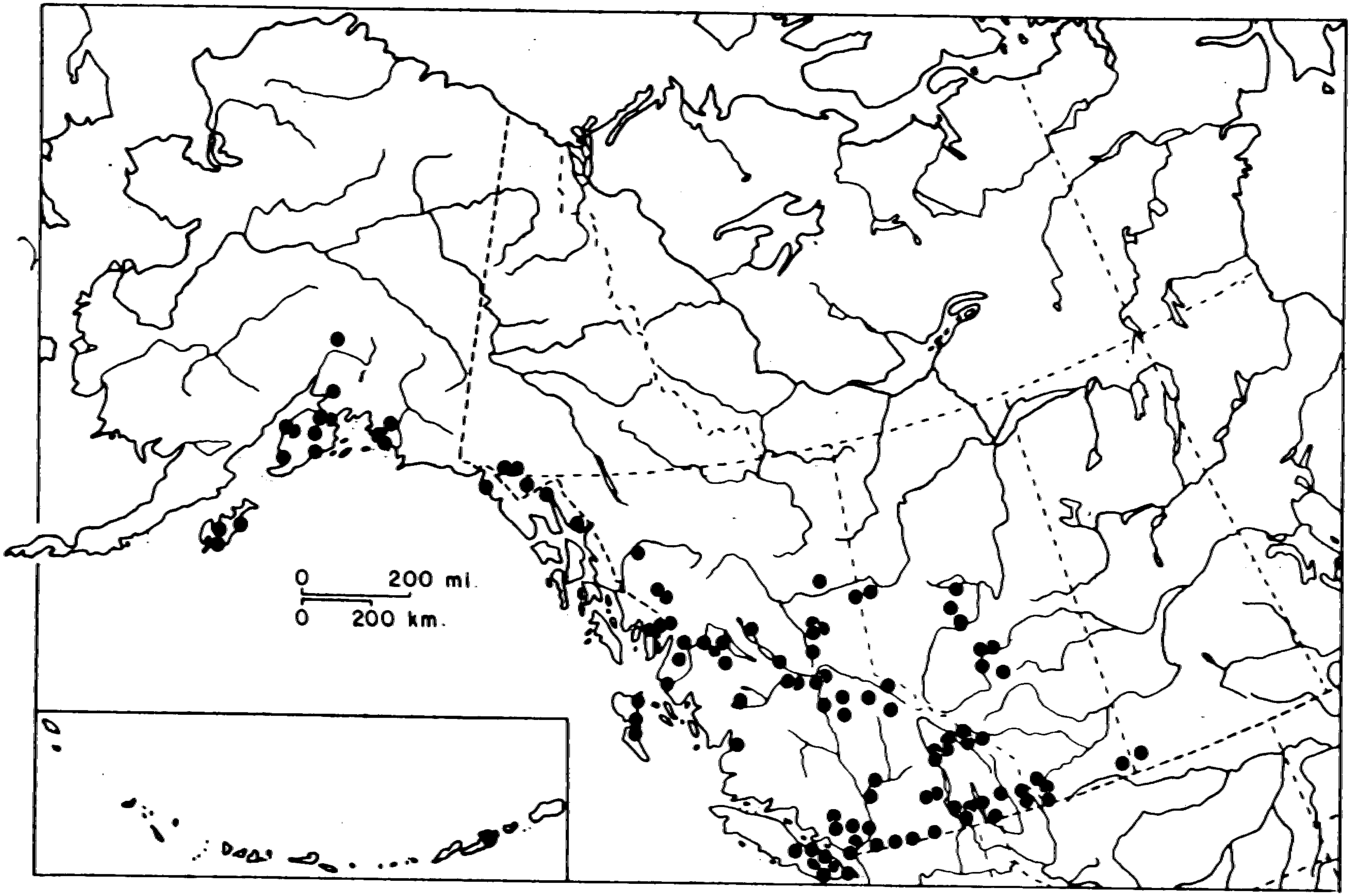


Figure 27. Distribution of *Carex pachystachya* (including 'stubby') for western Canada and Alaska.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From other members of the aggregate, the species is distinguished by the lusterous scales and perigynia, and more or less elongate inflorescence in which the perigynia tips are ascending to spreading. It shows the greatest amount of similarity to *C. macloviana,* but is distinguished from that species by those features discussed under *C. macloviana* and in the section of the taxonomy of the group.

This is a very variable species which may be a species complex in itself, and shows some similarities with the Cascadian and Californian species of Mackenzie's 'Festivae' category. Further investigation is needed to elucidate the relationship between *C. pachystachya* and these other species (i.e. *C. subfusca, C. teneraformis, C. mariposana, C. integra*). and to understand the biological reasons for its morphological and cytological variability.

This is the only member of the aggregate which shows a preference for coastal conditions. Aside from the factors which affect the distribution of the group as a whole, *C. pachystachya* may also have a requirement for either greater precipitation or humidity.

Representative Specimens: CANADA: SASKATCHEWAN: Cypress Hills, *Brietung 4355* (DAO); Cypress Hills, *Fraser 25* (NA); Cypress Hills, July 23, 1941, *Ledingham s.n.* (DAO); Cypress Hills, *Newsom 493-64* (SASK).

ALBERTA: Entwistle, *Hermann 12739* (ALTA); Lake Louise, *Malte 107692* (CAN, DAO); Dutch Creek, Livingston Valley, *Malte 107905* (CAN, DAO); Wabamun, *Moss 506* (ALTA, CAN); One-half mile west of Buck Lake, *Turner 7787* (ALTA, NA).

BRITISH COLUMBIA: Victoria, *Anderson 524* (UBC); Glacier, *Brown 633* (S); Imperial Street, West Point Gray, *Eastham 8935* (DAO, UBC); Hazelton, Skeena River, *Macoun 97980* (CAN); 129 km. south of Haines Jt. on Haines Road, *Whitkus 1681* (ALTA).

YUKON TERRITORY: Onion Lake, 46 miles south of Haines Jt., Kluane National Park, *Douglas and Douglas 7098* (ALA).

UNITED STATES OF AMERICA: ALASKA: Mendenhall, Juneau, *Anderson 6198* (ALA, CAN, DAO, RM, S, WTU); Between Lost and Situk River mouths, *Baten and Murphy 77-190* (ALA); 2 miles north of Steward, Kenai Peninsula, *Calder 6615* (ALA, DAO); Port Hobron, Kodiak Island, *Eyerdam 92* (CAN, S); Milepost 2 on road to Hope, Kenai Peninsula, *Whitkus 1497* ALTA).

WYOMING: Little Snake River, *Goodding 1718* (RM); Jackson Hole, *Williams 310* (RM).

IDAHO: 1 mile west of Bovill-Elk Rivers summit, *Cronquist 5881* (CAN, S).

WASHINGTON: Upper valley of the Nesqually River, *Allen 164* (RM); Deer Lake, Olympic National Park, *Eyerdam 6328* (CAN); Stevens Pass region, August, 1929, *Grant s. n.* (S); 20 miles west of Colville, *Hitchcock 17630* (WTU); Flat above Trapper Creek, Wind River Valley, *Ingram 1833* (ORE, OSC).

OREGON: Mt. Head, *Eastwood and Howell 3545* (S); Soda Meadow, *Ireland 2673* (ORE); Breitenbush Hot Springs trail, *Leach 4444* (ORE); Loewi, *Nelson 2212* (OSC); Near Mackenzie Pass, 7 miles west of summit of Cascade Mts., *Peck 9808* (OSC).

CALIFORNIA: Drakes Bad, *Howell 35653* (OSC); Drakes Bad, *Howell 359858b* (OSC).

Doubtful or Excluded Taxa

Carex microptera var. *crassinerva* F. J. Hermann, Rhodora 70: 240. 1968.

Type: Basin below Engineer Pass, Ouray County, Colorado, *W. M. Johnson 594* (US!, holotype).

Hermann (1968) distinguished the taxon on the basis of several strong nerves on the ventral side of the perigynia. Although the type is quite distinct in this character, the degree of the ventral nerves has been shown to be variable for all the species in the aggregate. In light of the difficulty that has been encountered in recognizing a variety in this aggregate, and as Hermann (1970) noted that the variety is infrequent, its status is doubtful. However, until further work is done on this taxon in Colorado where a number of problems have been uncovered (see discussion under *C. haydeniana* and *C. microptera*), it is not combined with *C. microptera*.

Carex olympica Mackenzie, Bull. Torrey Bot. Club 43: 610. 1916.

Mackenzie was normally very careful in noting the type of the species he described. However, for this species, he did not designate a type, and so the 17 specimens that he listed are syntypes. In his 1931-35 monograph, Mackenzie synonymized *C. olympica* and *C. pachystachya* var. *gracilis*, and noted the type ~~for~~ *C. olympica* came from the state of Washington. The only specimen from Washington that was collected in the Olympic Mountains (and presumably gave the name to the species) is *Elmer 2700* (ORE!, NY!), however, examination of this specimen shows that it is *C. preslii*, a species recognized by Mackenzie. Mackenzie (1916) noted the similarity between *C. preslii* and *C. olympica*, but separated the two by the reddish color of the scales and perigynia tips of *C. olympica*. However, *C. preslii* varies in color and can have either reddish or brownish scales and perigynia tips. Because of the ambiguity of the type for *C. olympica*, and since all of the syntypes from Washington could not be located and compared with the original description, the inclusion of this name in the aggregate is considered doubtful.

Carex pachystachya var. *monds-coulteri* Kelso, Biol. Leafl. 64: 2. 1953.
   C. pachystachya f. *monds-coulteri* (Kelso) F. J. Hermann, Leafl. W. Bot. 9: 16. 1959.
Type: Not located. Aspen, Pitkin County, Colorado, *Kelso 6662*.

The same problem in recognizing other varieties in *C. pachystachya* applies here. However, since the type was not seen, a decision could not be reached concerning the status of this taxon.

SUMMARY

The present investigation treats the *Carex macloviana* aggregate in a manner intermediate to those proposed in the past. Neither a single species, with numerous infraspecific taxa, as proposed by Kukenthal (1909), nor numerous, poorly delimited species, as proposed by Mackenzie (1931-35) has been recognized. Instead, grouping of taxa which failed to show consistent discontinuity in several rigorous morphological analyses, and continued recognition of taxa which maintained their idenity through the same analyses, as well as additional evidence from geographic distribution, ecological preferences and chromosome numbers, resulted in recognition of four species in western Canada and Alaska. Figure 28 presents a summary of this information. *Carex microptera* is expanded to encompass *C. festivella* and *C. limnophila.* Although it might be argued that the two latter taxa should be maintained at least at an infraspecific rank, evidence from this study failed to indicate a discontinuity in the continuum of morphological variation between them and "typical" *C. microptera.* *Carex haydeniana* possesses a number of similarities to *C. microptera*, but is maintained as a separate species until further evidence can show that there is a genetical base to these similarities. *Carex macloviana* and *C. pachystachya* are similar to one another as well, but maintain themselves, despite the opportunities the two species have for interbreeding (i. e. microsympatry).

Anyone who has intensely studies a group of organisms, and who has an interest in evolutionary theory, accumulated evidence naturally leads to speculation of the historical aspect of those organisms. For the present investigation, information for historical reconstruction may be viewed as inadequate, but certain lines of evidence provide a

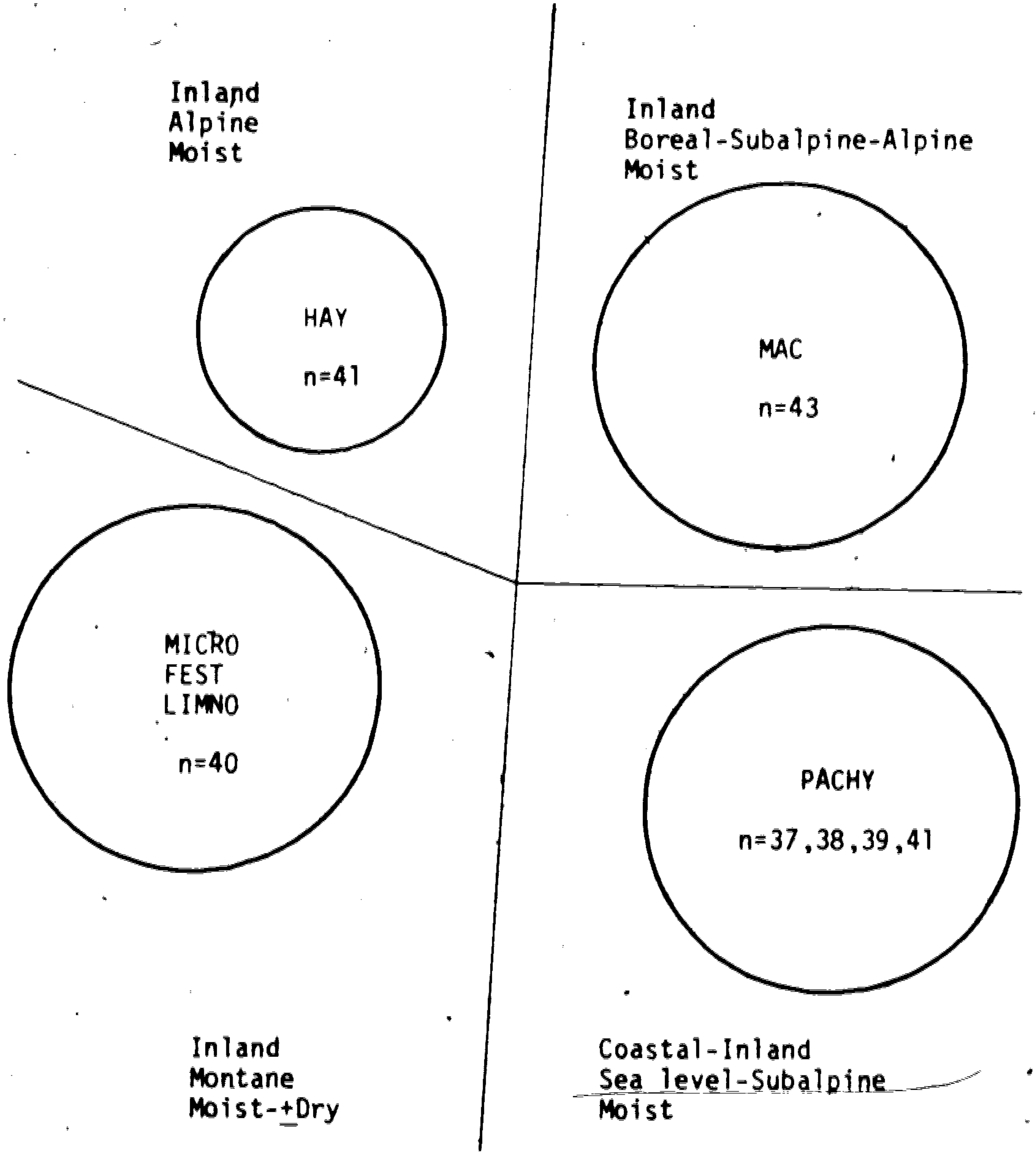

Figure 28. Summary of phenetic relationships, geographic distribution, ecological preferences and chromosome numbers for taxa of the *Carex macloviana* aggregate in western Canada and Alaska. Size of circles approximates the relative abundance of each species.

basis for some deductions. Low chromosome numbers, chromosome variability and morphological variability, suggest *Carex pachystachya* may be similar to, if not the progenitor, of the aggregate. From this species, fragmentation of chromosomes and reduction of morpholocical variability seems to follow a trend through *C. microptera, C. haydeniana* and *C. macloviana*. the problem with this trend is *C. macloviana* which is most similar to *C. pachystachya* on a morphological basis, and is the most widespread species in the aggregate. Younger species might be expected to occupy a smaller area, although they do not necessarily have to diverge a great deal from an ancestral species, expecially if they are directly descended from the progenitor. Actually, the progression of evolution within the aggregate is by no means fully understood, though *C. pachystachya* appears to be closest to the ancestral species.

Additional historical information can be drawn from the ecology of the group. All members of the aggregate perfer open, seral habitats, and occur frequently in mountainous regions, especially in the contiguous United States. Taken in conjunction with the diversity of the aggregate in western North America, and the fact that the species are very similar to one another, the following interpretation is plausible. During the Pleistocene glaciation, the ancestor of the aggregate existed in one of the refugial areas of the Rocky Mountains, or south of the ice sheet. With the retreat of the ice sheet at about 20,000 y.b.p., vast open areas became avaiable for plant establishment. Along with these open areas, the mountainous terrain provided a number of different environmental conditions which resulted in different selective pressures. With the opening of new areas, the progenitor of the group could have rapidly expanded into many different areas. This rapid expansion, along with varying selective pressures, may have been the impetus for the divergence of populations and establishment of discreet taxa. This proposal provides an explanation for two notable features present in the aggregate. First, the small amount of morphological differences among the various taxa may be a result of recent divergence (20,000 y.b.p.) without a concomitant loss of all intermediate forms (the 'stubby' form of *C. pachystachya*, for example). Second, the preference of the species for not only seral habitats, but glaciated regions as well. In Canada and Alaska, the aggregate is almost totally confined to glaciated areas (which precludes any likelihood of survival north of the ice sheet), while in the contiguous United States, it is generally restricted to mountainous areas where mountain glaciation was known to have occurred. Since the Pleistocene, the aggregate has expanded beyond the glaciated areas, but only to a limited degree: even *C. macloviana* occurs only in glaciated region of Greenland, Iceland, northwest Europe and South America.

Although this study in not complete, it has thoroughly examined the aggregate on a morphological level and provides a treatment which can be tested by other lines of investigation. Chemical studies can provide one means of testing, but crossing experiments would be the definitive test of the valididy of the proposed species. More cytological work on *Carex pachystachya* may provide an understanding of its variability in chromosome number, which may, in turn, explain its morphological variability. Further work in also needed on the two species complexes which are related but geographically peripheral to the aggregate, i. e. the *C. pachystachya-C. subfusca-C. teneraformis-C. mariposana-C. intergra* group, and the *C. microptera-C. haydeniana-C.*

ebenea group. A thorough understanding of all these species may not be attained, but it is felt that research towards this goal will not only contribute to a better understanding of the genus *Carex*, but may also provide information of taxa that have recently diverged and the processes involved.

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APPENDIX 1. SYNONYMY OF THE GENUS *Carex**

Carex Linnaeus, Sp. Pl. 972. 1753.

Ulva Adans. Fam. Pl. 2:496. 1763.
Physiglochis Neck. Elem. 3:245. 1790.
Cyperoides Tourn. Elem. Augm. 3:196. 1797.
Schelhammeria Moench, Meth. Suppl. 119. 1802.
Triplima Raf. Am. Mo. Mag. 4:195. 1819.
Scuria Raf. Jour. de Phys. 89:106. 1819.
Triodex Raf. Jour. de Phys. 89:106. 1819.
Vignea Beauv. in Lestib. Ess. Fam. Cyp. 22. 1918.
Trasus S. F. Gray, Nat. Arr. Brit. Pl. 2:53. 1821.
Phyllostachys Torr. Ann. Lye. N. Y. 3:404. 1836.
Olotrema Raf. Good Book 25. 1840.
Loxotrema Raf. Good Bood 25. 1840.
Loxanisa Raf. Good Book 25. 1840.
Anithista Raf. Good Book 26. 1840.
Edritria Raf. Good Book 26. 1840.
Olamblis Raf. Good Book 26. 1840.
Facolos Raf. Good Book 26. 1840.
Dewbya Raf. Good Book 26. 1840.
Diemisa Raf. Good Book 27. 1840.
Onkerma Raf. Good Book 27. 1840.
Loncoperis Raf. Good Book 27. 1840.
Kolerma Raf. Good Book 27. 1840.
Temnemis Raf. Good Book 27. 1840.
Neskiza Raf. Good Book 27. 1840.
Osculisa Raf. Good Book 27. 1840.
Itheta Raf. Good Book 28. 1840.
Forexeta Raf. Bood Book 28. 1840.
Maukschia Heuffel, Flora 27:527. 1844.
Psyllophora Heuffel, Flora 27:528. 1844.
Leucoglochin Heuffel, Flora 27:528. 1844.
Callistachys Heuffel, Flora 27:528. 1844.
Genersichia Heuffel, Flora 27:528. 1844.
Cryptoglochin Heuffel, Flora 27:528. 1844.
Pseudocarex Miq. Ann. Mus. Lugd. Bat. 2:146. 1865.
Vignantha Schur. Enum. Pl. Transsilv. 705. 1866.
Neilreichia Kotula. Spraw. Kom. Fizyogr. Krakow 17:136. 1883.
Caricina St. Lag. in Cariot. Etude Fl. ed. 8. 2:854, 872. 1889.
Caricinella St. Lag. in Cariot. Etude Fl. ed. 8. 2:855, 880. 1889.
Echinochlaenia Borner. Abh. Nat. Ver. Bremen 21:265. 1913.
Dapedostachys Borner. Abh. Nat. Ver. Bremen 21:265. 1913.
Kukenthalia Borner. Abh. Nat. Ver. Bremen 21:266. 1913.
Proteocarpus Borner. Abh. Nat. Ver. Bremen 21:266. 1913.
Limivasculum Borner. Abh. Nat. Ver. Bremen 21:268. 1913.
Bitteria Borner. Abh. Nat. Ver. Bremen 21:269. 1913.
Manochlaenia Borner. Abh. Nat. Ver. Bremen 21:271. 1913.
Lamprochlaenia Borner. Abh. Nat. Ver. Bremen 21:272. 1913.
Rhaptocalymma Borner. Abh. Nat. Ver. Bremen 21:272. 1913.

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*Based on Mackenzie(1931-35)

Rhynchopera Borner. Abh. Nat. Ver. Bremen 21:272. 1913.
Leptovignea Borner. Abh. Nat. Ver. Bremen 21:273. 1913.
Desmiograstis Borner. Abh. Nat. Ver. Bremen 21:274. 1913.
Thysanocarex Borner. Abh. Nat. Ver. Bremen 21:274. 1913.
Indocarex Borner. Abh. Nat. Ver. Bremen 21:275. 1913.
Vignidula Borner. Abh. Nat. Ver. Bremen 21:275. 1913.
Chionanthula Borner. Abh. Nat. Ver. Bremen 21:275. 1913.

APPENDIX 2. FORMULAE FOR STATISTIC AND NUMERICAL ANALYSES

Statistics

Mean (unbiased population estimate):

$$\overline{X} = S\ X\ /\ n,$$

where S is sigma, X the sample values, and n the sample size.

Standard deviation (unbiased population estimate):

$$s = [S(X-\overline{X})^2\ /\ n-1]^{1/2},$$

where n-1 is the degrees of freedom for the sample.

Standard error of the mean (unbiased population estimate):

$$\text{s.e. } \overline{X} = s\ /\ n^{1/2},$$

where s is the unbiased estimate of the population standard deviation.

Coefficient of variation:

$$\text{C.V.} = 100\ s\ /\ \overline{X}.$$

Similarity Coefficient

TAXMAP: The distance coefficient, which is the complement of similarity (Dist. = 1-Sim.), is calculated as the relative difference (D(i,j)) between the i-th and j-th OTU's:

$$D(i,j) = S[(d(i,j)k) \times W(k)]\ /\ S[W(k)],\ k = 1 \text{ to } n,$$

where S is sigma, d(i,j) the relative difference between the i-th and j-th OTU's for character k (see below), and W the weight of character k (see below).

The relative difference, d(i,j), between the i-th and j-th OTU's for a single character is given as:

$$d(i,j) = X(i) - X(j)\ /\ [X(\max) - X(\min)],$$

where X represents the states of the character. The difference between the two states is divided by the range of the character states to initally ensure each character has equal weight.

The weight of of a character is equal to its relative information content (I), which, for continuous, quantitative characters is given as:

$$I = \mathrm{Log2}(n),$$

where n is one more than the number of 95% confidence intervals in each character. In this study, the size of the 95% confidence interval was chosen as the largest power of 10 contained by a character. Thus, if the minimum and maximum values observed for a character are 2.5 and 37.9, respectively, the size of the 95% confidence interval is 10. With a range of 35.4, there are 3.54 confidence intervals, giving an n of 4.54 for the character, and an I of 2.18.

CLUSTAN: The correlation coefficient (r),which is a measure of similarity between two OTU's, is given as:

$$r(i,j) = \frac{S[(X(i) - \overline{X}(i))k \times (X(j) - \overline{X}(j))k]}{[S(X(i) - \overline{X}(i))^2 k \times S(X(j) - \overline{X}(j))^2 k]^{1/2}}, \quad k = 1 \text{ to } n,$$

where X is the character state value of the i-th OTU for character k, and $\overline{X}$ the mean of all character state values of OTU i. To ensure equal weighting of all characters, the raw values were standardized to give each character a mean of 0 and a standard deviation of 1.

APPENDIX 3. DATA MATRIX FOR 191 OTU's

```
TYPE01   0950407061731508012157095272405[illegible]3055092028
TYPE02   26003371321325164820153[illegible]3328
TYPE03   28703091323426091281[illegible]330
TYPE04   1810611162833111720185[illegible]218
TYPE05   13605541426429144252281[illegible]017
TYPE06   20307451325430152281432[illegible]013
TYPE07   20307551625331162251571[illegible]018
TYPE08   3200067081922004825115[illegible]013
TYPE09   10004861323336132201571[illegible]016
TYPE10   0650312091943307225125[illegible]022
MICRO01  134051116304411462517[illegible]16353072016
MICRO02  263025711254270329132[illegible]017
MICRO03  298042013254254325[illegible]020
MICRO04  2110722182543315427153[illegible]016
MICRO05  2940396132132812514212[illegible]018
MICRO06  1120516122271281[illegible]018
MICRO07  2850381342133308525138[illegible]022
MICROA1  1304751231429124251[illegible]4021
MICROA2  1290453152843008325143[illegible]2016
MICROA3  1530643193153515228158[illegible]8016
MICROA4  188035312223251172516014591[illegible]1019
MICROA5  187062417273311482516315515[illegible]8019
MICROA6  870051115213171822813312514[illegible]8016
MICRO[illegible]3020
MICRO[illegible]1017
MICRO[illegible]1017
MICRO[illegible]1017
MICRO[illegible]1018
MICRO[illegible]8024
MICRO[illegible]5019
MICROC[illegible]41740304102942213301[illegible]73021
MICROC[illegible]5165034511193241271381371[illegible]78014
MICROC[illegible]178134131121521688251182513150[illegible]76022
MICROC[illegible]1704302540922322362251181181311053057482027111013102361[illegible]75022
MICROC[illegible]124407151924416181[illegible]1017
MICROC[illegible]2182075213234161833015814314081572702511101010141471423022308020601317032505101321140805024051320051056017
HAYA01   05001701223429055301571631412067960273015102018145242004200901051010051805201020151006029040028015067014
HAYA02   103038113273331032825133341406309355203717202017152273200320070253510130021051015221711060270403024042071018
HAYA03   06402141221526085301231421108050075882034131010151461920032008027572310031904101723140905030041021036074014
HAYB01   037017209243160582813313015140600684820121320101714917200320083174710100023061020201408060220470326079065013
HAYB02   09703951328626091301551431312053097752048141010161651923042008023601017003104101715151007025048013040074012
HAYB03   10003891426430092301681781409063088772042141013171571720032007330301012002605101012150908026046019040074014
HAYB04   07703481430629080301631681500870082622039142015191611723032009023533030002503101015150805022041012030064012
HAYMIC01 08103311118325083251301101511053072432033131710161451420022009030532030001905101318150905024042026052073021
HAYMIC02 05502511017223080281331201814050070482033121310172411420022709030473030001905101025150904022046026061080024
LIMNOA01 09804521431533127281401421713057072552029171023141361523023009332772010001603101025130803022044019047081019
LIMNOA02 08804061433441124251421421115080067552528111027122361523022009013571013001604101323110803014044025040078016
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LIMNOB02 20008851429436152251811732015087082652528131020151431827032008710771013002105172725151004023049024057065019
LIMNOB03 09104121426433125271451421617070078622530131010102239172302200801367101010190713202014100402204903705407702 1
LIMNOB04 16206551632529144251481251412085070532028161010111138162702200801353171003190510172513090402505002605107401 9
LIMNOB05 05802710924420146231601083019070060472026111010102235152303270831347101000170210133012080302104901205907401 8
LIMNOB06 10704571223526158281371351510063067602528111320131301623032307710571010071805102025131004023047028065074021
LIMNOB07 05702501329424063281301131510063063432528111317142237153003200833057301007117031017271308030220460180530760 17
LIMNOB08 11704801427525088251581501520070073602529121013122401623022007317572310071908101725140904024048042050073020
LIMNOB09 12405351728331106251421301622063070582528111010151391523022009030573010001906102725130804023049032044072016
LIMNOC01 07602370825522161281130971413043057482025101013102341620022307713501010001503131330120903022047019050074020
LIMNOC02 06002880816423125231130981611048050432024101010132361527022008717631010031806102027130804021050033053067019
LIMNOC03 08803831123428096251151051210057055452025101020102291223012006010511310071304131325120703023045031053086024
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LIMNO004 130055212251331232512812512112730725120291110131013815200220070306320130118361017251308030200470330413076018
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FEST01   18916631625332215251751621751618    4 11253111101010140172003200971773201707220410131130904028050020053078017
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APPENDIX 4. DATA MATRIX FOR 7 OTU'a

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APPENDIX 5. STATISTICS OF THE 47 QUANTITATIVE CHARACTERS

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#1	*PACHY*	94	3.3-27.9	12.25	5.62	0.58	45.9
	STUB	17	4.6-16.2	9.19	3.78	0.92	41.1
	MAC	39	2.7-13.5	7.45	3.04	0.49	40.8
	FEST	14	6.9-20.0	12.58	4.36	1.17	34.7
	LIMNO	16	5.7-20.0	10.10	3.88	0.97	38.5
	HAY	7	3.7-10.3	7.54	2.61	0.99	34.6
	MICRO	26	4.0-24.4	11.69	5.82	1.14	49.8
#2	*PACHY*	94	16.4-107.3	47.61	18.53	1.91	38.9
	STUB	17	19.1-65.8	37.72	12.89	3.13	34.2
	MAC	39	9.5-58.6	32.36	12.04	1.93	37.2
	FEST	14	37.6-75.8	51.30	12.06	3.22	23.5
	LIMNO	16	23.7-88.5	44.53	17.25	4.31	38.7
	HAY	7	17.0-39.5	26.56	10.52	3.97	35.6
	MICRO	26	25.4-78.3	47.73	16.52	3.24	34.6
#3	*PACHY*	94	0.8-2.1	1.33	0.30	0.03	22.6
	STUB	17	0.8-1.6	1.15	0.24	0.06	20.9
	MAC	39	0.8-2.1	1.31	0.27	0.04	20.3
	FEST	14	1.0-2.2	1.44	0.28	0.07	19.2
	LIMNO	16	0.8-1.7	1.24	0.27	0.07	22.1
	HAY	7	0.9-1.4	1.26	0.17	0.06	13.7
	MICRO	26	0.9-1.9	1.33	0.28	0.06	21.3

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#4	*PACHY*	94	1.2-3.2	2.23	0.43	0.04	19.4
	STUB	17	1.6-2.7	2.15	0.31	0.07	14.3
	MAC	39	1.6-3.6	2.52	0.46	0.07	18.1
	FEST	14	2.0-4.7	2.71	0.67	0.18	24.6
	LIMNO	16	1.6-3.3	2.66	0.43	0.11	16.0
	HAY	7	2.1-3.0	2.56	0.31	0.12	12.1
	MICRO	26	1.9-3.1	2.45	0.32	0.06	13.1
#5	*PACHY*	94	2.0-6.0	3.56	0.87	0.09	24.5
	STUB	17	2.0-5.0	3.41	0.71	0.17	20.9
	MAC	39	2.0-6.0	4.05	0.97	0.16	24.0
	FEST	14	3.0-5.0	3.86	0.77	0.21	20.0
	LIMNO	16	3.0-5.0	4.13	0.72	0.18	17.4
	HAY	7	3.0-6.0	4.43	1.27	0.48	28.7
	MICRO	26	3.0-7.0	3.77	0.91	0.18	24.1
#6	*PACHY*	94	1.5-4.1	2.84	0.60	0.06	21.1
	STUB	17	2.1-3.6	2.69	0.40	0.10	14.8
	MAC	39	1.6-3.9	2.80	0.51	0.08	18.3
	FEST	14	2.3-3.9	2.98	0.45	0.12	15.1
	LIMNO	16	2.0-4.1	2.88	0.62	0.15	21.5
	HAY	7	1.6-3.3	2.70	0.54	0.20	20.1
	MICRO	26	2.1-4.1	3.02	0.50	0.10	16.6

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#7	*PACHY*	94	6.5-26.4	13.45	4.38	0.45	32.6
	STUB	17	7.1-18.9	12.59	3.37	0.82	26.7
	MAC	39	4.0-17.9	9.05	3.07	0.49	34.0
	FEST	14	8.4-22.9	14.26	4.65	1.24	32.6
	LIMNO	16	6.3-16.1	12.29	2.65	0.66	21.6
	HAY	7	5.5-10.3	8.06	1.79	0.68	22.2
	MICRO	26	6.2-21.0	12.94	4.10	0.80	31.7
#8	*PACHY*	94	1.2-2.5	2.03	0.24	0.03	12.1
	STUB	17	2.0-2.5	2.19	0.23	0.06	10.4
	MAC	39	1.7-2.5	2.01	0.18	0.03	9.1
	FEST	14	2.0-3.0	2.32	0.34	0.09	14.5
	LIMNO	16	2.0-2.8	2.53	0.22	0.05	8.6
	HAY	7	2.8-3.0	2.94	0.10	0.04	3.3
	MICRO	26	2.5-3.0	2.63	0.19	0.04	7.4
#9	*PACHY*	94	10.8-25.8	15.63	2.47	0.25	15.8
	STUB	17	7.8-15.2	12.07	1.89	0.46	15.7
	MAC	39	9.8-20.3	15.35	2.70	0.43	17.6
	FEST	14	13.2-20.0	16.02	2.17	0.58	13.6
	LIMNO	16	11.3-18.3	14.21	2.13	0.53	15.0
	HAY	7	12.3-20.5	15.77	2.64	1.00	16.8
	MICRO	26	11.2-17.5	14.20	1.49	0.29	10.5

CHARACTER	TAXON	N	RANGE	$\overline{X}$	S.D.	S.E.$\overline{X}$	C.V.
#10	*PACHY*	94	8.7-15.8	11.82	1.54	0.16	13.0
	STUB	17	7.7-13.0	10.57	1.50	0.36	14.1
	MAC	39	8.2-18.3	12.32	1.88	0.30	15.2
	FEST	14	12.3-16.8	14.22	1.47	0.39	10.3
	LIMNO	16	9.7-17.3	12.71	2.11	0.53	16.6
	HAY	7	13.0-17.8	15.10	1.86	0.70	12.3
	MICRO	26	10.5-15.5	12.91	1.29	0.25	10.0
#11	*PACHY*	94	1.0-7.0	2.07	0.82	0.08	39.5
	STUB	17	0.7-2.0	1.31	0.32	0.08	24.7
	MAC	39	1.3-3.7	2.04	0.61	0.10	30.0
	FEST	14	1.0-2.0	1.51	0.35	0.09	23.0
	LIMNO	16	1.1-3.0	1.67	0.53	0.13	31.6
	HAY	7	1.1-3.4	1.66	0.78	0.29	47.1
	MICRO	26	1.3-3.0	1.61	0.35	0.07	21.9
#12	*PACHY*	73	0.8-3.5	1.79	0.57	0.07	31.6
	STUB	17	0.8-1.8	1.25	0.33	0.08	26.6
	MAC	39	0.7-3.0	1.50	0.44	0.07	29.7
	FEST	13	0.7-1.8	1.31	0.36	0.10	27.7
	LIMNO	16	1.0-2.2	1.43	0.42	0.10	29.2
	HAY	7	0.8-1.4	1.10	0.26	0.10	24.1
	MICRO	26	0.8-2.0	1.25	0.33	0.66	26.7

CHARACTER	TAXON	N	RANGE	$\overline{X}$	S.D.	S.E.$\overline{X}$	C.V.
#13	*PACHY*	94	3.0-7.3	5.48	0.91	0.09	16.6
	STUB	17	3.3-6.7	5.04	1.17	0.28	23.2
	MAC	39	3.0-8.0	5.37	0.96	0.15	17.9
	FEST	14	5.7-10.0	7.28	1.42	0.38	19.6
	LIMNO	16	4.3-8.5	6.59	1.17	0.29	17.8
	HAY	7	5.0-7.0	6.14	0.75	0.29	12.3
	MICRO	26	4.0-8.7	6.55	1.03	0.20	15.8
#14	*PACHY*	94	4.7-9.0	6.68	0.81	0.08	12.1
	STUB	17	4.2-7.5	5.92	0.81	0.20	13.6
	MAC	39	5.7-10.5	7.34	1.03	0.16	14.0
	FEST	14	6.5-9.3	7.51	0.83	0.22	11.1
	LIMNO	16	5.0-8.2	6.69	0.91	0.23	13.5
	HAY	7	6.8-9.7	8.47	1.03	0.39	12.2
	MICRO	26	5.5-7.5	6.53	0.59	0.12	9.0
#15	*PACHY*	94	4.2-8.0	5.82	0.64	0.07	11.0
	STUB	17	4.2-5.7	4.94	0.48	0.12	9.7
	MAC	39	3.3-6.8	5.21	0.65	0.10	12.4
	FEST	14	5.2-6.3	5.67	0.37	0.10	6.6
	LIMNO	16	4.3-6.5	5.33	0.67	0.17	12.7
	HAY	7	4.8-7.7	6.36	1.05	0.40	16.5
	MICRO	26	4.7-7.0	5.62	0.53	0.10	9.5

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#16	*PACHY*	94	2.0-3.0	2.51	0.36	0.04	14.5
	STUB	17	2.0-2.5	2.21	0.25	0.06	11.5
	MAC	39	1.5-2.0	1.99	0.08	0.01	4.0
	FEST	14	2.0-2.5	2.25	0.26	0.08	11.5
	LIMNO	16	2.0-2.5	2.22	0.26	0.06	11.6
	HAY	7	2.0	2.00	--	--	--
	MICRO	26	2.0-2.5	2.27	0.25	0.05	11.2
#17	*PACHY*	94	2.7-4.3	3.28	0.32	0.03	9.8
	STUB	17	2.4-3.2	2.75	0.21	0.05	7.7
	MAC	39	2.7-4.0	3.24	0.26	0.04	7.9
	FEST	14	2.5-3.5	2.90	0.25	0.07	8.7
	LIMNO	16	2.4-3.5	2.80	0.25	0.06	8.9
	HAY	7	3.0-4.8	3.74	0.62	0.23	16.6
	MICRO	26	2.4-3.2	2.78	0.20	0.04	7.3
#18	*PACHY*	94	1.3-1.9	1.50	0.11	0.01	7.3
	STUB	17	1.3-1.9	1.51	0.16	0.04	10.4
	MAC	39	1.1-1.5	1.32	0.11	0.02	8.2
	FEST	14	1.0-1.5	1.19	0.21	0.06	17.5
	LIMNO	16	1.0-1.7	1.22	0.24	0.06	19.7
	HAY	7	1.3-1.7	1.43	0.14	0.05	9.7
	MICRO	26	0.9-1.3	1.07	0.11	0.02	9.9

CHARACTER	TAXON	N	RANGE	$\overline{X}$	S.D.	S.E.$\overline{X}$	C.V.
#19	*PACHY*	94	1.0-2.7	1.48	0.43	0.04	29.0
	STUB	17	1.0-2.3	1.51	0.47	0.11	31.2
	MAC	39	1.0-3.0	2.00	0.59	0.09	29.8
	FEST	14	1.0-2.3	1.23	0.41	0.11	33.7
	LIMNO	16	1.0-1.3	1.06	0.12	0.03	11.5
	HAY	7	1.0-2.0	1.43	0.53	0.20	37.4
	MICRO	26	1.0-1.3	1.01	0.06	0.01	5.8
#20	*PACHY*	94	1.0-3.0	1.95	0.56	0.06	28.8
	STUB	17	1.0-3.0	1.68	0.55	0.13	32.7
	MAC	39	2.0-3.0	2.74	0.38	0.06	14.0
	FEST	14	1.0-3.0	1.76	0.70	0.19	39.7
	LIMNO	16	1.0-3.0	1.58	0.68	0.17	42.7
	HAY	7	1.0-2.0	1.40	0.45	0.17	32.2
	MICRO	26	1.0-2.3	1.48	0.45	0.09	30.1
#21	*PACHY*	82	1.0-2.1	1.64	0.21	0.02	12.9
	STUB	17	1.0-2.0	1.53	0.28	0.07	18.3
	MAC	39	1.4-2.3	1.77	0.23	0.04	12.9
	FEST	14	0.9-1.9	1.34	0.35	0.09	25.9
	LIMNO	15	1.0-1.5	1.19	0.19	0.05	16.3
	HAY	7	1.5-1.9	1.70	0.13	0.05	7.6
	MICRO	26	0.9-1.4	1.17	0.16	0.03	13.5

CHARACTER	TAXON	N	RANGE	$\overline{X}$	S.D.	S.E.$\overline{X}$	C.V.
#22	*PACHY*	94	2.0-3.0	2.01	0.10	0.01	5.1
	STUB	17	2.0	2.00	--	--	--
	MAC	39	1.0-3.0	2.15	0.59	0.09	27.2
	FEST	14	1.0-3.0	1.50	0.76	0.20	50.6
	LIMNO	16	1.0-2.0	1.56	0.51	0.13	32.8
	HAY	7	1.0	1.00	--	--	--
	MICRO	26	1.0-2.0	1.23	0.43	0.08	34.9
#23	*PACHY*	94	3.3-5.0	3.95	0.36	0.04	9.2
	STUB	17	3.0-4.0	3.51	0.29	0.07	8.2
	MAC	39	3.5-4.4	4.04	0.25	0.04	6.3
	FEST	14	3.5-4.4	3.96	0.29	0.08	7.2
	LIMNO	16	2.9-4.3	3.74	0.32	0.08	8.5
	HAY	7	4.5-6.5	5.36	0.77	0.29	14.3
	MICRO	26	3.2-4.7	3.82	0.35	0.07	9.2
#24	*PACHY*	94	1.3-2.2	1.68	0.18	0.02	10.6
	STUB	17	1.3-2.0	1.54	0.17	0.04	10.8
	MAC	39	1.4-2.0	1.73	0.16	0.03	9.3
	FEST	14	1.4-2.3	1.74	0.21	0.06	12.3
	LIMNO	16	1.2-2.1	1.58	0.19	0.05	11.8
	HAY	7	1.7-2.4	1.94	0.29	0.11	15.1
	MICRO	26	1.3-1.8	1.50	0.12	0.02	8.1

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#25	*PACHY*	94	2.0-3.0	2.03	0.14	0.01	7.1
	STUB	17	1.7-2.0	1.98	0.07	0.02	3.7
	MAC	39	1.5-2.3	1.99	0.09	0.02	4.7
	FEST	14	2.0-3.0	2.37	0.35	0.09	14.7
	LIMNO	16	2.0-3.0	2.38	0.31	0.08	13.1
	HAY	7	2.0-2.3	2.09	0.15	0.06	7.0
	MICRO	26	2.0-3.0	2.32	0.32	0.06	13.6
#26	*PACHY*	94	0.1-0.3	0.22	0.05	0.01	22.5
	STUB	17	0.1-0.2	0.18	0.04	0.01	24.8
	MAC	39	0.2-0.4	0.28	0.04	0.01	15.2
	FEST	14	0.2-0.4	0.28	0.06	0.02	20.8
	LIMNO	16	0.1-0.3	0.23	0.06	0.02	26.0
	HAY	7	0.3-0.4	0.33	0.05	0.02	15.0
	MICRO	26	0.2-0.3	0.23	0.05	0.01	20.4
#27	*PACHY*	94	2.0-3.0	2.15	0.27	0.03	12.4
	STUB	17	2.0-3.0	2.09	0.25	0.06	12.0
	MAC	39	2.0-3.0	2.32	0.32	0.05	14.0
	FEST	14	2.0-2.3	2.06	0.13	0.03	6.2
	LIMNO	16	2.0-3.0	2.16	0.30	0.07	13.8
	HAY	7	2.0	2.00	--	--	--
	MICRO	26	2.0-2.3	2.06	0.12	0.02	5.9

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#28	*PACHY*	94	5.7-10.7	7.77	0.94	0.10	12.1
	STUB	17	6.3-8.3	7.42	0.54	0.13	7.2
	MAC	39	7.0-10.7	8.80	0.88	0.14	10.0
	FEST	14	6.0-9.7	7.63	1.12	0.30	14.7
	LIMNO	16	6.0-9.3	7.96	1.07	0.27	13.5
	HAY	7	7.0-9.0	8.09	0.77	0.29	9.5
	MICRO	26	6.0-10.0	7.94	0.92	0.18	11.6
#29	*PACHY*	94	1.0-3.0	2.56	0.53	0.05	20.7
	STUB	17	1.7-3.0	2.53	0.44	0.11	17.6
	MAC	39	1.3-3.0	2.63	0.48	0.08	18.3
	FEST	14	1.0-2.7	1.49	0.51	0.14	34.4
	LIMNO	16	1.0-3.0	1.64	0.76	0.19	46.3
	HAY	7	1.0-3.0	2.21	0.67	0.25	30.2
	MICRO	26	1.0-3.0	1.80	0.51	0.10	28.3
#30	*PACHY*	94	0.0-7.7	4.71	1.39	0.14	29.5
	STUB	17	1.7-5.0	3.05	1.00	0.24	32.4
	MAC	39	3.3-7.3	5.59	0.96	0.15	17.2
	FEST	14	2.0-7.3	5.24	1.57	0.42	30.0
	LIMNO	16	4.7-7.7	6.00	0.84	0.21	14.1
	HAY	7	3.0-6.0	4.74	1.11	0.42	23.5
	MICRO	26	1.3-7.7	4.82	1.57	0.31	32.6

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#31	*PACHY*	93	1.0-3.0	1.77	0.76	0.08	43.6
	STUB	17	1.0-3.0	2.47	0.59	0.14	23.9
	MAC	39	1.0-3.0	2.25	0.70	0.11	31.0
	FEST	14	1.0-2.3	1.31	0.48	0.13	36.4
	LIMNO	16	1.0-3.0	1.54	0.52	0.13	33.6
	HAY	7	1.0-3.0	1.47	0.83	0.31	56.4
	MICRO	26	1.0-3.0	1.41	0.64	0.13	45.3
#32	*PACHY*	93	1.0-3.0	1.24	0.47	0.05	38.1
	STUB	17	1.0-3.0	1.91	0.83	0.20	43.8
	MAC	39	1.0-2.3	1.20	0.36	0.06	30.0
	FEST	14	1.0-1.7	1.24	0.28	0.08	23.0
	LIMNO	16	1.0-1.3	1.06	0.12	0.03	11.5
	HAY	7	1.0-3.0	1.49	0.74	0.28	50.1
	MICRO	26	1.0-2.0	1.10	0.27	0.05	24.2
#33	*PACHY*	94	0.0-1.0	0.14	0.22	0.02	162
	STUB	17	0.0-0.7	0.18	0.28	0.07	156
	MAC	38	0.0-1.0	0.14	0.29	0.05	207
	FEST	14	0.0-1.0	0.55	0.43	0.12	78.4
	LIMNO	16	0.0-1.0	0.38	0.39	0.10	103
	HAY	7	0.0-0.5	0.11	0.20	0.08	178
	MICRO	26	0.0-0.7	0.11	0.21	0.04	188

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#34	*PACHY*	94	1.2-2.3	1.53	0.19	0.02	12.5
	STUB	17	1.1-1.7	1.39	0.16	0.04	11.2
	MAC	39	1.3-1.8	1.54	0.11	0.02	7.4
	FEST	14	1.3-2.1	1.90	0.21	0.06	10.9
	LIMNO	16	1.3-2.1	1.77	0.19	0.05	10.5
	HAY	7	1.8-3.1	2.33	0.45	0.17	19.3
	MICRO	26	1.5-2.5	1.84	0.22	0.04	12.1
#35	*PACHY*	94	0.3-1.2	0.62	0.16	0.02	25.4
	STUB	17	0.5-1.1	0.74	0.17	0.04	22.5
	MAC	39	0.4-0.9	0.65	0.11	0.02	17.6
	FEST	14	0.3-0.7	0.51	0.11	0.03	22.5
	LIMNO	16	0.2-0.8	0.46	0.17	0.04	36.1
	HAY	7	0.3-0.6	0.46	0.10	0.04	21.4
	MICRO	26	0.3-0.8	0.48	0.12	0.02	24.7
#36	*PACHY*	94	1.0-2.7	1.20	0.37	0.04	30.6
	STUB	17	1.0-2.3	1.40	0.43	0.11	30.9
	MAC	39	2.0-3.0	2.95	0.18	0.03	6.2
	FEST	14	1.0-1.3	1.02	0.08	0.02	7.9
	LIMNO	16	1.0-1.7	1.12	0.20	0.05	18.2
	HAY	7	1.0-2.0	1.14	0.38	0.14	33.1
	MICRO	26	1.0-1.3	1.01	0.06	0.01	5.8

CHARACTER	TAXON	N	RANGE	$\overline{X}$	S.D.	S.E.$\overline{X}$	C.V.
#37	*PACHY*	94	1.0-2.7	1.26	0.37	0.04	29.3
	STUB	17	1.0-2.3	1.50	0.40	0.10	26.6
	MAC	39	1.0-2.0	1.28	0.34	0.05	26.4
	FEST	14	1.0-3.3	1.74	0.57	0.15	32.6
	LIMNO	16	1.0-2.7	1.63	0.49	0.12	30.4
	HAY	7	1.0-2.0	1.41	0.41	0.16	29.3
	MICRO	26	1.0-3.0	1.77	0.61	0.12	34.6
#38	*PACHY*	94	2.0-3.0	2.73	0.28	0.03	10.3
	STUB	17	2.2-2.8	2.59	0.17	0.04	6.4
	MAC	39	2.2-3.0	2.80	0.20	0.03	7.2
	FEST	14	1.5-2.7	2.22	0.35	0.09	15.7
	LIMNO	16	2.0-3.0	2.51	0.26	0.06	10.3
	HAY	7	1.2-2.3	1.79	0.39	0.15	21.8
	MICRO	26	1.8-2.8	2.45	0.22	0.04	8.8
#39	*PACHY*	94	1.4-1.8	1.52	0.09	0.01	5.7
	STUB	17	1.4-1.6	1.49	0.08	0.02	5.3
	MAC	39	1.4-1.7	1.51	0.07	0.01	4.6
	FEST	14	1.2-1.4	1.33	0.07	0.02	5.5
	LIMNO	16	1.1-1.5	1.29	0.11	0.03	8.7
	HAY	7	1.4-1.7	1.50	0.10	0.04	6.7
	MICRO	26	1.1-1.4	1.24	0.09	0.02	7.6

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#40	*PACHY*	94	0.9-1.3	1.07	0.09	0.01	8.3
	STUB	17	0.9-1.1	0.98	0.05	0.01	5.4
	MAC	39	0.9-1.1	1.00	0.05	0.01	5.5
	FEST	14	0.8-1.0	0.91	0.06	0.02	6.8
	LIMNO	16	0.7-1.0	0.87	0.09	0.02	10.9
	HAY	7	0.8-1.3	1.00	0.17	0.06	18.0
	MICRO	26	0.7-1.0	0.84	0.06	0.01	7.6
#41	*PACHY*	94	0.3-0.5	0.41	0.05	0.01	13.3
	STUB	17	0.3-0.5	0.37	0.07	0.02	18.5
	MAC	39	0.4-0.6	0.52	0.05	0.01	9.8
	FEST	14	0.3-0.5	0.39	0.05	0.01	13.9
	LIMNO	16	0.3-0.4	0.36	0.05	0.01	14.4
	HAY	7	0.5-0.8	0.61	0.11	0.04	17.4
	MICRO	26	0.3-0.5	0.34	0.06	0.01	18.8
#42	*PACHY*	94	0.13-0.39	0.25	0.06	0.01	21.9
	STUB	17	0.17-0.39	0.24	0.06	0.02	25.4
	MAC	39	0.13-0.42	0.23	0.05	0.01	22.9
	FEST	14	0.17-0.36	0.24	0.05	0.01	21.2
	LIMNO	16	0.14-0.32	0.22	0.04	0.01	16.2
	HAY	7	0.22-0.30	0.26	0.03	0.01	12.1
	MICRO	26	0.15-0.34	0.24	0.05	0.01	19.7

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#43	*PACHY*	94	0.31-0.47	0.39	0.03	0.00+	7.5
	STUB	17	0.33-0.47	0.40	0.04	0.01	9.4
	MAC	39	0.34-0.44	0.38	0.02	0.00+	6.1
	FEST	14	0.37-0.51	0.48	0.03	0.01	7.2
	LIMNO	16	0.44-0.50	0.47	0.02	0.01	4.3
	HAY	7	0.40-0.48	0.43	0.04	0.01	8.2
	MICRO	26	0.43-0.53	0.48	0.02	0.00+	4.9
#44	*PACHY*	94	0.19-0.67	0.41	0.09	0.01	21.4
	STUB	17	0.40-0.79	0.53	0.11	0.03	21.4
	MAC	39	0.27-0.56	0.42	0.07	0.01	15.6
	FEST	14	0.16-0.46	0.27	0.08	0.02	29.5
	LIMNO	16	0.12-0.42	0.26	0.08	0.02	31.5
	HAY	7	0.12-0.28	0.10	0.06	0.02	30.3
	MICRO	26	0.16-0.40	0.26	0.06	0.01	22.3
#45	*PACHY*	94	0.34-0.80	0.55	0.08	0.01	15.3
	STUB	17	0.41-0.83	0.60	0.12	0.03	19.4
	MAC	39	0.36-0.75	0.52	0.08	0.01	15.7
	FEST	14	0.41-0.57	0.50	0.05	0.01	10.6
	LIMNO	16	0.40-0.65	0.52	0.06	0.01	11.5
	HAY	7	0.30-0.42	0.37	0.04	0.02	11.0
	MICRO	26	0.37-0.68	0.52	0.08	0.02	15.3

CHARACTER	TAXON	N	RANGE	$\bar{X}$	S.D.	S.E.$\bar{X}$	C.V.
#46	*PACHY*	94	0.69-0.97	0.83	0.05	0.01	6.5
	STUB	17	0.72-0.87	0.79	0.05	0.01	6.3
	MAC	39	0.68-0.95	0.80	0.06	0.01	7.1
	FEST	14	0.60-0.91	0.74	0.08	0.02	11.0
	LIMNO	16	0.65-0.88	0.75	0.06	0.02	8.0
	HAY	7	0.64-0.74	0.70	0.04	0.02	6.4
	MICRO	26	0.65-0.85	0.73	0.04	0.01	6.1
#47	*PACHY*	94	0.18-0.34	0.25	0.03	0.00+	12.9
	STUB	17	0.22-0.33	0.27	0.03	0.01	9.8
	MAC	39	0.16-0.27	0.21	0.03	0.00+	11.9
	FEST	14	0.14-0.20	0.18	0.02	0.01	11.3
	LIMNO	16	0.16-0.24	0.20	0.02	0.01	10.6
	HAY	7	0.12-0.18	0.14	0.02	0.01	14.7
	MICRO	26	0.14-0.24	0.18	0.02	0.00+	13.3

APPENDIX 6. CLUSTER MEMBERSHIP FOR TAXMAP ANAYLSES OF OTU's

```
MAP CLUSTER ANALYSIS:-CLUSTER ANALYSIS ON OTU'S, ALL CHARACTERS, LOG WEIGHTED

(MINIMUM NUCLEUS 0.166, MAXIMUM DROP 0.0183 BOTH ARE 110% OF NORMAL)
ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION CAPACITY

CLUS OTU DIST OTU  AVGOF  DROP FAR DIST FLAG NAME OF OTU
TER  NOS BEST BEST  NEW    IN  OTU FAR
NO.      LINK LINK LINKS  AVG.      OTU
---------------------------------------------------------
  1  166                                     PACHYE03
     183 0.07                                PACHYJ01
     165 0.08  166 0.091 0.019 183 0.10      PACHYE02
     144 0.09  165 0.111 0.020 183 0.13      PACHY18
     171 0.09  165 0.108-0.003 166 0.12      PACHYE08
     169 0.10  183 0.114 0.006 171 0.12      PACHYE06
       1 0.10  166 0.118 0.004 169 0.15      TYPE01
     153 0.10  169 0.130 0.012   1 0.16      PACHYB05
     146 0.10  171 0.141 0.011 153 0.16      PACHY20
     137 0.09  146 0.144 0.003   1 0.17      PACHY09
     170 0.09  137 0.131-0.012   1 0.16      PACHYE07
     136 0.10  137 0.127-0.004   1 0.15      PACHY08

     135 0.08  136 0.166 0.039 183 0.20 1000 PACHY06
---------------------------------------------------------
  2   17                                     MICR007
      29 0.07                                MICROC02
      21 0.08   17 0.103 0.030  29 0.12      MICROA04
      25 0.08   21 0.105 0.002  29 0.13      MICROB02
      73 0.08   25 0.114 0.009  29 0.15      FESTA06
      53 0.07   73 0.109-0.005  29 0.15      LIMNOB06
      71 0.09   73 0.116 0.007  29 0.15      FESTA04
      19 0.09   53 0.106-0.010  29 0.12      MICROA02
      12 0.09   19 0.130 0.023  29 0.16      MICR002
      64 0.09   73 0.125-0.004  29 0.17      FEST04
      72 0.09   25 0.112-0.013  71 0.13      FESTA05
      18 0.08   72 0.123 0.011  64 0.14      MICROA01
      16 0.10   21 0.127 0.004  64 0.15      MICR006
      60 0.08   16 0.130 0.002  29 0.15      LIMNOC04
      56 0.09   16 0.132 0.002  12 0.16      LIMNOB09
      15 0.09   16 0.115-0.017  64 0.14      MICR005
      13 0.10   15 0.128 0.014  71 0.15      MICR003
      54 0.10   13 0.152 0.024  71 0.19      LIMNOB07
      51 0.10   18 0.134-0.018  54 0.19      LIMNOB04
      22 0.09   51 0.164 0.029  54 0.25      MICROA05
      70 0.10   25 0.136-0.028  22 0.19      FESTA03
      27 0.10   71 0.136 0.000  54 0.18      MICROB04
      35 0.08   27 0.153 0.017  54 0.21      MICROD01
      32 0.10   13 0.130-0.023  22 0.19      MICROC05
      26 0.10   71 0.138 0.007  54 0.21      MICROB03
      28 0.10   19 0.123-0.015  22 0.16      MICROC04
      61 0.10   28 0.145 0.022  22 0.21      LIMNOC05
      69 0.10   29 0.139-0.005  22 0.19      FESTA02
      47 0.10   19 0.147 0.008  22 0.20      LIMNOA02
      23 0.11   21 0.134-0.013  54 0.20      MICROA06

      20 0.11   56 0.176 0.042  29 0.25 1000 MICROA03
---------------------------------------------------------
  3   80                                     MAC06
     108 0.08                                MACB14
```

```
       97 0.09    80 0.091 0.015 108 0.09        MACB03
       75 0.08    97 0.097 0.006 108 0.11        MACO1
      105 0.09    75 0.105 0.008 108 0.11        MACB11
      101 0.09   105 0.108 0.004 108 0.13        MACB07
       89 0.09   105 0.121 0.013  80 0.13        MAC15
      107 0.10    75 0.116-0.005  89 0.15        MACB13
       81 0.10   101 0.118 0.002  89 0.13        MACO7
      103 0.08    81 0.125 0.007  75 0.14        MACB09
       76 0.10   103 0.122-0.003  75 0.14        MACO2
       87 0.10   105 0.132 0.010 103 0.16        MAC13
       82 0.08    87 0.152 0.020  76 0.18        MACO8
       79 0.10   103 0.133-0.018  82 0.18        MACO5
      111 0.10    97 0.130-0.003  82 0.17        MACB17
       77 0.10    97 0.131 0.001  79 0.16        MACO3
       98 0.08    77 0.141 0.010  79 0.18        MACB04

       95 0.10    98 0.166 0.024  79 0.21  1000 MACB01
---------------------------------------------------------------
   4  172                                        PACHYF01
      174 0.08                                   PACHYF03
      173 0.11   172 0.128 0.049 174 0.14        PACHYF02

      146 0.12   172 0.130 0.002 173 0.14     4 PACHY20
        LINK TO CLUSTER  -1
---------------------------------------------------------------
   5  131                                        PACHY01
      142 0.08                                   PACHY15

      136 0.09   131 0.093 0.011 142 0.10     4 PACHY08
        LINK TO CLUSTER  -1
---------------------------------------------------------------
   6  135                                        PACHY06
      150 0.08                                   PACHYBO 1
* NEEDED .GT. FOUND FOR NEXT OTU **

      136 0.09   150 0.272 0.187   8 0.46  1004 PACHY08
---------------------------------------------------------------
   7   31                                        MICROC04
       57 0.09                                   LIMNOC01
       30 0.10    31 0.117 0.030  57 0.14        MICROC03
       10 0.11    31 0.139 0.022  30 0.17        TYPE10
       58 0.11    10 0.131-0.008  30 0.18        LIMNOC02
       52 0.11    57 0.144 0.013  10 0.17        LIMNOB05

       29 0.11    30 0.147 0.003  58 0.18     4 MICROC02
        LINK TO CLUSTER  -2
---------------------------------------------------------------
   8  126                                        STUBA05
      149 0.09                                   PACHYA05
      176 0.09   149 0.103 0.012 126 0.11        PACHYG02
      115 0.10   149 0.123 0.020 176 0.15        STUB02
      160 0.09   115 0.121-0.002 176 0.14        PACHYC03

      142 0.10   176 0.133 0.012 115 0.16     4 PACHY15
        LINK TO CLUSTER  -5
---------------------------------------------------------------
   9   44                                        HAYMIC01
       45 0.09                                   HAYMIC02
      138 0.13    45 0.150 0.059  44 0.17        PACHY10
```

```
     144 0.12  138 0.165 0.015  44 0.19     4 PACHY18
       LINK TO CLUSTER  -1
-------------------------------------------------------------
 10   50                                      LIMNOB03
      55 0.09                                 LIMNOB08

      70 0.11   50 0.122 0.031  55 0.13     4 FESTA05
       LINK TO CLUSTER  -2
-------------------------------------------------------------
 11    2                                      TYPE02
     102 0.09                                 MACB08
     117 0.11  102 0.121 0.029   2 0.14       STUB04

     146 0.10  117 0.128 0.007   2 0.14     4 PACHY20
       LINK TO CLUSTER  -1
-------------------------------------------------------------
 12  122                                      STUBA01
     127 0.09                                 STUBA06
     118 0.09  127 0.115 0.022 122 0.14       STUB05

     117 0.11  127 0.130 0.015 118 0.15     4 STUB04
       LINK TO CLUSTER -11
-------------------------------------------------------------
 13  157                                      PACHYB11
     162 0.09                                 PACHY004

     142 0.10  157 0.105 0.012 162 0.11     4 PACHY15
       LINK TO CLUSTER  -5
-------------------------------------------------------------
 14  156                                      PACHYB08
     182 0.10                                 PACHYI01

     137 0.10  156 0.107 0.011 182 0.11     4 PACHY09
       LINK TO CLUSTER  -1
-------------------------------------------------------------
 15  151                                      PACHYB02
     190 0.10                                 PACHYK10

     131 0.10  190 0.119 0.017 151 0.13     4 PACHY01
       LINK TO CLUSTER  -5
-------------------------------------------------------------
 16   96                                      MACB02
      99 0.10                                 MACB05

     105 0.10   96 0.116 0.014  99 0.13     4 MACB11
       LINK TO CLUSTER  -3
-------------------------------------------------------------
 17  121                                      STUB08
     148 0.10                                 PACHYA03

     160 0.11  121 0.134 0.031 148 0.16     4 PACHYC03
       LINK TO CLUSTER  -8
-------------------------------------------------------------
 18   14                                      MICRO04
      36 0.10                                 MICROD02
       6 0.11   14 0.128 0.025  36 0.15       TYPE06

      73 0.11   14 0.123-0.005   6 0.14     4 FESTA06
       LINK TO CLUSTER  -2
```

```
      --------------------------------------------------------------------------
       19  154                                              PACHYB06
           177 0.11                                         PACHYG03
           191 0.11   177 0.112 0.007 154 0.12              PACHYK11

           136 0.11   154 0.124 0.012 177 0.14           4  PACHY08
             LINK TO CLUSTER -1
      --------------------------------------------------------------------------
       20  119                                              STUB06
           159 0.11                                         PACHYC02

           160 0.11   119 0.112 0.006 159 0.12           4  PACHYC03
             LINK TO CLUSTER -8
      --------------------------------------------------------------------------
       21   88                                              MAC14
            94 0.11                                         MACA04
            86 0.11    88 0.127 0.020  94 0.14              MAC12
             3 0.12    86 0.149 0.022  94 0.18              TYPE03
           106 0.11     3 0.136-0.013  88 0.16              MACB12

            75 0.11   106 0.146 0.011  88 0.18           4  MAC01
             LINK TO CLUSTER  -3
      --------------------------------------------------------------------------
       22  164                                              PACHYE01
           189 0.11                                         PACHYK06
** NEEDED .GT. FOUND FOR NEXT OTU **

           142 0.11   189 0.284 0.174 188 0.46 1004 PACHY15
      --------------------------------------------------------------------------
       23  123                                              STUBA02
           124 0.11                                         STUBA03

           121 0.12   124 0.137 0.025 123 0.16           4  STUB08
             LINK TO CLUSTER -17
      --------------------------------------------------------------------------
       24   91                                              MACA01
            95 0.11                                         MACB01
           110 0.11    95 0.130 0.017  91 0.15              MACB16
** NEEDED .GT. FOUND FOR NEXT OTU **

            97 0.12   110 0.250 0.120  68 0.46 1004 MACB03
      --------------------------------------------------------------------------
       25  132                                              PACHY02
           163 0.11                                         PACHYD07
           147 0.12   132 0.152 0.038 163 0.18              PACHYA01
           140 0.12   147 0.156 0.005 163 0.20              PACHY13
           158 0.11   140 0.141-0.016 163 0.18              PACHYB12
** NEEDED .GT. FOUND FOR NEXT OTU **

           190 0.11   158 0.264 0.123 188 0.46 1004 PACHYK10
      --------------------------------------------------------------------------
       26   59                                              LIMNOC03
           128 0.12                                         STUBA07

           124 0.12   128 0.135 0.014  59 0.15           4  STUBA03
             LINK TO CLUSTER -23
      --------------------------------------------------------------------------
```

```
       27   41                                                HAYBO2
            42 0.13                                           HAYBO3

            39 0.15   41 0.166 0.041  42 0.18 1000 HAYAO3
     ------------------------------------------------------------------
       28  129                                                STUBBO1
           139 0.13                                           PACHY11

           190 0.13  139 0.138 0.013 129 0.15    4 PACHYK10
             LINK TO CLUSTER -15
     ------------------------------------------------------------------
       29   49                                                LIMNOBO2
            68 0.13                                           FESTAO1
            62 0.14   68 0.142 0.013  49 0.14      FESTO1
            20 0.14   62 0.142 0.000  49 0.15      MICROAO3

** NEEDED .GT. FOUND FOR NEXT OTU **

            27 0.14   62 0.236 0.094 112 0.46 1004 MICROBO4
     ------------------------------------------------------------------
       30  130                                                STUBBO2
           186 0.13                                           PACHYJO9

           147 0.13  186 0.135 0.006 130 0.14    4 PACHYAO1
             LINK TO CLUSTER -25
     ------------------------------------------------------------------
       31   33                                                MICROCO6
            34 0.13                                           MICROCO7

** NEEDED .GT. FOUND FOR NEXT OTU **

            58 0.13   33 0.293 0.164 188 0.46 1004 LIMNOCO2
     ------------------------------------------------------------------
       32  114                                                STUBO1
           120 0.13                                           STUBO7

           118 0.13  120 0.147 0.018 114 0.16    4 STUBO5
             LINK TO CLUSTER -12
     ------------------------------------------------------------------
       33   66                                                FESTO6
            67 0.13                                           FESTO7

            65 0.15   67 0.171 0.041  66 0.19 1000 FESTO5
     ------------------------------------------------------------------
       34   92                                                MACAO2
           109 0.13                                           MACB15

** NEEDED .GT. FOUND FOR NEXT OTU **

             2 0.13  109 0.294 0.163  68 0.46 1004 TYPEO2
     ------------------------------------------------------------------
       35  143                                                PACHY17
           179 0.13                                           PACHYGO5

           150 0.13  143 0.133 0.001 179 0.13    4 PACHYBO 1
             LINK TO CLUSTER  -6
     ------------------------------------------------------------------
       36  152                                                PACHYBO3
           161 0.13                                           PACHYDO1
```

```
      142 0.13   152 0.150 0.017  161 0.17     4 PACHY15
        LINK TO CLUSTER  -5
-----------------------------------------------------------------
  37   90                                          MAC16
      113 0.14                                     MACCO2

       77 0.14   90 0.162 0.026  113 0.19     4 MACO3
        LINK TO CLUSTER  -3
-----------------------------------------------------------------
  38  133                                          PACHYO3
      134 0.14                                     PACHYO4

      117 0.1[illegible]  134 0.157 0.020  133 0.18     4 STUBO4
        LINK TO CLUSTER -11
-----------------------------------------------------------------
  39  116                                          STUBO3
      185 0.14                                     PACHYJO7

      134 0.14   185 0.168 0.027  116 0.19  1004 PACHYO4
-----------------------------------------------------------------
  40   78                                          MACO4
      100 0.14                                     MACBO6
** NEEDED .GT. FOUND FOR NEXT OTU **

       99 0.14    78 0.301 0.157  188 0.46  1004 MACBO5
-----------------------------------------------------------------
  41   48                                          LIMNOBO1
       65 0.15                                     FESTO5

       67 0.15    65 0.151 0.005   48 0.15     4 FESTO7
        LINK TO CLUSTER -33
-----------------------------------------------------------------
  42  175                                          PACHYGO1
      180 0.15                                     PACHYGO6
** NEEDED .GT. FOUND FOR NEXT OTU **

      189 0.15   175 0.303 0.154   43 0.46  1004 PACHYKO6
-----------------------------------------------------------------
  43   11                                          MICROO1
       63 0.15                                     FESTO3
** NEEDED .GT. FOUND FOR NEXT OTU **

       13 0.15    11 0.304 0.154  188 0.46  1004 MICROO3
-----------------------------------------------------------------
  44   24                                          MICROBO1
       46 0.15                                     LIMNOAO1

       32 0.15    24 0.152 0.002   46 0.15     4 MICROCO5
        LINK TO CLUSTER  -2
-----------------------------------------------------------------
  45   39                                          HAYAO3
       40 0.15                                     HAYBO1

       53 0.15    39 0.159 0.007   40 0.17     4 LIMNOBO6
        LINK TO CLUSTER  -2
-----------------------------------------------------------------
  46  145                                          PACHY18
```

```
         178 0.16                                           PACHYG04

         177 0.16   178 0.178 0.023  145 0.20  1004 PACHYG03-
----------------------------------------------------------------------
   47    184                                           PACHYJ06
         187 0.16                                      PACHYK03

         169 0.16   184 0.157 0.001  187 0.16     4 PACHYE06
           LINK TO CLUSTER   -1
----------------------------------------------------------------------
   48     83                                           MAC09
          84 0.16                                      MAC10

         139 0.16    84 0.171 0.015   83 0.18     4 PACHY11
           LINK TO CLUSTER  -28
----------------------------------------------------------------------
   49    155                                           PACHYB07
         188 0.16                                      PACHYK05

         178 0.16   155 0.199 0.037  188 0.24  1004 PACHYG04
----------------------------------------------------------------------
   50     85                                           MAC11
         104 0.16                                      MACB10

         109 0.16   104 0.179 0.015   85 0.19     4 MACB15
           LINK TO CLUSTER  -34
----------------------------------------------------------------------
   51     37                                           HAYA01
          38 0.16                                      HAYA02

          21 0.17    38 0.172 0.008   37 0.18     4 MICROA04
           LINK TO CLUSTER   -2
----------------------------------------------------------------------

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
     52    4 TYPE04
     53    5 TYPE05
     54    7 TYPE07
     55    8 TYPE08
     56    9 TYPE09
     57   43 HAYB04
     58   74 FESTA07
     59   93 MACA03
     60  101 MACB07
     61  102 MACB08
     62  112 MACC01
     63  125 STUBA04
     64  141 PACHY14
     65  167 PACHYE04
     66  168 PACHYE05
     67  181 PACHYG11
```

```
MAP CLUSTER ANALYSIS:-CLUSTER ANALYSIS ON OTU'S, REP CHARACTERS, LOG WEIGHTED

(MINIMUM NUCLEUS 0.161, MAXIMUM DROP 0.0198 BOTH ARE 110% OF NORMAL)
ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION CAPACITY

CLUS OTU DIST OTU  AVGOF  DROP FAR DIST FLAG NAME OF OTU
TER  NOS BEST BEST  NEW    IN  OTU FAR
NO.      LINK LINK LINKS  AVG.      OTU
-----------------------------------------------------------
  1  135                                    PACHY06
     136 0.05                               PACHY08
     150 0.07  136 0.070 0.021 135 0.07     PACHYBO 1
     131 0.08  136 0.096 0.026 150 0.11     PACHY01
     142 0.08  131 0.096-0.001 150 0.13     PACHY15
     157 0.08  142 0.101 0.005 131 0.13     PACHYB11
     156 0.08  136 0.091-0.010 131 0.11     PACHYB08
     162 0.08  136 0.105 0.013 156 0.13     PACHYD04
     137 0.08  156 0.104-0.000 157 0.12     PACHY09
     189 0.08  136 0.112 0.007 137 0.16     PACHYK06
     170 0.09  137 0.121 0.010 157 0.15     PACHYE07
     146 0.09  137 0.119-0.002 189 0.14     PACHY20
     182 0.09  156 0.123 0.004 131 0.15     PACHYI01
     164 0.09  142 0.120-0.004 146 0.14     PACHYE01
     132 0.09  136 0.111-0.009 170 0.14     PACHY02
     163 0.09  132 0.135 0.024 164 0.16     PACHYD07
     172 0.10  146 0.149 0.014 182 0.18     PACHYF01
     174 0.07  172 0.145-0.003 182 0.19     PACHYF03
     143 0.10  136 0.132-0.014 172 0.17     PACHY17
     171 0.10  146 0.134 0.002 182 0.17     PACHYE08
     165 0.09  171 0.140 0.006 143 0.17     PACHYE02
     166 0.09  165 0.140-0.000 143 0.17     PACHYE03
     183 0.08  166 0.142 0.002 172 0.19     PACHYJ01
       1 0.10  165 0.146 0.004 157 0.18     TYPE01
     190 0.10  171 0.126-0.019 174 0.16     PACHYK10
     158 0.10  171 0.134 0.008 163 0.18     PACHYB12
     169 0.10  183 0.139 0.004 172 0.20     PACHYE06
     151 0 10  171 0 135-0 003 174 0.17     PACHYB02
     145 0.10  132 0.140 0.005 183 0.18     PACHY19
     153 0.10  169 0.144 0.004 172 0.20     PACHYB05
     117 0.10  171 0.141-0 004 143 0.18     STUB04
     102 0.10  117 0.156 0.015 143 0.20     MACB08
       2 0.10  102 0.173 0.017 169 0.20     TYPE02
     185 0.10  183 0.152-0.020 174 0.21     PACHYJ07
     134 0.10  131 0.130-0.022   2 0.17     PACHY04
     119 0.10  170 0.159 0.029 172 0.21     STUB06
     160 0.09  119 0.155-0.004   1 0.20     PACHYC03
     115 0.09  160 0.173 0.018 163 0.23     STUB02
     120 0.09  119 0.183 0.011 174 0.24     STUB07
     127 0.10  120 0.186 0.002 174 0.23     STUBA06
     122 0.09  127 0.195 0.010 182 0.25     STUBA01
     118 0.09  127 0.178-0.017 174 0.24     STUB05
     149 0.10  115 0.164-0.014 174 0.23     PACHYA05
     126 0.09  149 0.156-0.008 174 0.21     STUBA05
     176 0.10  149 0.148-0.008 172 0.19     PACHYG02

     173 0.10  172 0.171 0.023 169 0.22 1000 PACHYF02
-----------------------------------------------------------
  2   25                                    MICROB02
      73 0.06                               FESTA06
```

```
     53 0.07    73 0.077 0.013  25 0.08       LIMNOBO6
     21 0.07    25 0.090 0.013  53 0.11       MICROAO4
     71 0.08    21 0.081-0.009  25 0.09       FESTAO4
     26 0.08    21 0.091 0.010  53 0.10       MICROBO3
     19 0.07    26 0.090-0.001  21 0.11       MICROAO2
     17 0.08    21 0.101 0.010  53 0.11       MICROO7
     29 0.08    17 0.123 0.023  26 0.14       MICROCO2
     12 0.08    19 0.122-0.002  29 0.16       MICROO2
     11 0.09    21 0.116-0.005  29 0.14       MICROO1
     64 0.09    73 0.121 0.004  29 0.16       FESTO4
     72 0.09    25 0.119-0.001  11 0.15       FESTAO5
     51 0.08    72 0.121 0.002  11 0.17       LIMNOBO4
     18 0.08    72 0.127 0.005  11 0.17       MICROAO1
     22 0.08    51 0.148 0.021  29 0.20       MICROAO5
     35 0.09    25 0.120-0.028  22 0.17       MICRODO1
     27 0.08    35 0.110-0.010  22 0.17       MICROBO4
     32 0.09    27 0.120 0.010  22 0.17       MICROCO5
     23 0.09    21 0.116-0.004  18 0.14       MICROAO6
     70 0.09    53 0.119 0.003  22 0.17       FESTAO3
     14 0.09    21 0.126 0.007  29 0.16       MICROO4
     47 0.09    19 0.132 0 006  22 0.18       LIMNOAO2
     13 0.09    32 0.134 0.002  22 0.19       MICROO3

     54 0.10    13 0.165 0.030  22 0.24  1000 LIMNOBO7
---------------------------------------------------------
  3  31                                       MICROCO4
     57 0.08                                  LIMNOCO1
     30 0.10    31 0.116 0.039  57 0.13       MICROCO3
     10 0.10    31 0.134 0.018  30 0.17       TYPE10

     29 0.10    30 0.129-0.005  10 0.17     4 MICROCO2
      LINK TO CLUSTER  -2
---------------------------------------------------------
  4  75                                       MACO1
     97 0.08                                  MACBO3
     79 0.09    97 0.103 0.024  75 0.12       MACO5
    104 0.08    79 0.097-0.006  97 0.11       MACB10
     81 0.09    79 0.109 0.012 104 0.12       MACO7
    103 0.08    81 0.113 0.004  75 0.14       MACBO9
    110 0.09    97 0.115 0.001  79 0.14       MACB16
    101 0,09    81 0.113-0.002 103 0.13       MACBO7
     80 0.09    97 0.112-0.000 104 0.14       MACO6
    108 0.08    80 0.126 0.014 101 0.15       MACB14
    105 0.09    81 0.106-0.020  79 0.12       MACB11
     89 0.08   105 0.118 0.012  79 0.15       MAC15
     76 0.10    81 0.130 0.011 104 0.16       MACO2
     98 0.10   110 0.134 0.005 103 0.16       MACBO4
     77 0.09    98 0.121-0.014 104 0.15       MACO3
    109 0.10    77 0.143 0.022  80 0.17       MACB15
    107 0.10    75 0.130-0.013 109 0.17       MACB13
    106 0.10   110 0.139 0.010  76 0.18       MACB12
     90 0.10    98 0.135-0.004 106 0.16       MAC16
     92 0.10    77 0.141 0.006 107 0.17       MACAO2
     87 0.10    92 0.132-0.009 108 0.15       MAC13
     82 0.08    87 0.147 0.015 108 0.18       MACO8
     86 0.10    92 0.147-0.000  90 0.20       MAC12
     88 0.09    86 0.161 0.014  90 0.21       MAC14
    111 0.10    97 0.138-0.023  88 0.17       MACB17
     85 0.10   101 0.141 0.003 109'0.18       MAC11
     95 0.11    98 0.160 0.019  76 0.20       MACBO1
```

```
       96 0.11   105 0.135-0.025  88 0.17        MACB02
       99 0.10    96 0.128-0.006 111 0.16        MACB05

      102 0.11    77 0.151 0.023 107 0.18     4  MACB08
        LINK TO CLUSTER  -1
--------------------------------------------------------------
   5   15                                        MICR005
       60 0.08                                   LIMNOC04
       16 0.09    60 0.089 0.007  15 0.09        MICR006
       56 0.09    16 0.105 0.016  15 0.12        LIMNOB09
       20 0.10    56 0.143 0.038  15 0.19        MICROA03

       13 0.10    15 0.140-0.003  20 0.20     4  MICR003
        LINK TO CLUSTER  -2
--------------------------------------------------------------
   6  121                                        STUB08
      148 0.08                                   PACHYA03

      126 0.11   121 0.120 0.036 148 0.13     4  STUBA05
        LINK TO CLUSTER  -1
--------------------------------------------------------------
   7   50                                        LIMNOB03
       55 0.08                                   LIMNOB08

       22 0.10    55 0.115 0.031  50 0.13     4  MICROA05
        LINK TO CLUSTER  -2
--------------------------------------------------------------
   8  123                                        STUBA02
      124 0.09                                   STUBA03

      121 0.12   124 0.127 0.037 123 0.13     4  STUB08
        LINK TO CLUSTER  -6
--------------------------------------------------------------
   9   44                                        HAYMIC01
       45 0.09                                   HAYMIC02
       33 0.13    45 0.144 0.054  44 0.16        MICROC06

       27 0.11    33 0.154 0.010  45 0.18     4  MICROB04
        LINK TO CLUSTER  -2
--------------------------------------------------------------
  10  184                                        PACHYJ06
      191 0.10                                   PACHYK11
      177 0.11   191 0.124 0.024 184 0.14        PACHYG03
      154 0.11   177 0.121-0.002 184 0.15        PACHYB06

      135 0.11   191 0.132 0.010 154 0.15     4  PACHY06
        LINK TO CLUSTER  -1
--------------------------------------------------------------
  11   34                                        MICROC07
       69 0.10                                   FESTA02

       35 0.10    69 0.120 0.018  34 0.14     4  MICROD01
        LINK TO CLUSTER  -2
--------------------------------------------------------------
  12   28                                        MICROC01
       61 0.10                                   LIMNOC05

       27 0.11    61 0.107 0.004  28 0.11     4  MICROB04
        LINK TO CLUSTER  -2
--------------------------------------------------------------
```

```
13   49                                               LIMNOBO2
     68 0.11                                          FESTAO1
     62 0.12   68 0.128 0.022  49 0.14                FESTO1

     25 0.12   49 0.133 0.005  62 0.14              4 MICROBO2
      LINK TO CLUSTER  -2
---------------------------------------------------------------------
14   66                                               FESTO6
     67 0.11                                          FESTO7
     48 0.14   66 0.152 0.045  67 0.16                LIMNOBO1
     65 0.15   48 0.164 0.013  66 0.18                FESTO5

    174 0.15   48 0.215 0.080  65 0.25           1004 PACHYFO3
---------------------------------------------------------------------
15  140                                               PACHY13
    147 0.11                                          PACHYAQ1

    158 0.11  147 0.113 0.002 140 0.11              4 PACHYB12
      LINK TO CLUSTER  -1
---------------------------------------------------------------------
16  133                                               PACHYO3
    144 0.12                                          PACHY18

    150 0.12  144 0.139 0.021 133 0.16              4 PACHYBO 1
      LINK TO CLUSTER  -1
---------------------------------------------------------------------
17  139                                               PACHY11
    173 0.12                                          PACHYFO2

    140 0.12  139 0.145 0.026 173 0.17              4 PACHY13
      LINK TO CLUSTER -15
---------------------------------------------------------------------
18   36                                               MICRODO2
     74 0.12                                          FESTAO7
     39 0.12   36 0.151 0.028  74 0.18                HAYAO3

     50 0.12   74 0.157 0.006  39 0.19              4 LIMNOBO3
      LINK TO CLUSTER  -7
---------------------------------------------------------------------
19  152                                               PACHYBO3
    161 0.13                                          PACHYDO1

     64 0.13  152 0.163 0.035 161 0.20           1004 FESTO4
---------------------------------------------------------------------
20   59                                               LIMNOCO3
    128 0.13                                          STUBAO7

     30 0.13   59 0.146 0.016 128 0.16              4 MICROCO3
      LINK TO CLUSTER  -3
---------------------------------------------------------------------
21   41                                               HAYBO2
     42 0.13                                          HAYBO3

     39 0.16   41 0.171 0.040  42 0.18           1004 HAYAO3
---------------------------------------------------------------------
22  114                                               STUBO1
    129 0.1[illegible]                                STUBBO1
    159 0.13  129 0.137 0.005 114 0.14                PACHYCO2

    182 0.13  159 0.157 0.021 129 0.17              4 PACHYIO1
```

```
        LINK TO CLUSTER  -1
---------------------------------------------------------------------
 23   179                                            PACHYG05
      180 0.13                                       PACHYG06

      162 0.14   180 0.136 0.002  179 0.14    4 PACHYD04
        LINK TO CLUSTER  -1
---------------------------------------------------------------------
 24   130                                            STUBB02
      186 0.14                                       PACHYJ09

      190 0.14   186 0.157 0.018  130 0.17    4 PACHYK10
        LINK TO CLUSTER  -1
---------------------------------------------------------------------
 25   155                                            PACHYB07
      178 0.14                                       PACHYG04

      171 0.14   178 0.176 0.037  155 0.21 1004 PACHYE08
---------------------------------------------------------------------
 26     6                                            TYPE06
       54 0.14                                       LIMNOB07

       74 0.14     6 0.176 0.035   54 0.21 1004 FESTA07
---------------------------------------------------------------------
 27   100                                            MACB06
      138 0.14                                       PACHY10
       78 0.14   100 0.157 0.013  138 0.17          MAC04

       77 0.14    78 0.164 0.006  138 0.19    4 MAC03
        LINK TO CLUSTER  -4
---------------------------------------------------------------------
 28    24                                            MICROB01
       46 0.15                                       LIMNOA01
       52 0.15    24 0.165 0:020   46 0.18          LIMNOB05

       30 0.15    24 0.157-0.008   46 0.17    4 MICROC03
        LINK TO CLUSTER  -3
---------------------------------------------------------------------
 29    83                                            MAC09
       91 0.15                                       MACA01
** NEEDED .GT. FOUND FOR NEXT OTU **

       77 0.15    83 0.292 0.145   41 0.44 1004 MAC03
---------------------------------------------------------------------
 30    84                                            MAC10
      113 0.15                                       MACC02

      107 0.15    84 0.165 0.015  113 0.18    4 MACB13
        LINK TO CLUSTER  -4
---------------------------------------------------------------------
 31     3                                            TYPE03
       93 0.15                                       MACA03

      102 0.15    93 0.157 0.003    3 0.16    4 MACB08
        LINK TO CLUSTER  -1
---------------------------------------------------------------------
 32    94                                            MACA04
      168 0.15                                       PACHYE05
```

```
          2 0.15   94 0.164 0.009 168 0.17    4 TYPE02
          LINK TO CLUSTER  =1
    ------------------------------------------------------------
     33   141                                        PACHY14
          181.0.15                                   PACHYG11

** NEEDED .GT. FOUND FOR NEXT OTU **

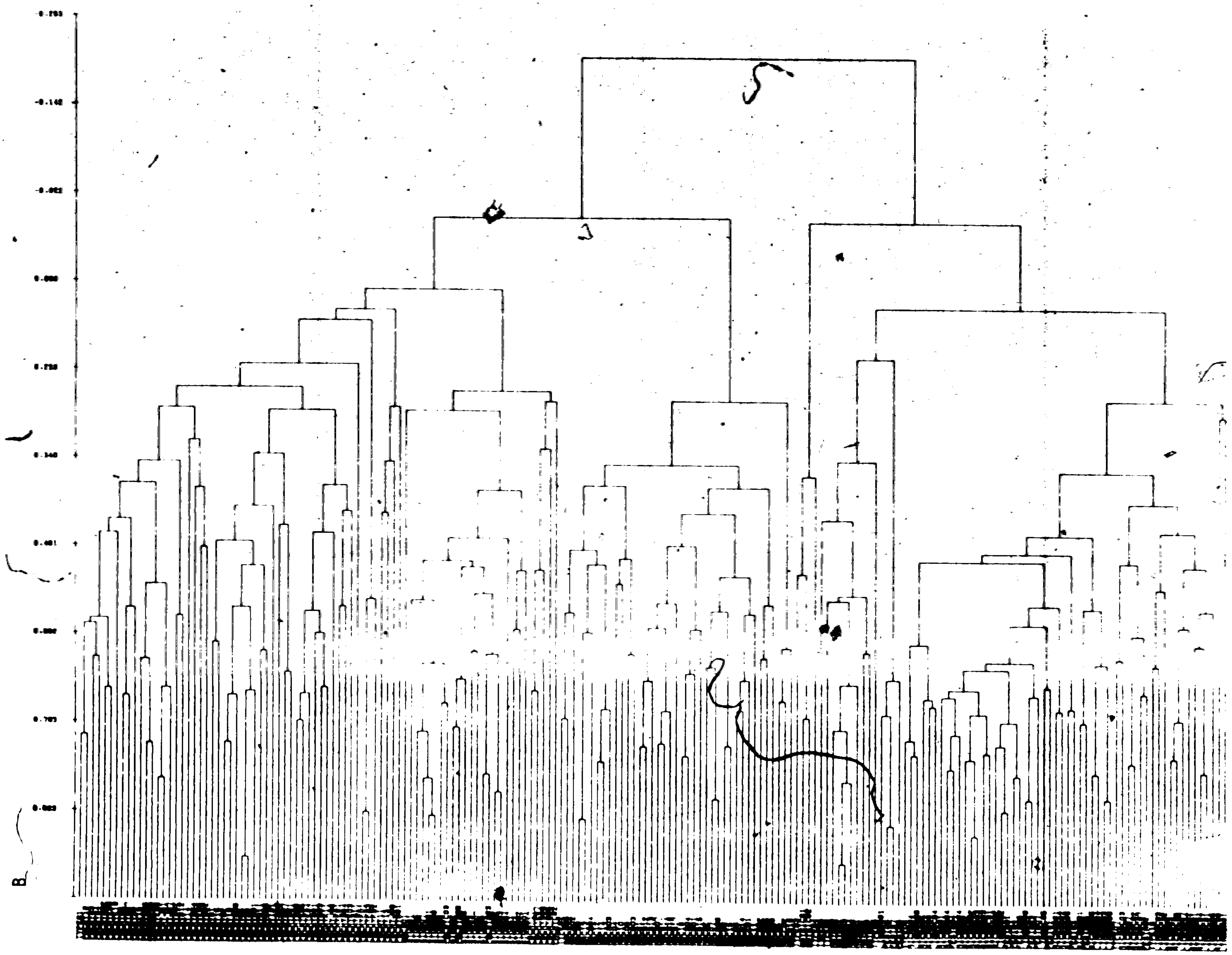
          109 0.15   181 0.296 Q.141   41 0.44 1004 MACB15
    ------------------------------------------------------------
     34    38                                        HAYA02
           40 0.16                                   HAYB01

           11 0.16   40 0.18[illegible] 0.025   38 0.21 1004 MICRD01
    ------------------------------------------------------------

    ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

    CLUSTER OTU LABEL
         35   4 TYPE04
         36   5 TYPE05
         37   7 TYPE07
         38   8 TYPE08
         39   9 TYPE09
         40  37 HAYA01
         41  43 HAYB04
         42  58 LIMNOCO2
         43  63 FEST03
         44 112 MACC01
         45 116 STUB03
         46 125 STUBA04
         47 167 PACHYE04
         48 175 PACHYG01
         49 187 PACHYK03
         50 188 PACHYK05
```

APPENDIX 7. PHENOGRAMS OF CLUSTAN ANALYSES
WITH OTU'S LABELED (A, analysis
with all characters; B, analysis
with reproductive characters)


B