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Cytotaxonomy of the Isoetes echinospora Complex[1]

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INTRODUCTION

The quillworts, or the genus *Isoëtes*, are among those fern-allies that are in great need of cytotaxonomical and experimental revision. Though Linnaeus (1753) recognized only a single species, later authors have generously described new species of this group even from very limited collections, with the result that Reed (1953) recognized over 610 names, representing, in the view of Lawrence (1951), only about 60 species. It is evident from the studies by Iversen (1928a,b) that several of the characters used for the separation of many of these taxa are taxonomically doubtful, and there is reason to believe that a few are only occasional edaphic modifications. Some are evidently good races which ought to be treated at the varietal or subspecific level, whereas still others are undoubtedly very good species.

Distinguishing four sections on the basis of surface characters of the megaspores, as proposed by Pfeiffer (1922), may be apparent rather than natural, but the morphological characters used in separating the monotypic genus *Stylites* (Amstutz, 1957) seem to be genuine. Though the distinction and relationship of Isoëtaceae to other ferns and fern-allies have been widely dis-

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cussed, the morphological method has been inadequate to decide if the family ought to be grouped as a class of its own (Lawrence, 1951), as a subclass of the Lycopsida (Pichi-Sermolli, 1959), or as an order between the Lycopsids and the eusporangiate ferns (Reed, 1953). The latter question is not likely to be solved by aid of biosystematic methods other than those utilizing biochemical approaches (cf. Bate-Smith, 1959), whereas cytological and experimental comparisons may contribute to the solution of the problems at a lower level.

Chromosome numbers from the diploid to the decaploid level are known from the genus *Isoëtes,* and distinct variations in length of the chromosomes and in the position of their centromeres perhaps may make it possible to recognize karyotypes and compare them from one taxon to another. The present study is an attempt to utilize some of these characters for the understanding of a disputed complex of such taxa, though it is perhaps most evident in this case that such methods are sometimes of a limited value as an additional indication of status, whereas they cannot and should not replace the classical morphological and geographical methods of approach.

OBSERVATIONS

ISOETES ECHINOSPORA Dur. *sensu stricto*

This species in its strict sense was described from Gironde in central France by Durieu (1861). It is a small plant with 10–30 submerged leaves, which vary in length between 5 and 50 cm. depending on locality and climate, soft and recurved. Stomata are usually absent on the leaves (cf. Iversen, 1928a). The sporangia are pale and unspotted, the velum is very narrow. The megaspores are 400–600 microns, densely echinate, with fine truncate spines, whereas the microspores are 20–35 microns in diameter. The taxon is distributed in boreal Eurasia but it is also met with in central Siberia (cf. Hultén, 1958). Its chromosome number was reported to be $2n = 22$ by Ekstrand (1920); this was confirmed by Ehrenberg (1945) though most of his plants seem to have had $2n =$ c. 100 chromosomes; this higher

number was also reported in a sample from Ireland by Manton (1950). It is possible that these latter numbers have been counted on hybrid populations or on specimens of *I. lacustris*, since the present writer found only $2n = 22$ chromosomes in plants from some localities in southern Sweden.

ISOETES MURICATA Dur.

A variable eastern North American species that was described by Durieu (1864) from live specimens sent from Woburn in Massachusetts and cultivated in the Botanical Garden at Bordeaux. In its typical form, var. *muricata*, it is a plant with rather long leaves, 10–15 cm. long, flaccid and commonly spirally twisted, slender and recurved. Stomata are present though not frequent on the leaves (Iversen, 1928a). The sporangia are pale and somewhat spotted, the velum covers ½ to ¾ of the sporangium. The megaspores are 200–700 microns, probably depending upon some environmental factors, covered with broad spinules that may be forked or toothed, whereas the microspores are 20–35 microns in diameter.

The variety *Braunii*, described by Durieu (1864) as a species from Lake Winnipesaukee in New Hampshire, is usually somewhat smaller, with leaves ranging in length between 5 and 30 cm. and there are a few stomata mainly on the tips of the leaves. The megaspores vary between 250 and 600 microns depending upon climate and locality: the smallest spores have been measured on plants from the deeper and colder parts of some Icelandic lakes, whereas in shallow and more warm parts of the same lakes the spores are invariably larger. The western extreme of var. *Braunii* is *I. echinospora* var. *truncata* A. A. Eaton (in Gilbert, 1901), whereas var. *Savilei* Boivin (1961) is either a forma, or, more likely, an arctic modification comparable to the plants from the deeper parts of cold Icelandic lakes mentioned above. The microspores of var. *Braunii* are 20–35 microns in diameter.

The variety *hesperia* was described by Reed (1945) from Bear Creek in Idaho, at the altitude of 2,250 meters. It is distinctly

smaller than typical and even arctic var. *Braunii*, with 10–20 leaves that are only about 5–15 cm. long. The sporangia are pale-spotted but the velum is narrow, covering about ¼ of the sporangium. The megaspores on specimens seen by the writer are 400–600 microns with long and fine spines, whereas the microspores are 25–35 microns in diameter.

As shown by Reed (1945), the typical var. *muricata* is distinctly an eastern American boreal plant. The var. *Braunii* is a transcontinental, and in the east somewhat more northern plant reaching to western Greenland and Iceland (Hultén, 1958; Löve & Löve, 1961a), whereas the var. *hesperia* is a plant of the western American mountains.

The chromosome number of eastern North American plants of var. *muricata* was reported as $2n = 24–26$ by Dunlop (1949), but Löve & Löve (1961a) found $2n = 22$ only in Icelandic material of the var. *Braunii*. This same number has also been confirmed by the writer on Quebec material of var *muricata*, on material from New Hampshire and Manitoba of var. *Braunii*, and on plants from the southern Canadian Rocky Mountains belonging to var. *hesperia*.

ISOETES MARITIMA Underw.

This is a plant with a few leaves, only 5–20, which are 2–5 cm. long, slender but rather rigid with fine-pointed tips; the stomata on the leaves are always numerous and scattered all over the surface. The sporangia are pale-spotted, the velum is narrow and covers ¼ to ½ of the sporangium. The megaspores are 350–600 microns, with rather thick and blunt spines, white; microspores are usually 30–40 microns in diameter.

This species was described by Underwood (1888) from a salt marsh near Alberni on Vancouver Island in British Columbia. It is distributed near the coast of the State of Washington, British Columbia, and Alaska to the Aleutian Islands and Commander Islands (Hultén, 1948) and seems to prefer somewhat saline localities. In the southernmost part of this area the taxon is represented by a variety *Flettii* (A. A. Eaton) Reed, which differs mainly in the width of the velum that covers ½ to ⅔ of

the sporangium. It is often so vaguely distinct from the main type that the writer hesitates to regard it as anything more than a southern ecotype.

Material from a salt marsh in western British Columbia near Vancouver, belonging to the typical race, was found to have $2n = 22$ chromosomes.

ISOETES ASIATICA (Makino) Makino

An eastern Asiatic plant distributed from Honshu to Sakhalin and the Kurile Islands and also met with in Kamtchatka (Hultén, 1958) and, according to Boivin (1961) reaching Alaska. It was described by Makino (1904) as a variety of *I. echinospora*, but later Makino (1914) lifted it to specific rank. The type locality is at Lake Nojiri in the mountains of the province Shinano in central Honshu, but the plant seems to be rare in the Japanese mountains. It differs from *I. echinospora sensu stricto*, in having a broader velum that covers $\frac{2}{3}$ to $\frac{3}{4}$ of the sporangium, and also in having coarser spinules on the macrospores and smoother microspores. There are usually only 5–30 leaves, 3–15 cm. long and rather rigid, without stomata. The chromosome number of this taxon is $2n = 22$, according to Takamine (1921).

CHROMOSOME MORPHOLOGY

The fixations used for this study were not made specially with studies on the morphology of the chromosomes in mind. However, the chromosomes of all the taxa mentioned above are rather long though distinctly variable in size within each chromosome complement. Their centromeres are usually median or submedian, but sometimes subterminal, and by aid of the centromere position and studies of the variations in length it is possible to recognize some of the chromosome pairs with reasonable certainty even when fixed with chromosome number determinations alone in mind. Comparisons of the chromosome complements of the taxa available to the writer seemed to indicate that possible differences in chromosome size and morphology between these taxa are not greater than variations met within each taxon, so it seems reasonably safe to conclude that these taxa at least

do not show any distinct differences in the morphology of their chromosomes; and the chromosome number $2n = 22$ is characteristic of them all.

TAXONOMICAL CONCLUSIONS

It has been concluded recently by Hultén (1958) that the main taxa here studied should be treated as varieties, or at most as subspecies, of a single circumpolar species. This is supported by the spore morphology of all the taxa and, also, by the stomatal characters studied by Iversen (1928a). Since the cytological observations seem to support the view that these taxa are only vaguely dissimilar though geographically and ecologically somewhat distinct, the writer agrees that they are conspecific races. Because the four main taxa constitute morphologically somewhat distinct regional groups of populations, they are logically treated at the subspecific level, whereas their somewhat more local minor races are distinguished as varieties only (Löve & Löve, 1961b). This has been proposed recently for the populations of the western Atlantic region by Löve & Löve (1961a) and, independently, by Boivin (1961).

Although the name of the European species, *I. echinospora* Dur., which is traditionally very well established, seems to be the oldest valid epithet within this group, it has been pointed out by Rothmaler (1944) that it is antedated by two other names. The oldest one is that of *I. setacea* described by Lamarck (1789), but since that name has not been used in this sense but rather in the sense of Delile (1827), Rothmaler (1944) proposed that it be rejected as a "nomen confusum"; in this the present writer agrees. The second valid name, according to Rothmaler (1944), should be *I. tenella* Leman (in Desvaux, 1827), which was based on the variety *tenella* of *I. lacustris* described by Leman (1822); the holotype of this name is the Tab. 191 in Flora danica (Oeder, 1766).

The description by Leman (1822) is short: "Une troisième variété, l'*isoëtes tenella*, croî en Danemarck: elle offre un très petit tubercule, d'oú partent six ou huit frondes sétacées, molles,

longues de trois pouces environ. Elle est figurée, planche 191 de la Flore danoise."

Since the description is inconclusive for a distinction between *I. lacustris* and *I. echinospora,* only the picture is left for the identification of the new spcies. Although Rothmaler (1944) did not hesitate to identify the picture with *I. echinospora,* Lange (1887)thinks it is *I. lacustris* and adds the remarks: "Nomine *Isoëtis lacustris* specimen delineatum est, ad Norderhoug Norvegiae lectum. Figura nimis imperfecta est ad dijudicandum, utrum *I. lacustris* L. vera, an *I. echinospora* D.R. pictori ante oculus fuit. Secundum Blytt (Norg. Fl. 3, p. 1238) utraque species hinc inde in Norvegia occurrit, locus autem in Fl. Dan. indicates inter stationes l.c. enumeratas non invenitur."

The present writer has seen the plate in question and agrees with Lange (1887) that it cannot be identified with any assurance with either *I. lacustris* or *I. echinospora.* Since not only Oeder (1766) himself but also Lange (1887) named it *I. lacustris,* the safest conclusion seems to be that this is correct, and the identification of this picture with *I. echinospora* as proposed by Rothmaler (1944) must be regarded as doubtful enough to be rejected.

The first certain name for a plant of the circumpolar group here treated is, thus, *I. setacea,* but since it is a "nomen confusum," the valid name is *I. echinospora* Dur. The typical subspecies of this taxon is, then, ssp. *echinospora*; the common North American plant is ssp. *muricata* (Dur.) Löve & Löve; the race in the salt marshes of the western coast of North America is ssp. *maritima* (Underw.) Löve, whereas the eastern Asiatic plant is to be named ssp. *asiatica* (Makino) Löve. The many formae listed by Reed (1953) on the authority of Gandoger (1891) and Iversen (1928a) can be dismissed, though the spore characters used by the latter certainly are important. The Asiatic and west-coast American races show small variations of little phytogeographical interest, whereas the more common North American race, ssp. *muricata,* includes at least three geographically somewhat distinct and ecologically remarkable varieties

of taxonomical interest, or var. *muricata,* var. *Braunii,* and var. *hesperia* (cf. Reed, 1945). A review of these taxa and their essential synonyms is given below.

ISOETES ECHINOSPORA Dur.

I. setacea Lamarck, 1789, non Bosc ex Delile 1827, nomen confusum.
I. tenella, sensu Rothmaler, 1944, non Leman, 1822.
I. echinospora Durieu, Bull. Soc. Bot. Fr. **8**: 164. 1861.
Calamaria echniospora Kuntze, Rev. Gen. Pl. **2**: 828.

ssp. ECHINOSPORA

I. echinospora s.str. auct. Eur. bor. et occid.

LOCUS CLASSICUS: Gironde, France.

GEOGRAPHICAL AREA: Northern and western Europe, from northern Spain to northern Norway, from Ural west to Ireland and the Faeroes; central Siberia, not in Iceland.

spp. MURICATA (Dur.) Löve & Löve

I muricata Durieu, Bull. Soc. Bot. Fr. **11**: 100. 1864.
I. echinospora ssp. *muricata* (Dur.) Löve & Löve, Bot. Notiser **114**: 49. 1961a. Boivin, Amer. Fern Journ. **51**: 83. 1961.

var. MURICATA

I. muricata Durieu (1864), 100, *sensu stricto.*
I. echinospora var. *muricata* (Dur.) Engelmann, in Gray's Manual ed. 5, 676. 1867.
I. Boottii Engelmann, in Gray's Manual ed. 5, 676. 1867.
I. echinospora var. *robusta* Engelmann, Transact. St. Louis Acad. Sci. **4**: 380. 1882.
I. echinospora Braunii f. *muricata* (Dur.) Clute, Fern Bull. **16**: 55. 1908.

LOCUS CLASSICUS: Woburn, Massachusetts.

GEOGRAPHICAL AREA: Eastern North America, from Novia Scotia south to New Jersey, west to Ohio and Michigan.

var. BRAUNII (Dur.) Löve & Löve

I. echinospora ssp. *muricata* var. *Braunii* (Dur.) Löve & Löve, Bot. Notiser **114**: 49. 1961a.
I. Braunii Durieu, Bull. Soc. Bot. Fr. **11**: 101. 1864, non Unger in Bruckman, 1850.
I. echinospora var. *Braunii* (Dur.) Engelmann in Gray's Manual ed. 5, 676. 1867.
I. echinospora ssp. *muricata* var. *Savilei* Boivin, Amer. Fern Journ. **51**: 85. 1961.

I. echinospora var. *Flettii* A. A. Eaton. Fern Bull. **13**: 51. 1905.

LOCUS CLASSICUS: Lake Winnipesaukee, New Hampshire.

GEOGRAPHICAL AREA: North America: Western Greenland and Newfoundland to Alberta and Yukon, south to Pennsylvania, Ohio, Minnesota, and Saskatchewan; Europe: Iceland.

var. **hesperia** (Reed) Löve, comb. nov.

I. muricata var. *hesperia* Reed, Amer. Fern Journ. **35**: 84. 1945.

LOCUS CLASSICUS: Bear Creek, Idaho.

GEOGRAPHICAL AREA: Alpine regions of western North America, from California, Idaho, Colorado, and Utah north to Alaska and Yukon.

spp. **maritima** (Underw.) Löve, comb. nov.

I. maritima Underwood, Bot. Gazette, **13**: 94. 1888.

I. Macounii A. A. Eaton, Fern Bull. **8**: 12. 1900.

I. echinospora var. *truncata* A. A. Eaton, in Gilbert, List North Amer. Pteridoph. 27. 1901.

I. echinospora var. *maritima* (Underw.) A. A. Eaton, Fern Bull. **13**: 52. 1905.

I. echinospora var. *Braunii* f. *maritima* (Underw.) Clute, Fern Bull. **16**: 55. 1908.

I. Braunii var. *maritima* (Underw.) Pfeiffer, Ann. Mo. Bot. Gard. **9**: 174. 1922.

I. beringensis Komarov, Bull. Jard. Bot. Acad. Sci. USSR **30**: 196. 1932.

LOCUS CLASSICUS: Alberni, Vancouver Island, British Columbia.

GEOGRAPHICAL AREA: Near the coast of western North America, from State of Washington, British Columbia and Alaska to the Aleutian Islands and Commander Islands.

ssp. **asiatica** (Makino) Löve, comb. nov.

I. echinospora var. *asiatica* Makino, Bot. Mag. Tokyo **18**: 129. 1904.

I. asiatica (Makino) Makino, Bot. Mag. Tokyo **28**: 184. 1914.

LOCUS CLASSICUS: Lake Nojiri, in the Shinano province, central Honshu.

GEOGRAPHICAL AREA: Japan, from Honshu to Hokkaido, in the mountains; Kurile Islands, Kamtchatka, Alaska (Boivin, 1961).

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A Resume of the Taxonomic Reorganization of Equisetum, Subgenus Hippochaete, IV.

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HYBRIDS

In the previous papers of this series I have given a key to, and short descriptions and discussions of, the sections, subsections, species, subspecies, and varieties of *Hippochaete*. My taxonomic system may appear simpler than those of previous workers. Probably the single most important factor contributing to an understanding of the taxa and their relationships was the discovery of extensive hybridization in the subgenus. To find six hybrids between various pairs among seven species certainly is unexpected, particularly in an ancient group of plants presumed to be evolutionarily static.

The identification of these hybrids was based on three kinds of evidence: spore abortion, morphology, and geographic distribution. Specimens with aborted spores, together with those vegetative specimens closely resembling them, were segregated into a group and their measurable characters were analyzed sta-