

## A Re-evaluation of *Isoetes savatieri* Franchet in Argentina and Chile

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**ABSTRACT.**—*Isoetes savatieri* has traditionally been interpreted as being a uniform aquatic ranging from the southernmost regions of South America to the central Andes of Chile and Argentina. An examination of herbarium material supports the recognition of two taxa, a southern *I. savatieri* and a more northern *I. chubutiana*, from central Chile and Argentina. The latter taxon is hexaploid and described here as a new species. The morphology of these species suggest that they are sister species resulting from divergence following a polyploidy event. These species, and several other species pairs, provide the best and, to date, only examples of allopatric divergence in polyploid *Isoetes*.

*Isoetes* is a nearly cosmopolitan genus of aquatic to sub-aquatic perennial lycopsids. Estimates of species number has ranged from 60 (Pfeiffer, 1922) to 150 (Tryon & Tryon, 1982). Recent systematic work in North America (e.g., Brunton & Britton, 1997, 1998; Caplen & Werth, 2000, 2000b) and South America (Small & Hickey, 2001; Hickey, 1994), however, indicates that even 150 is likely to be an underestimate. The actual number of species worldwide is probably closer to 350. There are several reasons for this large disparity. Despite a long history of systematic and morphological interest, the genus is poorly collected (Hickey *et al.*, 1989) and only sporadically studied. Aside from the classic 19<sup>th</sup> Century works of Baker (1880) and Motelay & Vendryès (1882) there has only been one modern systematic treatment of the genus worldwide (Pfeiffer, 1922). Pfeiffer's monograph stands as the classic treatment of the genus despite a number of significant but unavoidable flaws. Most significant among these is the lack of adequate Neotropical collections examined during the study. Pfeiffer, working out of the Missouri Botanical Garden, relied almost exclusively on specimens housed at F, GH, MO and US. She did not examine the many important collections held in Europe and Latin America and, as a result, was unable to develop a full appreciation of the diversity of the genus as it occurs in South America.

South America appears to be the center of both morphological and taxonomic diversity for *Isoetes* (Hickey, 1990). The richness of the South American flora was first evidenced in the work of Ulrich Weber (1922). In a revision of the South American species, he recognized 18 taxa, 11 of which he described as new. Weber's work, while certainly not complete or entirely



accurate, stands in contrast to the work of Pfeiffer which recognized only seven species for all of South America. The next significant work on South American *Isoetes* was that of Fuchs-Eckert (1982) in which he recognizes 75 species. In an overly conservative work, Hickey (1985) recognized 47 South American species but has since accepted considerably more (Hickey, 1994; Small & Hickey, 2001).

This paper adds to our knowledge of the genus in South America by describing a new species, allied to *Isoetes savatieri* Franchet. This new taxon was first recognized as distinctive by Fuchs-Eckert (1982) but was never validly published. We compare both species and continue a discussion (Hickey et al., 1989) on speciation in the genus.

***Isoetes savatieri*** Franchet, Bull. Soc. Bot. France 31:395. 1884. *Calamaria savatieri* (Franchet) Kuntze, Rev. Gen. Pl. 2:828. 1891–1893. *Isoetes lechleri* var. *savatieri* (Franchet) L. D. Gomez, Brenesia 18:5. 1980.—TYPE: Argentina, Puerto Bueno, 15 Feb 1877, *Savatier s.n.* (Holotype: P), *ex char.* Figs. 1–3.

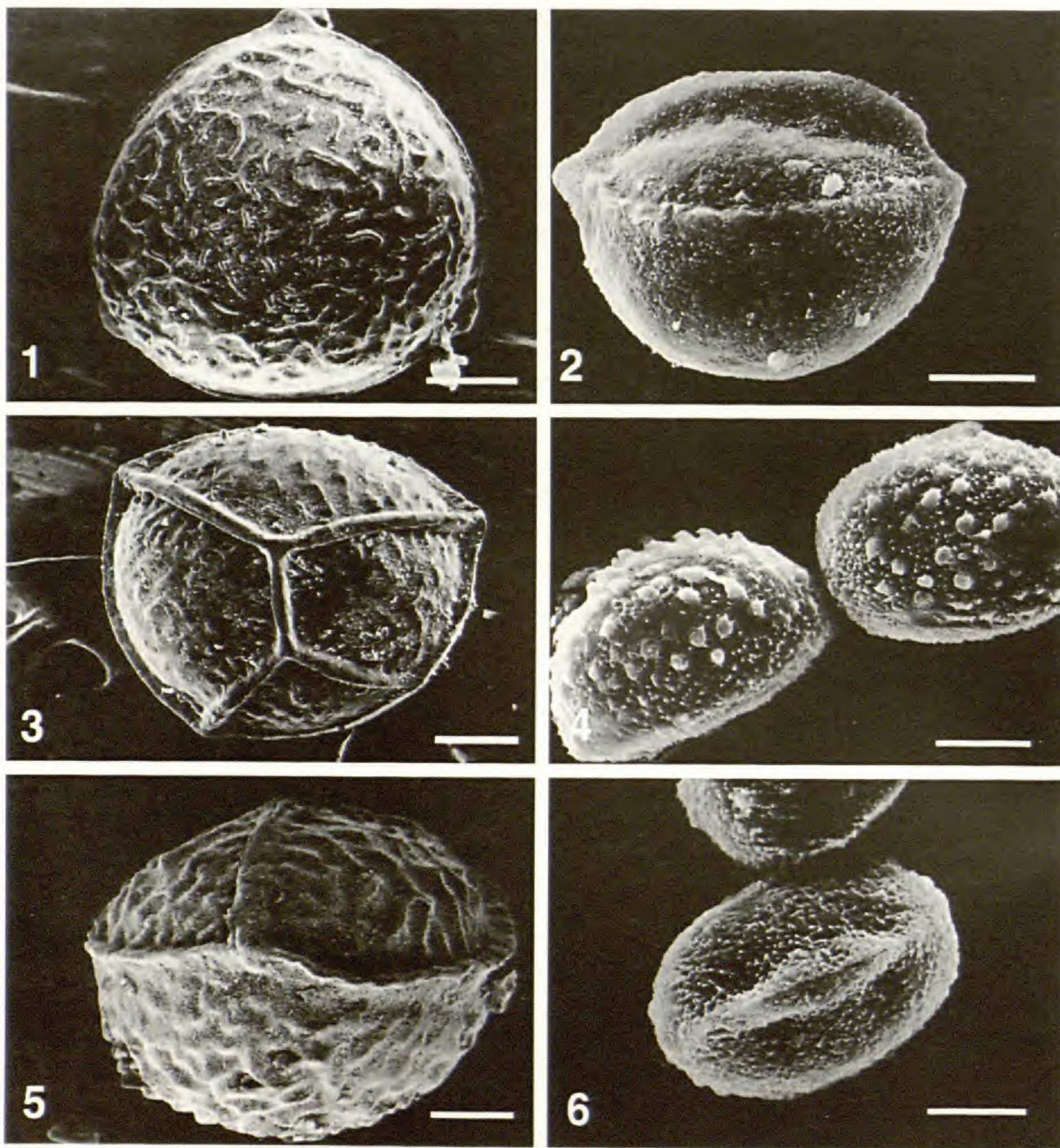
*Corm* globose to somewhat laterally elongate, 9–12 mm wide, 8–10 mm high, 2-lobed; *roots* dichotomous, arising synchronously within the continuous circumbasal fossa. *Leaves* 6–22, stiffly erect or slightly recurved, brittle, 42–163 mm long, 7–14 mm wide at the base, 1.8–5.0 mm wide at mid length; *alae* hyaline and chartaceous proximally, dark green and membranaceous distally, 1.0–3.5 mm wide at the sporangium, 12–65 mm long (extending up for 29–65% of the leaf length), each apex obtuse; *subula* terete, dark green, the apex short acuminate; *fibrous bundles* absent; *stomates* absent; *scale leaves* and *phyllopodia* absent. *Sporangium* circular to elliptic, hyaline, tan, concolorous, 3.0–9.5 mm long, 3.5–6.2 mm wide, basal. *Velum* incomplete, extending (0.5)1.5–2.5 mm down from the top of the sporangium. *Ligule* deltate to widely ovate, hastate-auriculate, delicate and ephemeral, 2.5–3.0 mm long, 1.8–3.3 mm wide. *Labium* inconspicuous, represented by a low, entire or scalloped ridge, light green, membranaceous, 40–60  $\mu\text{m}$  high, 70–100  $\mu\text{m}$  wide. *Megaspores* white to off-white, frequently lustrous, 370–580 ( $\bar{x}$  = 479)  $\mu\text{m}$  in diameter, rugulate or rarely tuberculate, *girdle* sparsely ornamented; *equatorial* and *proximal ridges* straight, distinct, as high as broad. *Microspores* light gray, 35.0–46.3 ( $\bar{x}$  = 39)  $\mu\text{m}$  long, 25.0–33.8 ( $\bar{x}$  = 29)  $\mu\text{m}$  wide, laevigate. *Chromosome number* unknown.

**DISTRIBUTION.**—Endemic to the low coastal regions around Tierra del Fuego in Chile.

**ECOLOGY.**—The limited ecological data suggest that this species is typically found below 200 m. The plant is apparently an obligate aquatic, inhabiting the shallows of streams and lake margins. Vegetative reproduction is frequent and is accomplished by the production of cortical gemmae. This species produces megaspores and microspores January through April.

*Isoetes savatieri* is characterized by an acuminate leaf apex, a hastate-auriculate ligule, a partial velum, and a minute labium. It differs from *I.*





FIGS. 1–6. SEM images of *Isoetes* megaspores and microspores. 1. Distal view of *I. savatieri* megaspore (Borge s.n., NY). 2. Equatorial view of *I. savatieri* microspore (Borge s.n., NY). 3. Proximal view of megaspore of *I. savatieri* showing tetra-*radiate* proximal ridges (Borge s.n., NY). 4. Distal views of *I. chubutiana* microspores showing broad echinate surface markings (Taylor 6168, LP). 5. Equatorial view of megaspore from *I. chubutiana* (Taylor 6168, LP). 6. Proximal view of *I. chubutiana* microspore showing mono-*lete* suture (Taylor 6168, LP). Bars in figs. 1, 3, and 5 are 100 $\mu$ m; those in 2, 4 and 6 are 10 $\mu$ m.

*chubutiana* in leaf shape, in particular leaf width and apex shape, and to a lesser extent in spore morphology (Table 1). *Isoetes savatieri* has a blunt apex with a distinct acumen, whereas *I. chubutiana* generally has a more tapering apex and less obvious acumen. *Isoetes savatieri* has broad, short leaves; the range in leaf width is 2–5 mm, with a mean and mean of 3 mm. The leaf width/



TABLE 1. Comparison of traits in *Isoetes savatieri* and *I. chubutiana*.

	<i>I. savatieri</i>	<i>I. chubutiana</i>
Leaf width (mm)	1.8–5.0 ( $\bar{x} = 3$ )	1.5–2.2 ( $\bar{x} = 1.7$ )
Leaf width/length ratio	9–47 ( $\bar{x} = 24$ )	19–98 ( $\bar{x} = 62$ )
Leaf apex shape	blunt	tapering
Acumen	distinct	weak
Alae development: % of leaf length	29–65	18–30[45]
Alae apex shape	obtuse	attenuate
Megaspore surface morphology	rugulate to rarely tuberculate	sparsely to densely rugulate, to cristate, to reticulate
Megaspore size ( $\mu\text{m}$ )	370–580 ( $\bar{x} = 479$ )	460–750 ( $\bar{x} = 595$ )
Microspore surface morphology	laevigate	sparsely to densely echinate; the spines narrow to broad based
Microspore length ( $\mu\text{m}$ )	35.0–46.3 ( $\bar{x} = 39$ )	33.8–41.3 ( $\bar{x} = 39$ )
Microspore width ( $\mu\text{m}$ )	25.0–33.8 ( $\bar{x} = 29$ )	26.2–33.8 ( $\bar{x} = 30$ )

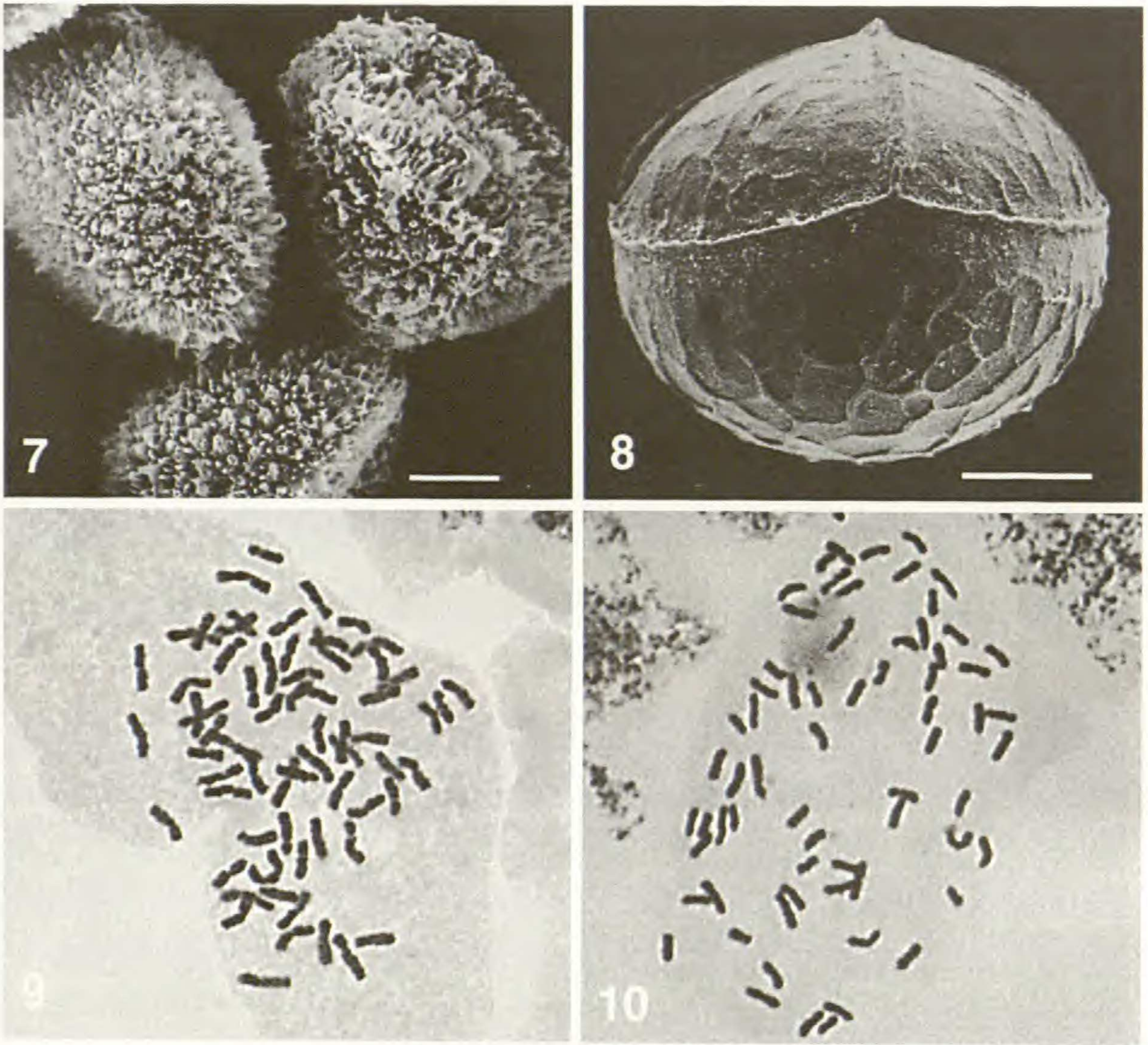
length ratio ranges from 9 to 47 with a mean of 24. In *I. chubutiana*, the leaves are narrower; leaf width ranges from 1.5–2.1 mm with a mean of 1.7 mm and a mode of 1.5 mm. The leaf length/width ratio ranges from 19 to 98 with a mean value of 62.

Megaspores of *I. savatieri* are rugulate except in some individuals of *Donat 380* where the spores are tuberculate. Some of the spores of this collection have the tubercles confluent to form short muri, approaching a rugulate condition. The megaspores of *I. chubutiana* are more variable; they range from sparsely to densely rugulate to cristate and finally to reticulate. Although there is a tendency in the latter species to produce a greater number of leaves and to have larger megaspores, these differences are not reliable enough for identification purposes. The microspores of *I. savatieri* are laevigate, whereas in *I. chubutiana* they are sparsely to densely echinate. In all other characters the two taxa are virtually indistinguishable. *Isoetes savatieri* is geographically separated from *I. chubutiana* by some 1000 km.

The megaspores of *Isoetes savatieri* are about the same size as those of the hexaploid *Isoetes chubutiana* suggesting they are the same ploidy level (Small & Hickey, 2001; Troia, 2001).

**SPECIMENS EXAMINED.**—**CHILE. Magallanas:** Laguna Maravilla, in altitudine bimetralli, 22 Mar 1899, *Borge s.n.* (GH, NY, US); Lago del Toro (L. Maravilla), La Península, 10 Mar 1941, *Santesson 1747* (S); Region Riesco; 22 Mar 1931, *Donat 380* (BM, F, GH, LIL, M, NY, SGO, U); en charcos con gramineas, Jun 1972, *Gomez PAT3803* (CR); Isla Desolación, Puerto Angosto, 6 Apr 1896, *Dusen 705* (LIL, MO, O, S, UPS[2]); SE of Caleta, Josefina (Onaisin) on rd to Río Chico, 53°32'S, 69°09'W, *Bolax-Empetrum* heath near lake, 11 Nov 1971, *Moore 2423* (H, HIP); Laguna "El Parrilar;" sumergida a +/- 10 cm bajo nivel inferior de las aguas, entre piedras, suelo arenoarcilloso, 7 Feb 1971, *Pisano 2938* (HIP); arrojado a la playa por las olas, 26 Jan 1973, *Pisano 3871a* (HIP); Isla Rennel Norte, Canal Smyth, 74°12'S, 51°54'W, river bottom, rocky bottom w/ ferric accumulation, submerged +/- 0.3 m, *Transecta Botánica de Patagonia Austral 1151* (HIP-2); consolidated organic mud rich in iron, *Transecta Botánica de Patagonia Austral 1205* (HIP).





FIGS. 7–10. *Isoetes chubutiana*. 7. Proximal and equatorial view of microspores (Taylor 6171, LP); scale bar = 10  $\mu$ m. 8. Equatorial view of megaspore with smooth girdle and retate surface markings (Taylor 6171, LP); bar = 100  $\mu$ m. 9. Root tip squash of  $2n = 66$  (Taylor 6171, MIL). 10. Root tip squash of  $2n = 66$  (Taylor 6168, MIL).

*Isoetes chubutiana* Hickey, Macluf & W. C. Taylor, *spec. nov.*—TYPE: Argentina: Gob. Rio Negro, Lago Hess, 10 Jan 1945, Meyer 8077 (holotype: LIL; isotypes: NY, UC). Figs. 4–10.

*I. valdiviensis* H. P. Fuchs, *nom.nud.*, Proc. Kon. Ned. Akad. Wetensch. C85:255. 1982.

*I. Meyeri* Fuchs, *nom. nud.*, Proc. Kon. Ned. Akad. Wetensch. C85:231, 241, 242, 255. 1982. Based on: Argentina; Gob. Rio Negro, Cascado del Rio Manso, 30 Jan 1945, based on Meyer 8238 (LIL!).

*Cormus* globosus usque lateraliter elongatus, bilobatus, 4–23 mm latus, 3–10 mm elatus; *radices* dichotomae, e fossa singulari circumbasali exoriente. *Folia* 9–30, rigide erecta vel raro recurva distale, fragilia, 40–280 mm longa, 6.0–9.0



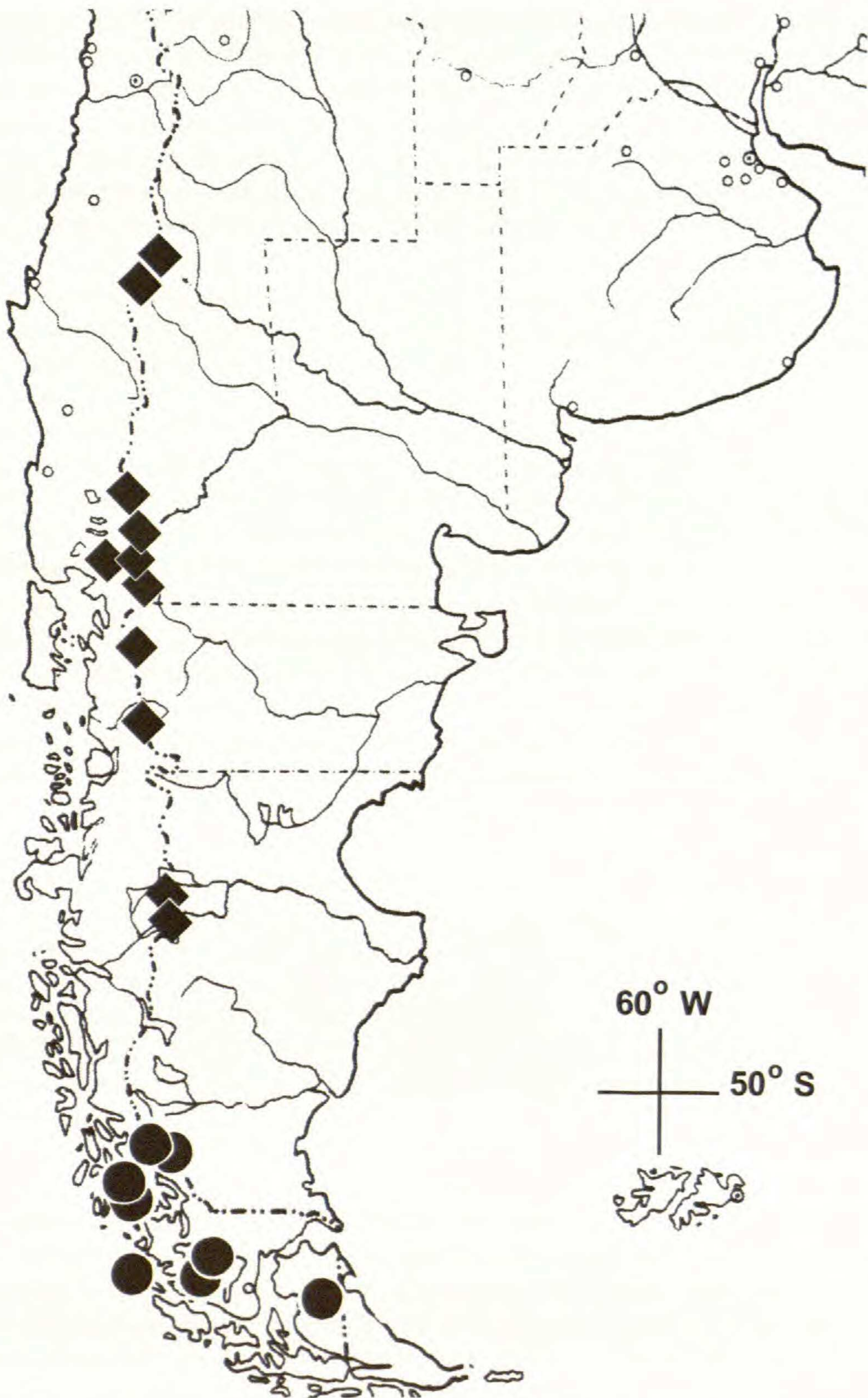


FIG. 11. Distribution of *Isoetes savatieri* (circles) and *I. chubutiana* (diamonds).



mm basi lata, 1.5–2.2[3.0] mm medio lata; *alae* proximale hyalinae et chartaceae, distale atrovirides et membranaceae, 11–55 mm longae (18–30[45]% per foliae longitudinem ascendentes), apicibus attenuatis; *subula* teres, atroviridis, apice longe acuminato; *fasciculi fibrosi peripherici*, *stomata*, *squamae* et *phyllodia absentia*. *Sporangium* circulare usque ellipticum, hyalinum, concolor, 2.8–6.7 mm longum, 2.8–5.7 mm latum, basale. *Velum* incompletum, descendens ad 0.7–2.7 mm. *Ligula* deltata usque late ovata, cordata usque hastata, viridi-nigra, tenella atque fugax, 1.5–3.0+ mm elata, 1.7–2.3 mm lata. *Labium* inconspicuum usque absens. *Megasporae* albae usque cretaceae, saepe nitidae, 460–750 ( $\bar{x} = 595$ )  $\mu\text{m}$  diametro, rugulosae usque rugulosae-cristatae vel reticulatae; *zona* non dissimilis usque laevis; *cristae* aequatoriae proximalisque rectae, distinctae, non altiores quam latae. *Microsporae* cinereae usque brunneae, 33.8–41.3 ( $\bar{x} = 39$ )  $\mu\text{m}$  longae, 26.2–33.8 ( $\bar{x} = 30$ )  $\mu\text{m}$  latae, sparse usque dense echinatae. *Chromosomatum numerus*  $2n = 66$ .

*Corm* globose to somewhat elongate laterally, 4–23 mm wide, 3–10 mm high, 2-lobed; *roots*, dichotomous, arising synchronously within the continuous circumbasal fossa. *Leaves* 9–30, stiffly erect or more rarely recurved distally, brittle, 40–280 mm long, 6.0–9.0 mm wide at the base, 1.5–2.2(3.0) mm wide at mid length; *alae* hyaline and chartaceous proximally, dark green and membranaceous distally, 1.2–3.0 mm wide at the sporangium, 11–55 mm long (extending up for 18–30(45)% of the leaf length), each apex attenuate; *subula* terete, dark green, the apex long acuminate; *fibrous bundles* absent; *stomates* absent; *scale leaves* and *phyllodia* absent. *Sporangium* circular to elliptical, hyaline, tan, concolorous, 2.8–6.7 mm long, 2.8–5.7 mm wide, basal. *Velum* incomplete, extending 0.7–2.7 mm down from the top of the sporangium. *Ligule* deltate to widely ovate, chordate to hastate, black, delicate, ephemeral, 1.5–3.0+ mm high, 1.7–2.3 mm wide. *Labium* inconspicuous to absent. *Megaspores* white to off white, often lustrous, 460–750 ( $\bar{x} = 595$ )  $\mu\text{m}$  in diameter, rugulate, rugulate-cristate, to reticulate, *girdle* undifferentiated to smooth; *equatorial* and *proximal ridges* straight, distinct, as high as broad. *Microspores* light grey to dark brown, 33.8–41.3 ( $\bar{x} = 39$ )  $\mu\text{m}$  long, 26.2–33.8 ( $\bar{x} = 30$ )  $\mu\text{m}$  wide, sparsely to densely echinate. Chromosome number  $2n = 66$ .

DISTRIBUTION.—Endemic to the central Andes of Chile and Argentina.

ECOLOGY.—*Isoetes chubutiana* grows at elevations of 750 to 1300 m as a submerged aquatic in the shallows of streams and lakes. Collections from November, January, February, March and April have megaspores and microspores. Collections from May have only microspores. The absence of collections from the rest of the year precludes further statements about yearly phenology. *Isoetes chubutiana*, like a number of species of the central and south central Andes, reproduces asexually by the production of cortical gemmae.

In technical characters of the sporangium, velum, and ligule, *I. chubutiana* is indistinguishable from *I. savatieri*. It can be distinguished from it however by leaf form, as described under *I. savatieri*, and to a lesser extent by megaspore morphology.



The names *I. valdiviensis* and *I. meyeri* were published by Fuchs-Eckert (1982) without latin or english descriptions as part of an enumeration of South American species. In addition, *Diem 1105* (GH) is annotated as the type of the unpublished "herbarium" name *Isoetes chilensis*. This plant and those annotated as *I. Meyeri* and *I. valdiviensis* are best accommodated within *I. chubutiana*.

Megaspore and microspore ornamentations are extremely variable in this otherwise uniform taxon. The most common megaspore type in the southern portion of the range is rugulate while the more northerly collections are typically reticulate. In all other South American species with reticulate megaspore ornamentation the microspores are laevigate. In this species, however, the microspores generally have an underlying or dominant echinate surface pattern. The presence of reticulate megaspores in this species provides additional evidence of convergence in spore morphology and seriously undermines the recognition of a Section *Terrestres* (*sensu* Fuchs, 1982; = *Reticulatae* of Pfeiffer, 1922), a section currently based almost exclusively on the presence of reticulate megaspores.

PARATYPES.—**CHILE. Aysen:** Lago Gral, Paz, 15 Apr 1943, *Maldonado 288* (LP); Chile chico, a orillas del algo, 3 Dec. 1946, *Castillo s.n.* (CONC); Ventisquero Soler, 24–25 Mar 1967, *Seki 581III* (CONC). **Llanquihue:** La Turbina, Payne, en orillas del Río Payne, después del Salto Chico, 22 Feb 1974, *Pisano 4304* (HIP); Puerto Varas, Puella, Rigi, 125 m, 41°06'S, 72°02'W, Mar 1967, *Zollitsch 298* (CONC). **Osorno:** Isla de Rupanco, hidrofito crece a poca profundidad (1 m) orillas, 15 Mar 1978, *Godoy s.n.* (SGO); Isla de Rupanco, acuática, se desarrolla a 1 m de profundidad en el lago Rupanco, 7 Mar 1979, *Godoy 3* (SGO); Isla de Rupanco, acuática, se desarrolla a 1 m de profundidad y en orillas sobre arena, 7 Mar 1979, *Godoy s.n.* (SGO); Lago Rupanco, Río Pecaderos, 8 Dec 1945, *Rudolph 43,676* (CONC); Lago Puyehue, (Isla Fresia), costa en sur y vuelta (en el agua), 5 Feb 1954, *Levi Heins 1744* (CONC).

**ARGENTINA. Neuquen:** Depto. Minas, Lagunas Epu-Lauquen, Aduana Vieja, sumergida en las orillas de las lagunas, +/- 50 cm de profundidad, 1300 m, 15 Jan 1964, *Boelcke et al. 10871* (BAA, SI); extremo norte de la laguna Varvarco Campos, orillas, 2 Feb 1970, *Boelcke et al. 14336* (BAA), *14337* (MU, SI); Puerto Manzano, 13 Feb 1934, *Burkart 6499* (BM, SI); Lago Espejo y correntoso, 1 m profundidad, 16 Apr 01, *Meier s.n.* (LP); Lago Lacar, playa cerca a San Martín de Los Andes, 1 Mar 1966, *Burkart & Troncoso 26447* (SI, UC); Lago Totoral, bei niedrigem wasserstand beinahe ausserhalb des Wassers, 900 m, 22 Feb 1970, *Diem 3379* (L, M, NY); Quetrihue, en aguas tranquilas, 1 m bajo el agua, 30 May 1942, *Diem 646* (SI); Punta Quethihue, en playas inundadas, formando comunidades puras y numerosas, 770 m, 8 Mar 1959, *de la Sota 2167* (LIL). **Rio Negro:** Lago Nahuel Huapi: Puerto Pañuelo, a 1–2 m de profundidad en las aguas, 15 Feb 1934, *Burkart 6548* (SI); Puerto Pañuelo, Feb 1911, *Hauman 1* (LIL); Parque Nacional Nahuel Huapi, E side of Lago Guillermo, plants firmly anchored in sandy humus among rocks, submerged 0.75–1.0 m, elev. 840 m, 41°22.3'S, 71°29.7'W, 17 Mar 2001, *Taylor 6168* (LP,



MIL); Parque Nacional Nahuel Huapi, S side of Lago Mascardi, plants firmly anchored in sandy humus among rocks, submerged 0.75–1.0 m, 41°21.35S, 71°34.3'W, 822 m, 17 Mar 2001, *Taylor 6171* (LP, MIL); Lago Frias, 1–2 m bajo agua en extensas colonias enterreno arcuosa-arculoso, 800 m, 1 Nov 1947, *Diem 1105* (GH). Cascado del Río Manso, 30 Jan 1945, *Meyer 8238* (LIL). **Chubut:** Lago Futalaufquen, 14 Jan 1945, *Castellanos 114242* (AA); Lago Futalaufquen, Reserva Nacional de los Alerces, 27 Mar 1949, *Pedersen 302* (C, S); Lago Verde, Parque Nac. Los Alerces, sumergida en el río, 25 Feb 1950, *Soraimo 4287* (BAA).

An interesting aspect of both species is the sporadic occurrence of irregular spores. In *Donat 380* (*I. savatieri*) the megaspores show a high degree of size dimorphism whereas the microspores show ca. 70% spore abortion. *Borge s.n.* (*I. savatieri*) contains megaspores with occasional tetraradiate meiotic scars (Fig. 3), often an indication of meiotic irregularity, but shows only 1–2% microspore abortion. In *I. chubutiana*, a plant from *Castellanos 11424* has very irregular megaspores, both in size and shape, yet has perfectly normal microspores. Such situations are frequent in other species of the genus, for example, in occasional specimens of *I. storkii* Palmer from Cerro de la Muerte of Costa Rica and in *I. Luetzelburgii* Weber of Brazil. More comparable is the situation in the *Isoetes lechleri* Mett. complex of Peru and Bolivia (Hickey, 1994). In that complex both of the currently recognized members, *I. lechleri* and *I. herzogii* Weber, appear to be tetraploid and, like the two members of the *I. savatieri* complex, reproduce asexually by means of cortical buds. Members of the *I. lechleri* complex are notorious for their high rate of megaspore abnormalities, reminiscent of meiotic irregularity. Hickey (1994) hypothesized that this phenomenon was the result of polyploidy followed by differential gene silencing and, through subsequent out-crossing, the accumulation of reciprocal gene silencings (Werth and Windham, 1991). The spore abortion seen in *I. savatieri* and *I. chubutiana* is likely to be of similar origin.

The hexaploid *I. chubutiana* is probably the result of stabilization through polyploidy of a sterile triploid, with the triploid springing from a hybridization event between a tetraploid and a diploid. A number of features suggest that the tetraploid parent was a member of the *I. lechleri* complex. That complex and the members of the *I. savatieri* complex share cortical gemma production and a turgidly brittle leaf habit, both unusual features in the genus. In addition, they share a similar habit, similar spore morphology, and have nearly contiguous ranges. The rugulate *I. herzogii* is more likely involved than the laevigate *I. lechleri*. The diploid parent might be *I. boliviensis* Weber of Bolivia and Peru or *I. alcalophila* Halloy (interpreted here as including *I. escondidensis* Halloy) of northern Argentina. *Isoetes hieronymii* Weber is another possibility, being found in northern Argentina and proximate to the range of the *Isoetes lechleri* complex, but its chromosome number is not yet known.

Taylor and Hickey (1992) discussed the mechanisms of speciation in *Isoetes* and have noted two predominant patterns. The first is characteristic of lowland diploid taxa and involves allopatric divergence. The second is allopolyploidy. The latter is common in “social” species, typically aquatics of temperate or



tropical upland regions. Little attention has been given to the origin of lowland polyploids nor has convincing evidence been provided for divergence subsequent to a polyploid event. Perhaps the best potential example of polyploid divergence was to be found in the *Isoetes riparia* Engelm. complex of eastern North America (Proctor, 1949). This assemblage of tetraploids includes several specific and subspecific segregates that have variously been elevated in rank or subsumed since their initial descriptions. The two best known segregates are *I. saccharata* Engelm. and *I. canadensis* (Engelm.) A. A. Eaton. Recently, however, it has been shown that this *I. riparia* complex is polyphyletic and consists of a number of similar but phylogenetically distinct polyploids sharing some but not all ancestors (Caplen & Werth, 2000a, 2000b).

In South America, there are several good candidates for divergence following polyploidy. Within the *Isoetes lechleri* complex, there is a tremendous amount of inter-populational differentiation, and a number of specific segregates have been proposed (Fuchs-Eckert, 1982; Hickey, 1985). Hickey (1994) argued that most of these segregates are best accommodated in a more inclusive *I. lechleri*. However, the populations from central and southern Bolivia form a cohesive assemblage distinct enough from the northerly *I. lechleri* to be recognized at the specific level as *I. herzogii*. Similarities in morphology, identical chromosome number, spore abortion, and cortical gemmae in *I. lechleri* and *I. herzogii* argue strongly for a divergent rather than an independent origin for these tetraploids. Likewise, similarity in morphology, spore ornamentation, spore size, and geography supports an allopatric-divergence model for the *I. savatieri-chubutiana* polyploid pair. These examples then represent the best evidence to date for allopatric speciation in polyploid *Isoetes*.

The combination of a high incidence of polyploidy in the genus (58.1%, Troia, 2001) and the rarity of allopatric polyploid speciation is surprising. It suggests that *Isoetes*, which appears to date back to the earliest Triassic (Grauvogel-Stamm and Lugardon, 2001), as *Isoetites*, has persisted through geologic time primarily as basic diploids. It further suggests that either polyploidy is a relatively recent process in the genus and/or that polyploids are ephemeral taxa that position themselves temporarily in vacant niches. Support for both of these models comes from the modern distribution of polyploids: most polyploids being found in fairly recent habitats such as temperate, glaciated regions, areas affected by such glaciations, or high altitude páramos and lakes. These models are also supported by allozyme studies: polyploid *Isoetes* appear to retain fixed heterozygosity and show little or no evidence of extensive diploidization (Caplen and Werth, 2000a, 2000b), suggesting relatively recent origins. The preponderance of data concerning *Isoetes* evolution suggest that polyploids are of little consequence from a divergence standpoint, but certainly do evolve by way of additional rounds of polyploidy.

Morphological, geographic and cytological data from the *I. savatieri-I. chubutiana* and the *I. lechleri-I. herzogii* pairs provide an arena to test whether there is a third model of speciation, divergence following polyploidy, occurring in the genus. Other wide-ranging tetraploids such as the lowland *I. panamensis* Maxon & C. V. Morton, which ranges from Central America to



Paraguay, and the *I. triangula* complex of Mexico, Venezuela, Brazil, and French Guiana (Stolze and Hickey, 1983; Hickey, 1985; Hickey, 1988) should be studied for additional examples of this evolutionary model.

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