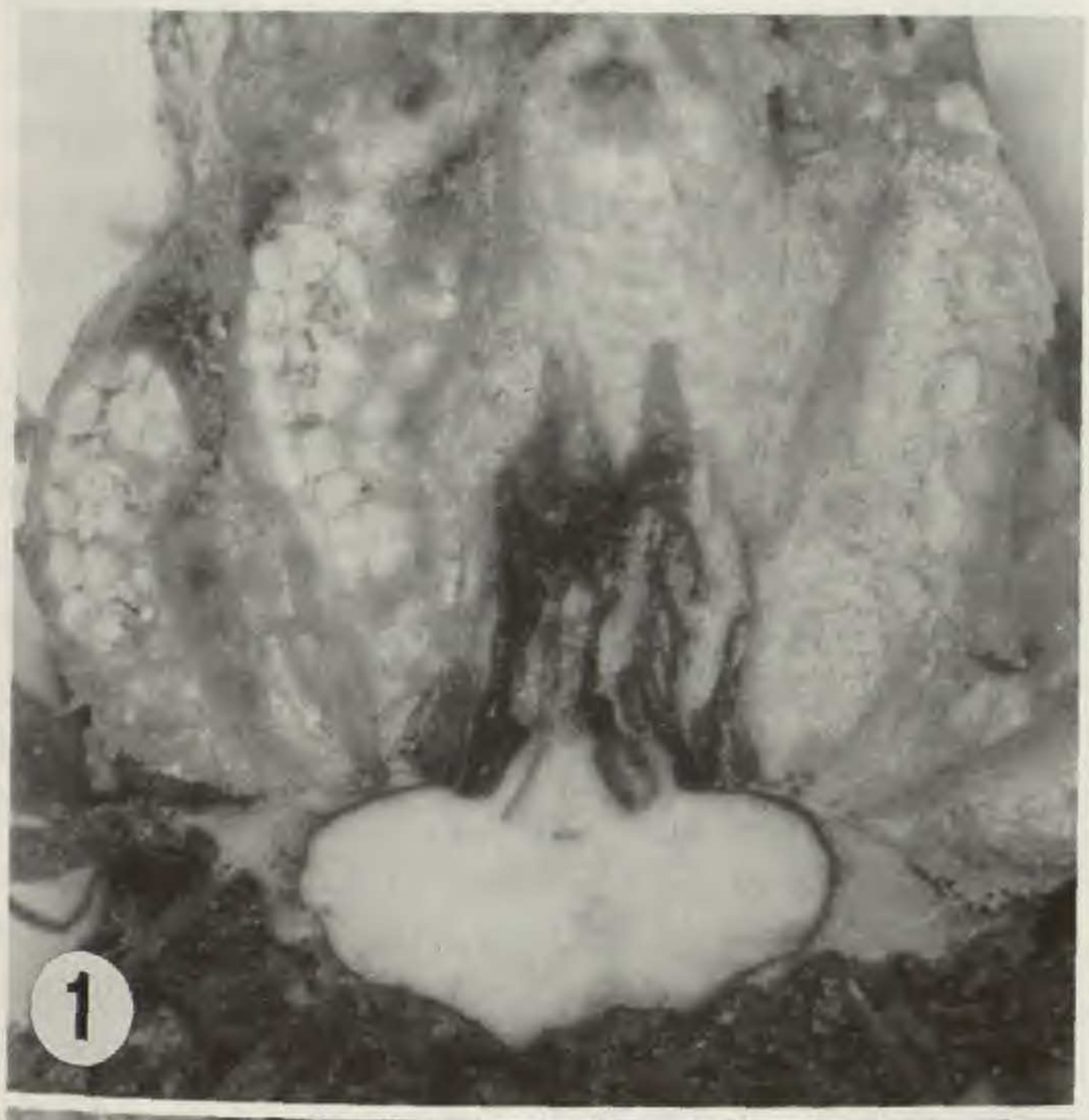
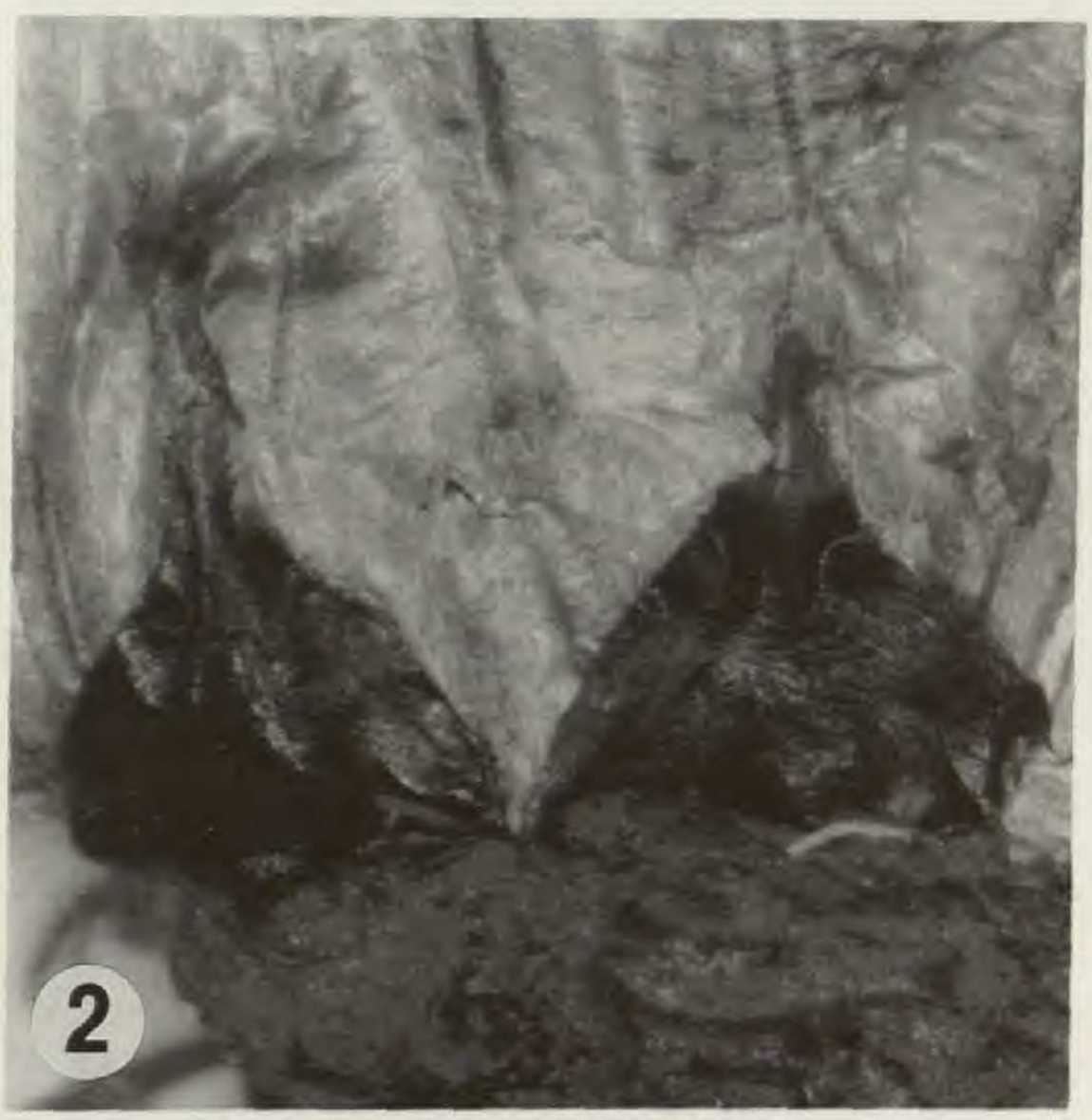
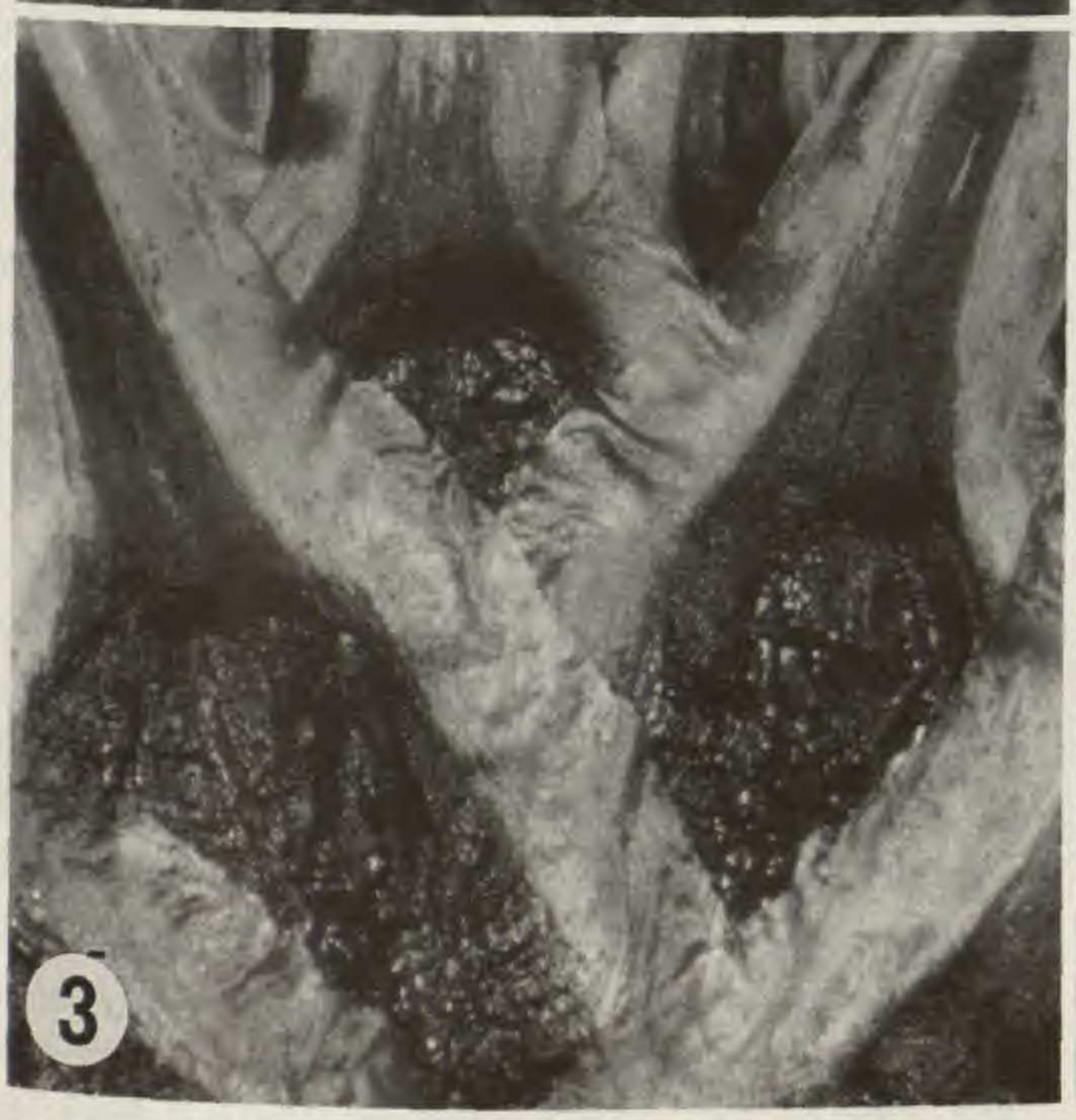
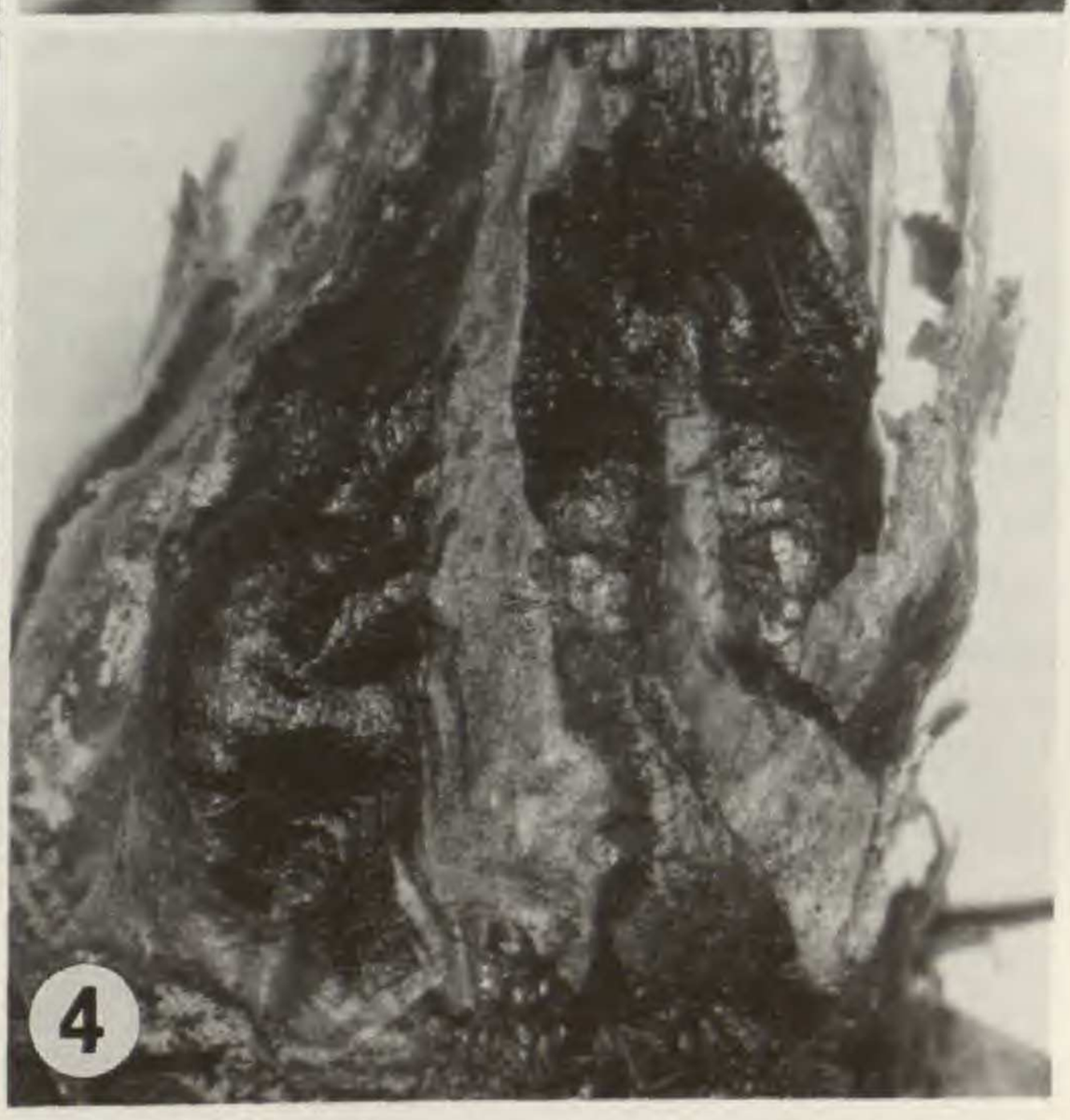








FIGURES 1–4. Scales and phyllopodia in *Isoetes*.—1. Transection through corm and leaf bases of *I. nuttallii*. Scales surround corm apex during summer dormancy.—2. Leaf bases of *I. nuttallii* surrounded by scales. Near end of growing season, scales have been displaced to peripheral position by current season's growth.—3. Sclerified leaf bases of *I. howellii* near end of growing season.—4. Phyllopodia (remnants of sclerified leaves) surround corm apex during summer dormancy.

This group of nonsclerotic species, defined by scarious, persistent leaf bases, is centered in India and represents a distinctive element within subgenus *Isoetes*:

Isoetes sect. **Coromandelina** Hickey & Taylor, sect. nov.

TYPE: *I. coromandelina* L.f., Suppl. Pl. 447. 1781.

Species foliorum basibus scariosis, persistentibus.

The remaining species of subgenus *Isoetes* comprise section *Isoetes*, which is here redefined as those subulate taxa that have, or were presumably derived from taxa that had, the ability to produce sclerotic pigmentation in leaf primordia, leaf bases, or sporangial tissue. As so defined, section *Isoetes* contains most of the extant species of the genus. It is an extremely diverse assemblage including both terrestrial and aquatic species, which are found throughout Africa, Australia, Europe, Asia, and the New World. By comparing the morphology of these species with that found in subgenus *Euphyllum* and section *Coromandelina* of subgenus *Isoetes*, we can polarize several included characters (Watrous & Wheeler, 1981). Notable among these are velum and labium development. Analyses in-

TABLE 1. Polyploid series for North American aquatic species of *Isoetes*.

Species	Chromosome number ($2n$)
I. lacustris	110
I. occidentalis	66
I. maritima, I. riparia, I. tuckermanii	44
I. bolanderi, I. echinospora, I. engelmannii, I. prototypus	22

dicate that the absence of a velum and the presence of a large, well-developed labium are plesiomorphic conditions (Hickey, 1985). In addition, the generalized condition of tuberculate (sensu Pfeiffer, 1922) megaspores is likewise plesiomorphic. When section *Isoetes* is analyzed for these character state distributions, two facts are immediately evident. First, species retaining all plesiomorphic conditions are terrestrial or amphibious; and second, nearly all aquatic species have derived or intermediate states for these characters, regardless of their geographic location. These data strongly suggest that the aquatic condition seen in most temperate and high-altitude tropical species is a secondarily derived condition that has evolved independently in unrelated lineages (Hickey, 1985).

The more plesiomorphic taxa of section *Isoetes* show a distinctly southern or Gondwana distribution, most evident in Africa and South America, whereas derived members of the section are generally Laurasian, but with close affinities to species of proximate Gondwana landmasses. These observations, coupled with data on section *Coromandelina*, suggest that subgenus *Isoetes* had its origin within Gondwana and subsequently radiated northward into Laurasia. Such hypotheses are strongly corroborated by the distribution of other character states, including the persistence of leaves during cold and drought periods, megaspore surface morphology, and electrophoretic anomalies such as the migrational location of TPI-2 (triosephosphate isomerase-2) and the presence or absence of anomalous TPI-3 activity (Hickey et al., 1989a).

RECENT SPECIATION

In North America, species of *Isoetes* vary in habit from ephemeral terrestrials to evergreen aquatics. Terrestrial *Isoetes* are found in seasonally wet soils where, in general, plants are active in spring when the soil is saturated with water and dormant in summer when the soil is dry. In the southern United States, terrestrial species may be found as isolated populations in soil pockets on sandstone, limestone, or granite. *Isoetes melanopoda* is widespread in the central and eastern United States where it is found in meadows, fields, and soil pockets on sandstone outcrops. *Isoetes butleri* occurs in the south-central and southeastern United States in calcareous soils over limestone. *Isoetes piedmontana* grows in soil pockets on granite outcrops in the southeastern United States. *Isoetes melanospora* inhabits shallow pools on isolated granite domes and flatrocks in the Piedmont of Georgia and South Carolina. *Isoetes tegetiformans* occurs in pools on porphyritic granite flatrocks in the Piedmont of Georgia (Rury, 1985). *Isoetes lithophila* is found in temporary pools on granite domes in central Texas. In the western United States, *I. howellii* and *I. nuttallii* inhabit seasonally wet meadows, lake margins, and vernal pools and streams. All of these terrestrial species have the lowest diploid chromosome number found in the genus ($2n = 2x = 22$). These basic diploids appear to represent examples of gradual speciation due to spatial isolation of ancestral populations followed by genetic divergence.

Aquatic *Isoetes* occur mostly in glacially formed lakes, ponds, and streams. In contrast to the terrestrial species, which occur mainly as isolated populations, two or more aquatic species frequently grow together. For example, in the northeast, *I. echinospora*, *I. engelmannii*, *I. riparia*, *I. tuckermanii*, and *I. lacustris* may all grow in the same body of water. Likewise, in the northwest, *I. echinospora*, *I. bolanderi*, *I. maritima*, and *I. occidentalis* could occur in the same lake. Such assemblages, which might have resulted as divergent species of *Isoetes*, were brought together by foraging water fowl, which carried spores into bodies of water left by retreating glaciers. Because gametes of different species can readily mingle in these aquatic habitats, the potential exists for interspecific hybridization. The existence of a polyploid series among the aquatic taxa (Table 1) implies that some species could be allopolyploids, which have evolved through interspecific hybridization and chromosome doubling. In addition to cohabitation and chromosome numbers, further evidence for hybridization and allopolyploidy come from spore morphology and viability, *in vitro* hybridizations, and electrophoretic profiles of leaf enzymes. How these sources of evidence support an allopolyploid mode of evolution in aquatic *Isoetes* are shown by

two examples, the evolution of *I. riparia* in eastern North America and the evolution of *I. brochonii* in western Europe.

THE EVOLUTION OF *ISOETES RIPARIA* IN EASTERN NORTH AMERICA

In the early summer of 1895, A. A. Eaton discovered unusual plants of *Isoetes* growing along the Powwow River in southeastern New Hampshire. Dodge (1897) described these unusual plants as a new species, *I. eatonii*. Dodge noted his new species to be "peculiar" in several ways. First, he mentioned that *I. eatonii* "seldom is found growing very near another of its species" and that plants "are from a foot to ten feet apart." By contrast, he noted the associated species *I. echinospora*, *I. engelmannii*, and *I. riparia* grow "for the most part gregariously." Dodge also reported his new species to be exceptionally vigorous. He mentioned vernal leaves attaining a length of 28 inches and the plants producing from 50 to nearly 200 leaves. Further, Dodge noticed the "straightness" of the radial ridges on the proximal side of the megaspore and "the low angle they form with the equatorial plane." Such a configuration imparts a proximally flattened, nearly lenticular form to the megaspore. Species of *Isoetes* typically have curvilinear radial ridges conforming to a rounded proximal hemisphere and a globose megaspore.

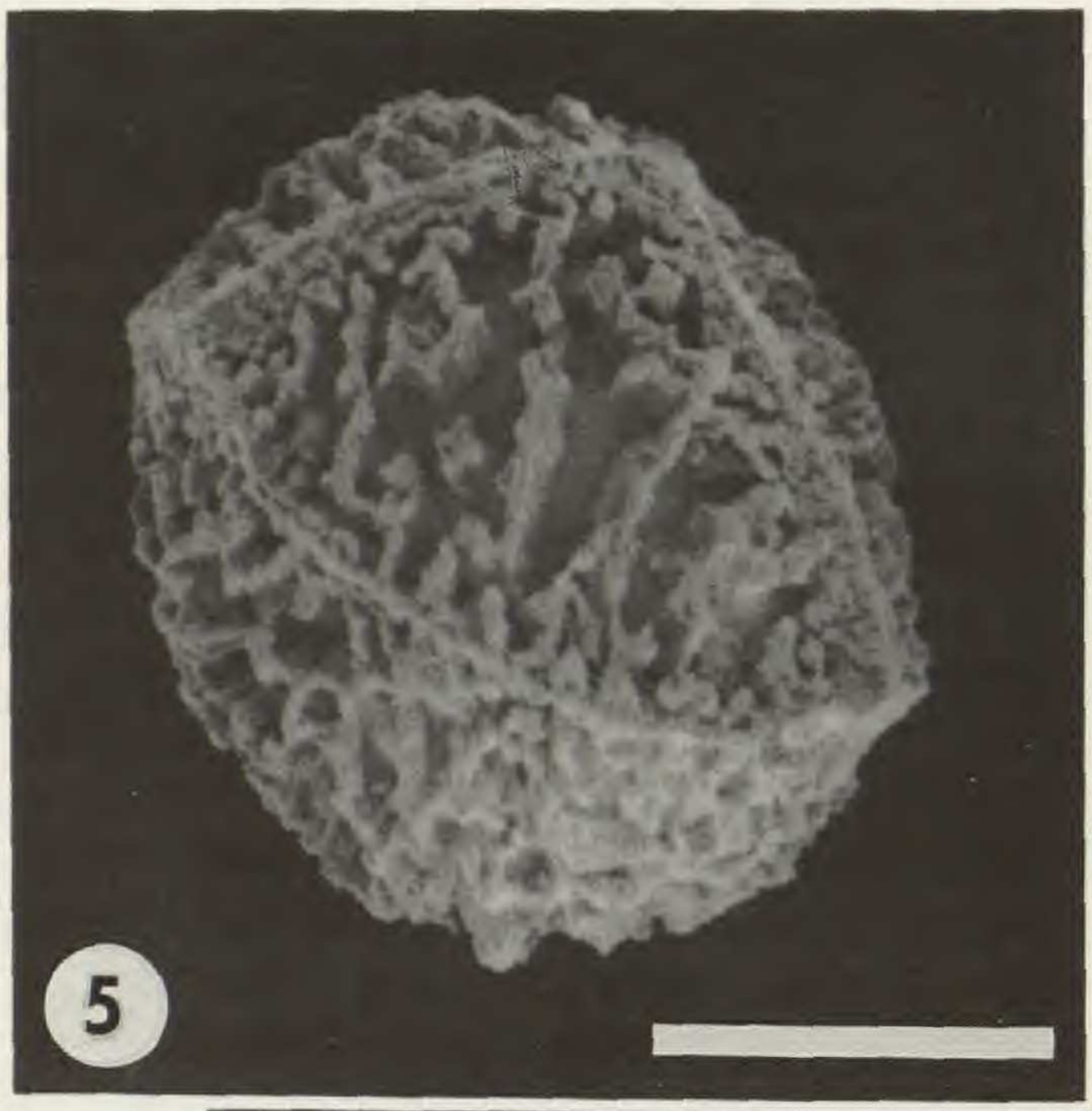
Taylor et al. (1985) reported that the megaspores of *I. echinospora*, *I. engelmannii*, and *I. riparia* readily germinated and formed megagametophytes in culture, but megaspores of *I. eatonii* did not germinate. They also showed that *I. eatonii* had been found almost entirely within the overlapping ranges of *I. echinospora* and *I. engelmannii* and that hybrids between these two species are readily produced in culture. They concluded that *I. eatonii* ($2n = 2x = 22$) represented a sterile, basic diploid hybrid between the basic diploids *I. echinospora* and *I. engelmannii* (both $2n = 2x = 22$).

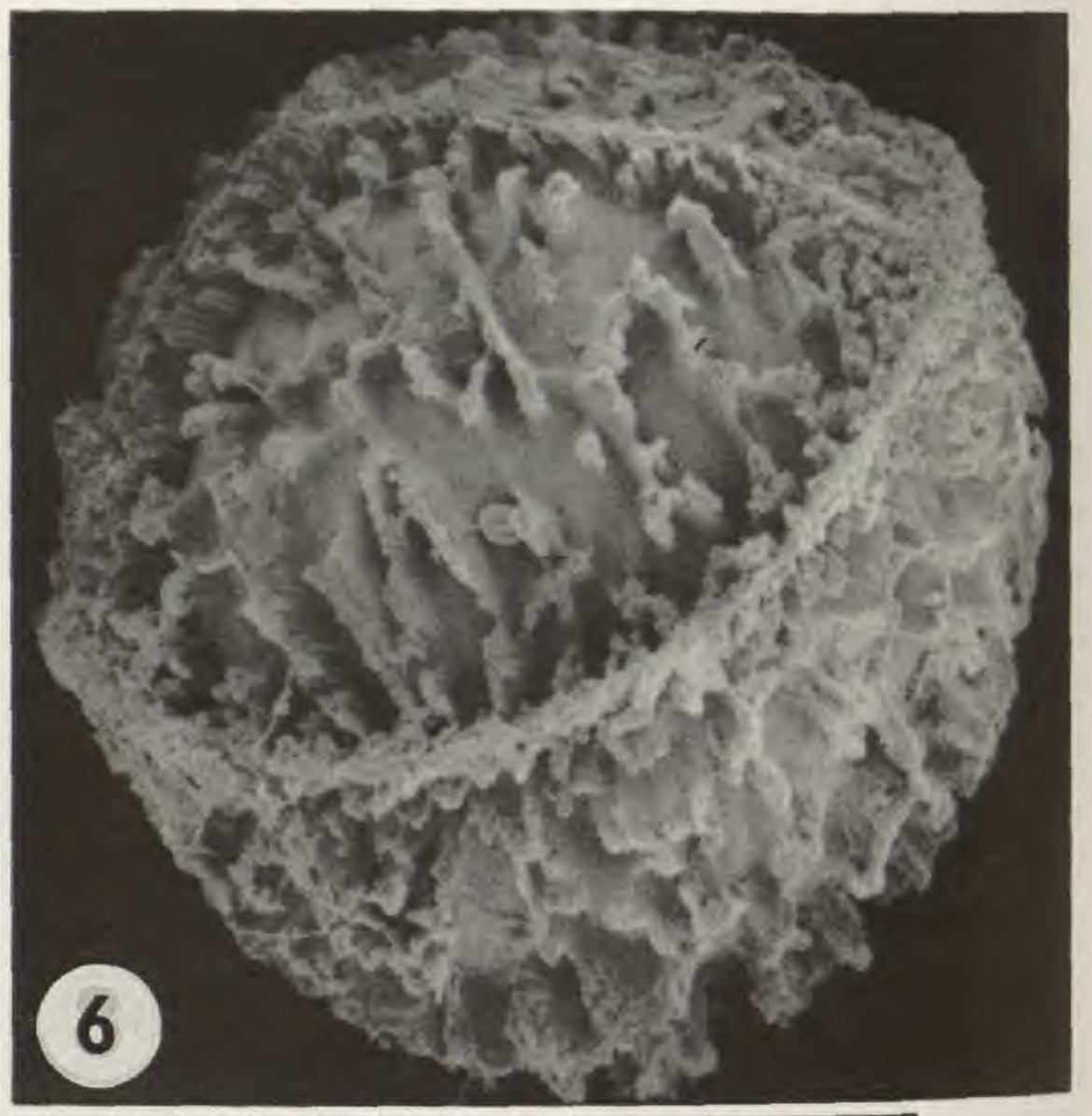
Although the megaspores of *I. eatonii* are described most often as small and flattened, with a labyrinthiform-convolute (brain coral) surface texture, larger, globose megaspores are produced occasionally (Fig. 5). The cristate surface texture of the larger, globose megaspore of *I. eatonii* appears intermediate between the echinate megaspore of *I. echinospora* (Fig. 7) and the reticulate spore of *I. engelmannii* (Fig. 8). Furthermore, the larger, cristate megaspore of *I. eatonii* resembles the even larger, globose megaspore of *I. riparia* (Fig. 6), a fertile tetraploid ($2n = 4x = 44$) occurring in northeastern North America, throughout the range of *I. eatonii*. If *I. eatonii* is the sterile, diploid hybrid between *I. echinospora* and *I. engelmannii*, could *I. riparia* be its fertile, allotetraploid derivative?

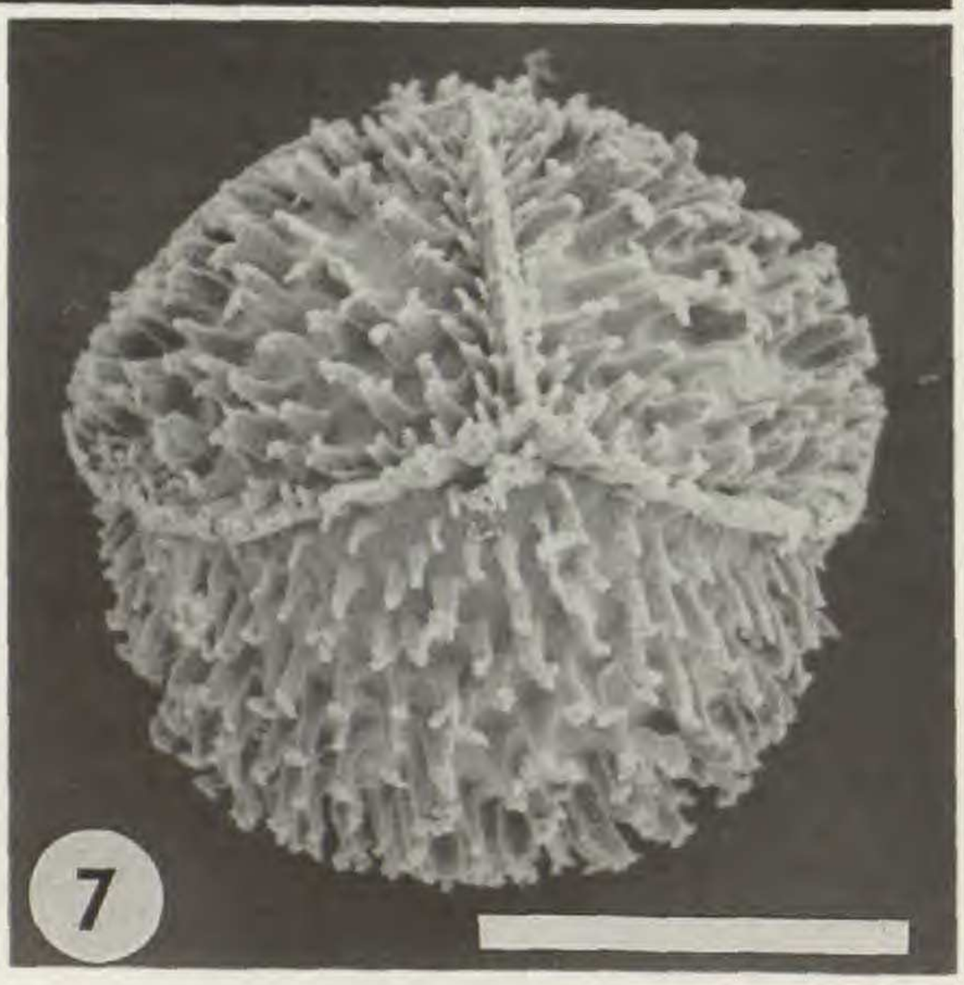
Electrophoretic profiles of triosephosphate isomerase (TPI) from *Isoetes* leaves help to answer this question. Leaves of *I. echinospora*, *I. engelmannii*, *I. eatonii*, and *I. riparia* were crushed and ground in Tris-HCl buffer-PVP solution. The resulting mixtures were absorbed onto filter paper wicks and subjected to horizontal starch gel electrophoresis. Electrophoretic procedure, composition of grinding, gel, and electrode buffers, and staining method follow Soltis et al. (1983). Electrophoresis was conducted using electrode and gel buffer system 7 in a 12% starch gel at 4°C with a constant current of 35 mamp for 8.5 hr. Wicks were removed from the gel after 15 min. The gel was sliced, incubated in substrate at 37°C for 1 hr. in the dark, rinsed in distilled water, and photographed.

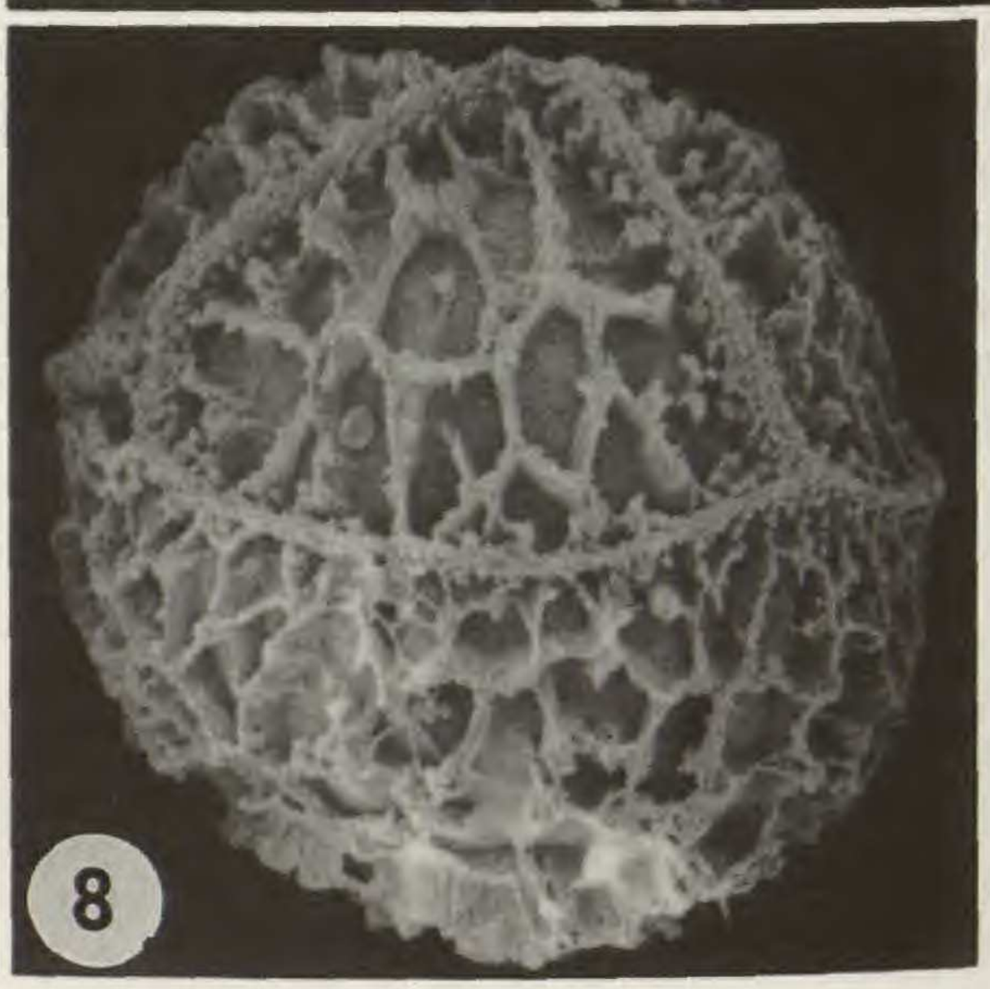
Electrophoretic profiles of *I. echinospora*, *I. engelmannii*, *I. eatonii*, and *I. riparia* support the hypothesis that *I. eatonii* is a sterile hybrid between *I. echinospora* and *I. engelmannii* and that *I. riparia* could be an allotetraploid derivative of *I. eatonii*. In Figure 9, TPI, a dimeric enzyme, requiring the combination of two subunits to form an active enzyme, is expressed by two loci, TPI-1 and TPI-2. TPI-1 appears single-banded, and invariant for the taxa sampled. TPI-2, composed of subunits designated "a" and "b," shows variability that distinguishes *I. echinospora* and *I. engelmannii* and relates *I. eatonii* to *I. riparia*. *Isoetes echinospora* expresses the band "aa," whereas *I. engelmannii* expresses the band "bb." *Isoetes eatonii* and *I. riparia* express bands "aa" and "bb" in addition to the heterodimeric band "ab," which is not present in either parent. The profiles of TPI-2 for *I. eatonii* and *I. riparia* are similar and additive for *I. echinospora* and *I. engelmannii*. Lighter bands cathodal to bands "aa" and "ab" may represent subbands. A subband is formed when an additional, charged component attaches to an enzyme thereby changing its charge, possibly its size and shape, and thus its migration (Buth, 1990). Subbanding for "bb" is not evident in Figure 9.

Evidence from distribution patterns, spore morphology and viability, *in vitro* hybridizations, and electrophoretic profiles of leaf enzymes supports the hypothesis that *I. echinospora* has crossed with *I. engelmannii* to form the sterile hybrid *I. eatonii*,









FIGURES 5–8. Scanning electron micrographs of *Isoetes* megaspores.—5. *I.* × *eatonii.*—6. *I. riparia.*—7. *I. echinospora.*—8. *I. engelmannii.* Scale bar = 0.25 mm.

which then doubled its chromosome number to form the fertile allotetraploid *I. riparia.*

THE EVOLUTION OF *ISOETES BROCHONII* IN WESTERN EUROPE

In October 1983, a mass collection of *I. echinospora* and *I. lacustris* was made from Neva Lake in northern Wisconsin to obtain spores for germination and hybridization experiments. Neva Lake is a small, glacially formed, soft-water lake with a sand, gravel, and muck bottom. Examination of plants from this collection revealed several individuals bearing megaspores that were far more variable in size, shape, and surface texture than typical megaspores of *I. echinospora* or *I. lacustris.*

Isoetes echinospora and *I. lacustris* grow together in many lakes in northeastern North America and Europe. Although they can look alike vegetatively, these two species are readily distinguishable by their spores, which differ in size and surface texture. *Isoetes echinospora* produces echinate megaspores about 400–500 μm in diameter, whereas *I. lacustris* bears cristate megaspores mostly 600–800 μm in diameter. Scanning electron photomicrographs show that megaspores from the unusual Neva Lake plants bear a spine and ridge texture that seems to combine the patterns of *I. echinospora* and *I. lacustris* (Fig. 10).

Megaspores from these plants are not viable. Using the procedure described by Taylor & Luebke (1986) for germinating spores of aquatic *Isoetes*, *I. echinospora* and *I. lacustris* megaspores germinated and formed megagametophytes in culture, but megaspores from the unusual Neva Lake plants did not germinate.

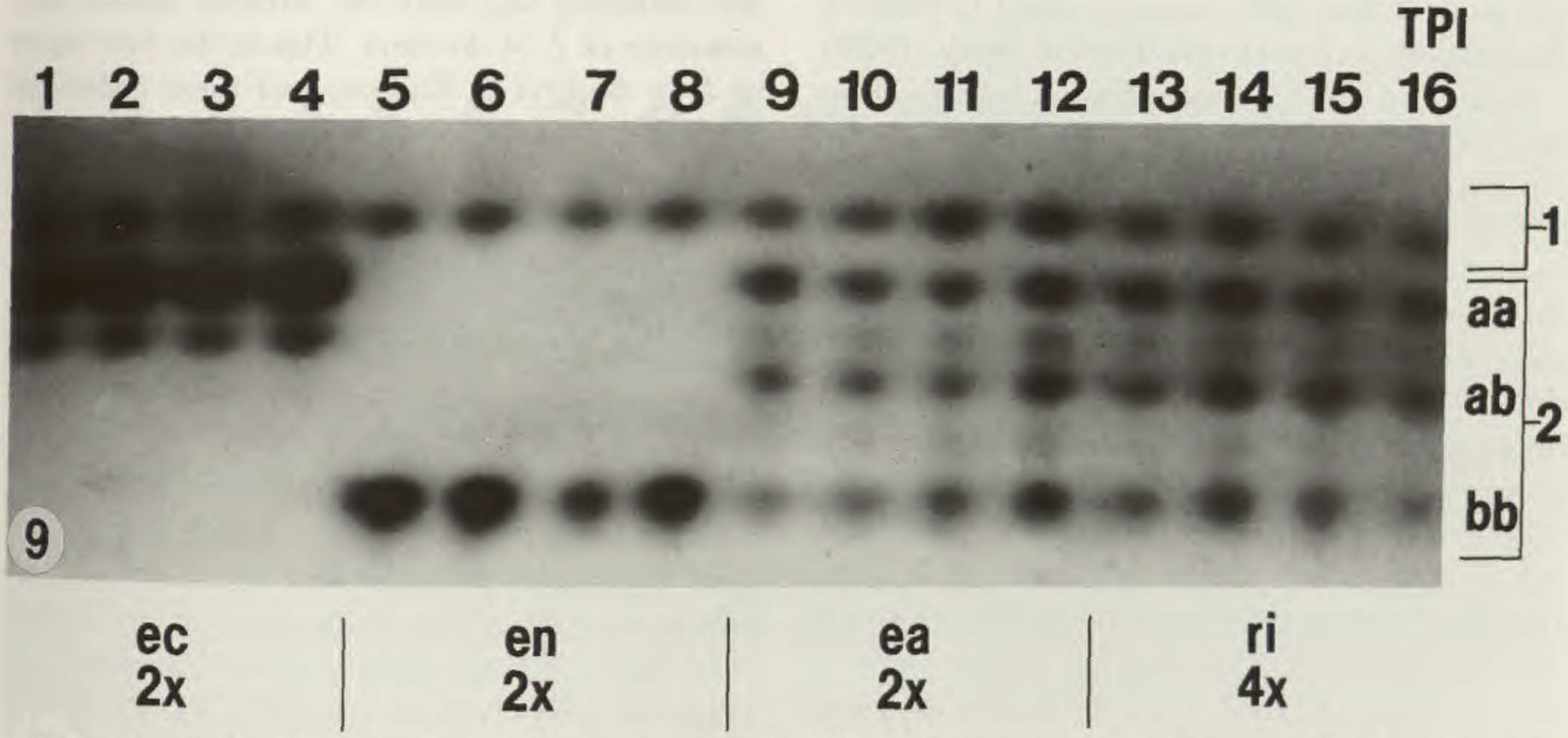
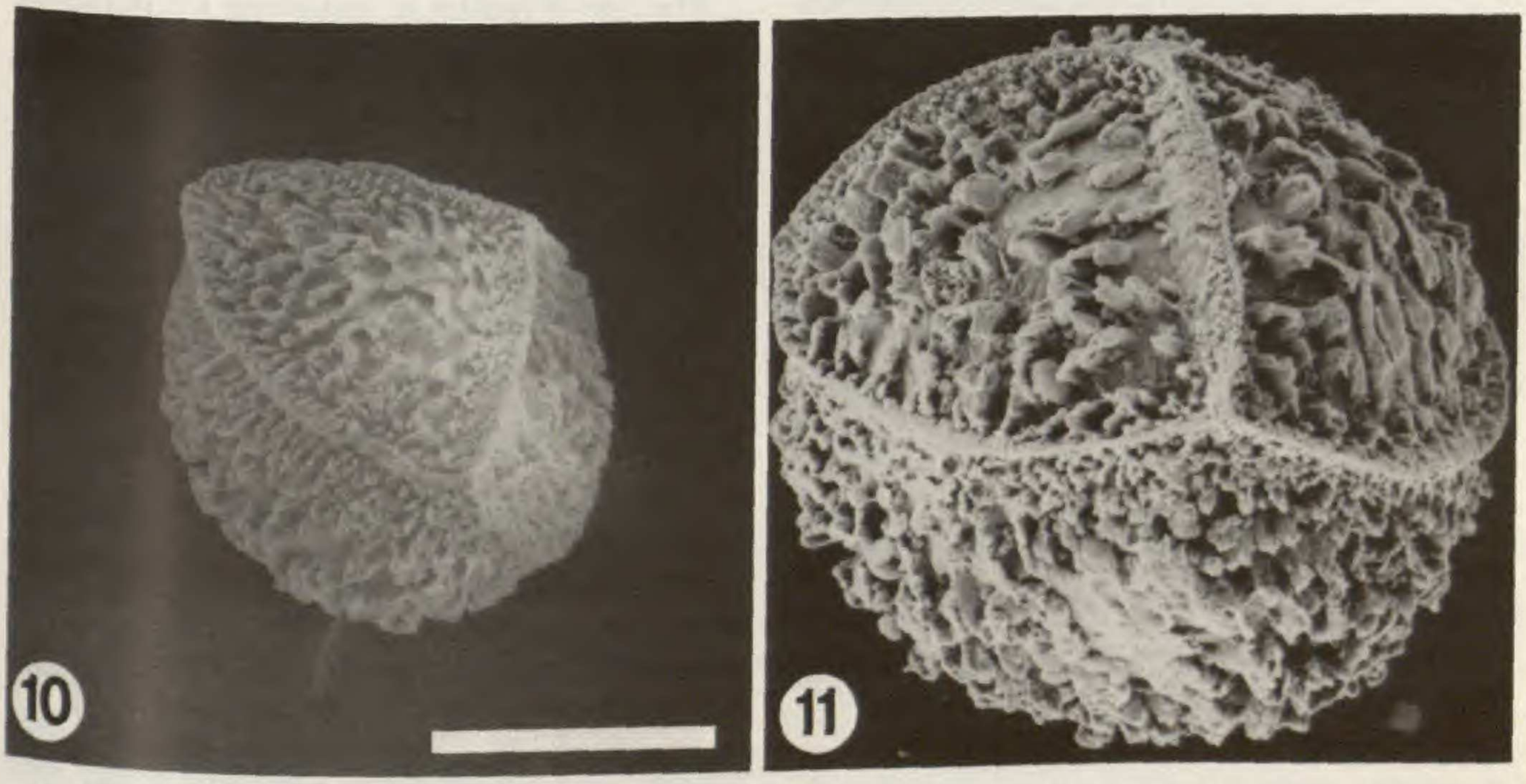


FIGURE 9. TPI (Triosephosphate isomerase) zymogram of *Isoetes* leaves.—Lanes 1–4. ec = *I. echinospora*.—Lanes 5–8. en = *I. engelmannii*.—Lanes 9–12. ea = *I.* × *eatonii*.—Lanes 13–16. ri = *I. riparia*. $x = 11$, chromosome base number for *Isoetes*.

A hybrid between the basic diploid ($2n = 2x = 22$), *I. echinospora*, and the decaploid ($2n = 10x = 110$), *I. lacustris*, should have a chromosome number of $2n = 6x = 66$, the sum of 11 chromosomes from a haploid gamete of *I. echinospora* and 55 chromosomes from a haploid gamete of *I. lacustris*. Root tip squashes of the unusual Neva Lake plants show cells containing the predicted 66 chromosomes for a hybrid between a diploid and a decaploid (Taylor & Luebke, 1988).

Based on megaspore morphology, production of nonviable megaspores, and chromosome number, it appears that these unusual Neva Lake plants are sterile, interspecific hybrids between *I. echinospora* and *I. lacustris*. This hybrid has been named *I.* × *hickeyi* (Taylor & Luebke, 1988).

Isoetes brochonii, a poorly known taxon, has been collected from several lakes in the Pyrenees of France where it grows with *I. echinospora* and *I. lacustris*. Since its description by M. L. Motelay (1892), the taxonomic status of *I. brochonii* has been debated, and it has been treated as a distinct



FIGURES 10, 11. Scanning electron micrographs of *Isoetes* megaspores.—10. *I.* × *hickeyi*.—11. *I. brochonii*. Scale bar = 0.25 mm.

species or it has been variously allied to either *I. echinospora* or *I. lacustris* (Prelli & Bock, 1989).

In August 1987, *I. brochonii* was collected from Lac Vivé, just west of Lac Bouillouses in the western Pyrenees of France. Specimens from this collection were cultured to provide root tips for chromosome counts and leaves for enzyme electrophoresis. Of initial interest in this collection was the surface texture of *I. brochonii* megaspores (Fig. 11). Although they were globose, and uniform in shape, size, and surface texture, these megaspores had a surface texture like many of the megaspores of *I.* × *hickeyi* from Neva Lake, Wisconsin. Chromosome counts from root tip squashes revealed *I. brochonii* to be dodecaploid ($2n = 12x = 132$), double the chromosome number of *I.* × *hickeyi*. If *I.* × *hickeyi* is the sterile, hexaploid hybrid between *I. echinospora* and *I. lacustris*, could *I. brochonii* be the fertile, allododecaploid derivative?

Electrophoretic profiles of malate dehydrogenase (MDH) from *Isoetes* leaves help to answer this question. Leaves of *I. echinospora*, *I.* × *hickeyi*, *I. brochonii*, and *I. lacustris* were crushed and ground in phosphate-PVP buffer solution. The resulting mixtures were absorbed onto filter paper wicks and subjected to horizontal starch gel electrophoresis. Electrophoretic procedure and composition of grinding buffer and staining method follow Soltis et al. (1983). Electrophoresis was conducted using an electrode and gel buffer system by Clayton & Tretiak (1972) adjusted to pH 6.0 with N-3 (3-aminopropyl)-morpholine in a 12% starch gel at 4°C at a constant current of 40 mamp for 6 hr. Wicks were removed from the gel after 30 min. The gel was sliced, incubated in substrate at 37°C for 30 min. in the dark, rinsed in distilled water, and photographed.

Electrophoretic profiles of *I. echinospora*, *I.* × *hickeyi*, *I. brochonii*, and *I. lacustris* support the hypothesis that *I.* × *hickeyi* is a sterile hybrid between *I. echinospora* and *I. lacustris* and that *I. brochonii* could be an allododecaploid derivative of *I.* × *hickeyi*. In Figure 12, MDH profiles of *I.* × *hickeyi* and *I. brochonii* appear similar and additive for their suspected parents *I. echinospora* and *I. lacustris*, but it is impossible to precisely interpret the MDH band patterns until variation in parental species is identified and segregation studies are conducted.

Isoetes × *hickeyi* has recently been collected from Lac Long and Lac Font Vivé in the western Pyrenees of France, within the range of *I. brochonii* (Carmen Prada, pers. comm.). Prada's plants are hexaploid and have the variable spores characteristic of *I.* × *hickeyi*. This is the first report of *I.* × *hickeyi* in Europe, and these collections represent a geographically closer link to *I. brochonii*.

Evidence from distribution patterns, spore morphology and viability, chromosome numbers, and electrophoretic profiles of leaf enzymes supports the hypothesis that *I. brochonii*, like *I. riparia*, is an allopolyploid species formed through interspecific hybridization and chromosome doubling.

In addition to the allopolyploid evolution of *I. riparia* and *I. brochonii* described here, allopolyploid origins for several other polyploid taxa are being disclosed as we learn more about *Isoetes*. With nearly 60 percent of the known species being polyploid, allopolyploidy may be a significant speciation mechanism in this genus.

Thus, species of *Isoetes* appear to have evolved in two ways. First, species have developed gradually by isolation and genetic divergence as taxa adapted to terrestrial and aquatic habitats. Second, species have formed through interspecific hybridization and chromosome doubling as divergent species migrated into the same aquatic habitats. Interspecific hybridization produces plants of more or less intermediate morphology and the inclusion of such hybrids within species descriptions has confused species distinctions. Allopolyploidy fixes this intermediate, hybrid morphology in fertile, polyploid species (Hickey et al., 1989b).

Conclusions

The role of habitat in explaining the phylogeny of *Isoetes* has only recently been recognized, but there is a growing body of evidence indicating that the major clades of the genus radiated subsequent to environmental shifts. Initially *Isoetes* species were evergreen aquatics with lacunate, laminate, nonsclerified leaves without peripheral fibrous bundles. The evolution of novel character states occurred as members of the genus radiated into terrestrial habitats following the Cretaceous. Peripheral fibrous bundles for support, sclerified leaves and leaf bases for protection, subulae, and ephemeral leaves to reduce water loss were derived as plants adapted to more xeric environments. Subsequently, many of these novel states were lost as plants reverted to aquatic habitats perhaps during wetter periods. These serial environmental shifts resulted in a tremendous amount of parallelism and convergence as characters or character states were gained, lost, or modified.

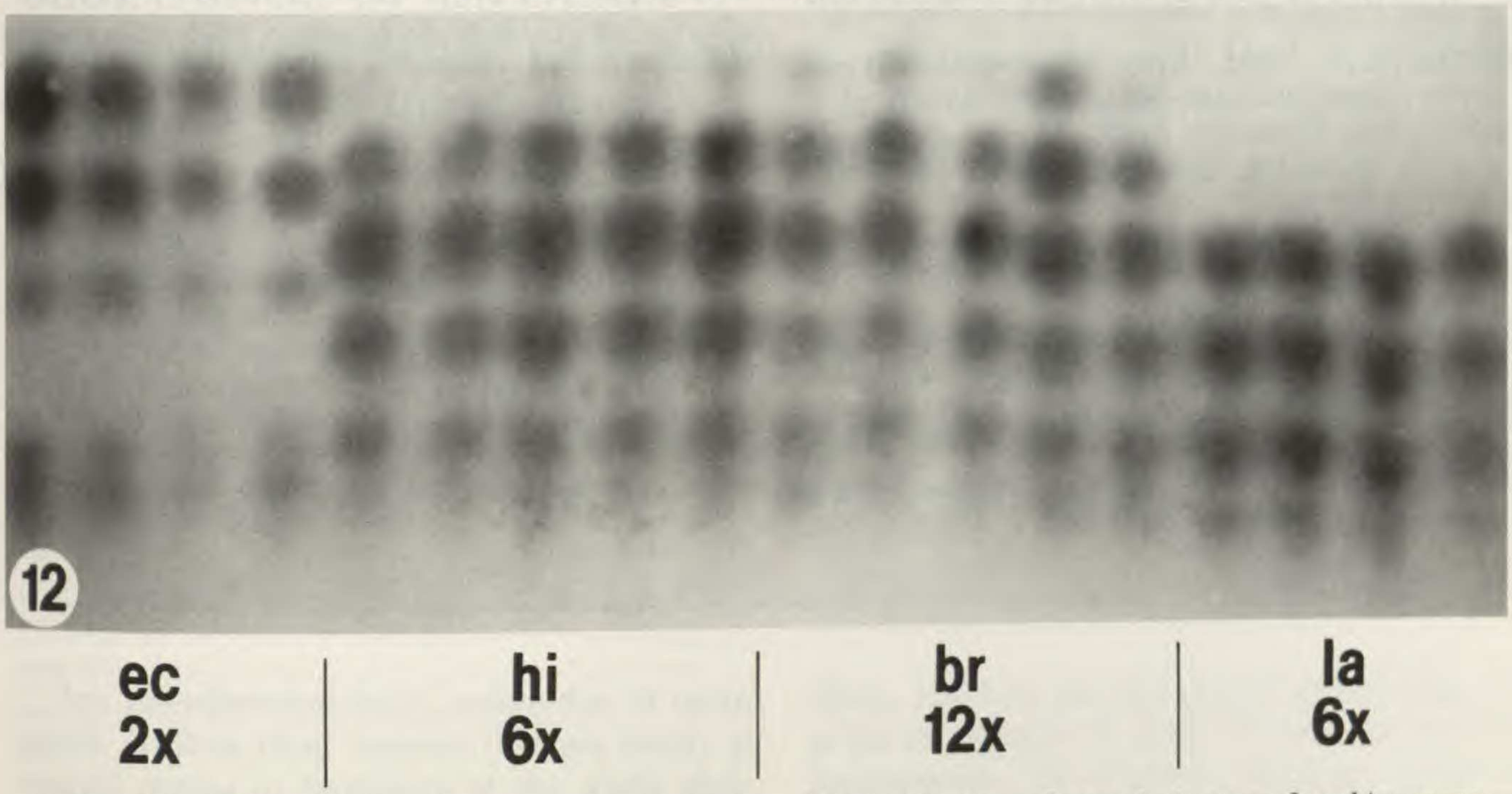


FIGURE 12. MDH (Malate dehydrogenase) zymogram of *Isoetes* leaves.—Lanes 1–4. ec = *I. echinospora.*—Lanes 5–9. hi = *I.* × *hickeyi.*—Lanes 10–14. br = *I. brochonii.*—Lanes 15–18. la = *I. lacustris.* $x = 11$, chromosome base number for *Isoetes.*

Because of their terrestrial habit these species had little or no long-range dispersal ability during continental movements, and their geography can be explained largely on the basis of vicariant events.

Extant species can be viewed loosely as being either terrestrial or aquatic. The assemblage (non-phylogenetic) of extant aquatic species can be characterized as being highly polyploid, "social" (co-existing with one or more additional taxa), and promiscuous. The terrestrial taxa are quite the opposite. These taxa are generally diploid, often exist in monospecific populations, and rarely hybridize. These differences appear to be tied to the mode and frequency of dispersal events. Ponds and lakes may be good "visual targets" for migrating waterfowl that carry spores of *Isoetes.* This increases the opportunity both for long-distance dispersal and for commingling of species. This sociality of aquatic *Isoetes* species in turn leads to a greater opportunity for hybridization and evolution via subsequent polyploidy. Terrestrial species, by contrast, produce mature spores as or when their habitats, ephemeral ponds or moist glades, are drying out. The habitats of terrestrial species may then be poor "visual targets" for waterfowl, at least during the time of year necessary for dispersal. This would lead to a reduced number of dispersal events and a decrease in sociality of species.

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PALEOZOIC HERBACEOUS LYCOPSIDS AND THE BEGINNINGS OF EXTANT *LYCOPODIUM* SENS. LAT. AND *SELAGINELLA* SENS. LAT.

Barry A. Thomas[1]

ABSTRACT

Devonian and Carboniferous herbaceous Lycopsids are reviewed to illustrate their diverse morphologies. The problem of interpreting small fragments of Lycopsids as either the remains of herbaceous plants, or as terminal portions of much larger plants, is highlighted. Lycopsids resembling the extant genera *Lycopodium* and *Selaginella* are known from the Carboniferous onward. The problems of assigning these herbaceous taxa to extant genera are discussed. The presence of both isophyllous and heterophyllous *Selaginella*-like plants in the Carboniferous supports the idea that the genus should be divided into at least two genera.

Any paleobotanical study, unlike that of extant plants, involves plant remains that are nearly all isolated organs or fragments of the whole plant. Much effort is expended trying to reconstruct whole plants from these remains, often with quite striking and valuable results. People should not, however, become accustomed to looking at plant fossils as though they are all fragments of large plants. This is clearly not the case; herbaceous plants were probably present in large numbers in most of the many diverse floras that have existed from the late Paleozoic onward. They would have formed the ground cover in open habitats or the floor layer of the more closed forest communities. Unfortunately, remains of these herbaceous plants might easily be misidentified as fragments of much larger plants, or just overlooked.

LOWER PALEOZOIC LYCOPSIDS

Herbaceous lycopsid-like plants are known from the Upper Silurian onward. The earliest, *Baragwanathia* Lang & Cookson, 1935, came from Upper Silurian strata of Victoria, Australia (Garratt et al., 1984). It was very similar to *Drepanophycus spinaeformis* Goeppert, 1852, and *Asteroxylon mackiei* Kidston & Lang, 1920, from the Lower Devonian of the present Northern Hemisphere, in having a partly creeping and partly erect habit with lateral branching and spirally arranged microphylls. They must have been very similar to living *Huperzia selago* (L.) Bernh. ex Schrank & Mart., 1829, in size and general morphology and, as far as we know, in stelar anatomy and in being homosporous. The problem, however, is that although these early land plants resembled lycopsids vegetatively, their sporangia were cauline rather than being on the adaxial surfaces of sporophylls. This cauline arrangement is more like that of such plants as *Zosterophyllum* Penhallow, 1892, and *Sawdonia* (Dawson) Hueber, 1971, which are included in the Zosterophyllophytina. One other genus very similar to *Asteroxylon* is the Lower/Middle Devonian *Kaulangiophyton* Gensel, Kasper & Andrews (1969). It was described as having prostrate, dichotomously branching rhizomes and dichotomizing aerial axes with scattered spiny leaves. The ovoid sporangia borne on some of the upright branches terminated well-developed lateral stalks. They were not associated in any regular manner with the sterile spines. Schweitzer (1980), however, concluded that the type species, *K. akantha*, was conspecific with *Drepanophycus devonicus*, so that *Kaulangiophyton* should be regarded as a synonym of *Drepanophycus*.

Various suggestions have been made about the taxonomic relationships of these early lycopsid-like forms. Banks (1968) described them as transitional between the Zosterophyllopsida and the Lycopsida. Bierhorst (1971) argued that they should be placed in a new order, the Asteroxylales, within the class Zosterophyllopsida. Rayner (1984) stressed their dissimilarities even further by suggesting that a new class, the Drepanophycopsida, is needed for

[1] Department of Botany, National Museum of Wales, Cathays Park, Cardiff CF1 3NP, United Kingdom.

plants intermediate in organization between the Zosterophyllopsida and the Lycopsida. It may, however, be a little premature to accept this new class because most species of *Drepanophycus* have been included in the genus solely on vegetative characters; the genus could easily represent several unrelated species. Grierson & Banks (1983) implied this by segregating *D. gaspianus* as a new genus, *Haskinsia*.

The recognition of the first undisputed lycopsid is difficult, as only a relatively simple change of sporangial position was needed to derive the first lycopsid from its drepanophycopsid ancestor. The earliest homosporous lycopsids diversified and radiated in many ways, as hybridization was probably easily accomplished through the plants' relatively simple genetic make-up (Banks, 1968). Some forms of plants seem to have continued almost unchanged to the present day. Others evolved into further homosporous herbaceous forms or into heterosporous ones, while some evolved along quite different paths that gave rise to the arborescent Carboniferous lycopsids and eventually to the extant *Isoetes* (Snigirevskaya, 1980; Pigg & Rothwell, 1983; Karrfalt, 1984).

Lycopsids are perhaps the most common plant fossils found in Devonian rocks around the world. This may reflect a greater tolerance of climatic and other ecological conditions, and/or their better potential for fossilization. Nevertheless, this wider distribution is generally taken as evidence for a uniform worldwide flora in mid-Devonian times (Fairon-Demaret, 1974; Gould, 1975; Anderson & Anderson, 1985, Edwards & Benedetto, 1985).

Many of these Devonian and subsequent Carboniferous adpression lycopsids have been described as herbaceous, although they are known only as fragmentary remains of leafy axes or even axes with scars marking the former attachment of leaves. For example, Grierson & Banks (1963, 1983) described *Archaeosigillaria* Kidston, 1901, *Protolepidodendron* Krejci, 1880, *Colpodexylon* Banks, 1944, *Eleutherophyllum* Stur, 1877, *Sugambrophyton* Schmidt, 1954 and *Zimmermannia* Gothan & Zimmermann, 1932, as herbaceous on such evidence.

The recent description of pyritic axes from the Tournaisean of Ireland (Matten, 1989) highlights the similar problem of recognizing herbaceous lycopsids when they are preserved as permineralizations. The specimens, described as a new genus *Wexfordia*, have only primary tissues and a combination of characters intermediate between the Devonian Protolepidodendrales and the Upper Carboniferous Lepidodendrales. However, these features are not reliable enough to prove that the fragments came from a herbaceous plant for, as Matten has indicated, *Wexfordia* might instead represent the distal portions of a larger plant such as *Cyclostigma* or even fragments of a rhizome.

Ligules and Taxonomic Problems

In living lycopsids ligules are restricted to heterosporous genera. However, in fossils it is often impossible to determine whether leafy shoots are ligulate or eligulate. One exception is the Lower Carboniferous eligulate leafy shoot *Stansburya petersenii* Tidwell & Jennings (1986). There is a general assumption that fossil lycopsids that are known to be ligulate are also heterosporous and vice versa, even though the homosporous Devonian *Leclercqia* has been shown to be ligulate (Grierson & Bonamo, 1979; Bonamo et al., 1988). This genus has been described from several North American localities (Kasper & Forbes, 1979) and from Australia (Fairon-Demaret, 1974) and was evidently widespread.

Ligulate lycopsids continued to evolve rapidly during the Carboniferous. There were a number of recognizably different forms. The morphologically simplest erect isophyllous axes, with unknown reproductive features, were worldwide during the Lower Carboniferous, but became more restricted during the Upper Carboniferous and Permian. Large numbers eventually survived only in the colder area of what is now Siberia (then Angaraland). Meyen (1976) suggested that they may have escaped competition here from more vigorous plants that were evolving elsewhere. Similar genera have been described from the northern slope of Alaska, which suggests that this area of land was once closer to, or part of, Angaraland (Thomas & Spicer, 1986; Spicer & Thomas, 1987).

Such sterile axes are referred to genera solely on morphological characters related to phyllotaxy, leaf morphology, or to features visible after leaf fall such as the leaf cushion, leaf scar, ligule pit, and infrafoliar bladder (Thomas & Meyen, 1984a). This is a workable system provided that its more important limitations are understood. These are: (1.) The systematic, taxonomic, and evolutionary relationships of fragmentary adpression axes are impossible to assess accurately without details of any reproductive organs. An overly simplistic approach can lead to generalized comparisons and statements that are impossible to prove. For that reason, Thomas & Brack-Hanes (1984) suggested an alternative method of classifying lycopsids where only bisporangiate whole plants or fructifications,