

A description of the basic body plan in *Isoëtes* by means of regressions: results of an exemplary study

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One of the well-known difficulties in the identification of *Isoëtes* species is the extreme phenotypic plasticity within the species. Kott & Britton (1985) recognized that leaf length and leaf number are not diagnostic. However, accounting for one species, *Isoëtes lacustris*, and for one site, Szmeja (1993a,b) obtained several regressions between morphology and fertility features. Vöge (1997a,b) studied the species in more than 50 lakes throughout Europe and established eight highly significant regressions. The number of leaves per rosette proved to be the most important plant feature, related with corm width, total root length, rosette surface area, number of spores per macrosporangium, the number of macrospores per plant, and the number of macrosporophylls per plant (Fig. 1).

Isoëtes lacustris is an evergreen perennial, inhabiting commonly clear soft water lakes between 40° and 70° North latitude in Europe. *Isoëtes echinospora*, the second species studied, occurring in this area, is rather rare. The studied sites comprised natural lakes without conspicuous signs of anthropopressure, as well as humic, eutrophicated and acidified lakes, experiencing different climate conditions. The mean number of leaves per rosette varied among the lakes studied and could be explained by the number of months with mean temperatures > 10° C per year, the water colour (given by Hazen number) or by (m) Secchi depth).

The basic body plan in *Isoëtes* was described by Kott & Britton (1983): The corm supports spirally arranged leaves surrounding the central shoot apex. Roots originate from the corm. Microsporangia and macrosporangia are produced by mature plants on the adaxial surfaces of the leaf bases. The older leaves become displaced towards the periphery of the corm by new leaves which are produced by the apical meristem. The authors emphasize that this basic body plan is very similar for all species whether they are aquatic, emergent, or terrestrial in habit. The body plan was described for both European species by five regressions. It was the aim to examine further *Isoëtes* species, by way of example: aquatic or terrestrial, in and out of Europe, in order to recognize if the the validity of the regressions may be extended to further species.

Material and methods

The author received living sporogenous plants from D. Brunton (Canada), K. Heafner (USA), C. Taylor (USA), and A. Troia (Italy). The samples are detailed in Tab. 1. Species or hybrids 1-8 are aquatic, the species 9 and 10 are terrestrial. The aquatic specimens belong to one of the four major groups of North American taxa and occur in northeastern North America. Taylor & Hickey (1992) characterize the assemblages of these extant aquatic species as being highly polyploid, „social“ and promiscuous; the sociability leads to a great opportunity for hybridization and evolution via subsequent allopolyploidy. In fact, from the species 1-4, *Isoëtes lacustris* (macrospora), *I. echinospora*, *I. riparia*, and *I. tuckermanii*, the hybrids (no. 6-8) *I. X harveyi*, *I. X dodgei*, and *I. X hickeyi* were born (Fig. 2). *Isoëtes prototypus* (no. 5) is an unique species and a global rarity. The species appears to contain many characters to be plesiomorphic in *Isoëtes*: the sporangium is entirely enclosed in translucent saccate membrane and the velum covers the entire sporangium (Brunton & Britton, 1993). The aquatic specimens have been collected during summer, the terrestrial species in early spring, as their leaves are ephemeral. The terrestrial taxa are generally diploid, often exist in monospecific

populations and rarely hybridize (Taylor & Hickey, 1992). *Isoëtes melanopoda* belongs to the *I. melanopoda* complex, a group of North American taxa and found in the southeastern USA. All species of this complex are tropical in origin (Hickey et al., 1989). *Isoëtes melanopoda* is endemic to granite outcrops. *Isoëtes histrix* occurs in Mediterranean coastal areas of southern Europe.

The specimens were studied as described (Vöge 1997a,b) except the samples per site were smaller: 3 to 10 plants each. The following 9 plant parameters were determined: number of leaves per rosette (n), mean leaf length (a), mean leaf width (b), height of rosette, number of microsporophylls, number of macrosporophylls (bearing mature macrospores), number of spores per macrosporangium, total root length, and corm width. When counting the leaves, all green leaves were taken into account, even when incomplete, possibly by collecting. The rosette surface area was calculated from $2 \cdot n \cdot a \cdot b$. Mean values have been calculated for each species or hybrid examined even if one species was collected in different locations.

The regressions 1-5 (Fig. 1) were selected with the aim of using all plant features determined, accounting for the corm, the rosette assimilatory surface area, the roots enabling the uptake of carbon dioxide, and the number of macrospores per plant characterizing the reproduction chance, together with the more numerous microspores. These are the regressions used for quantitative description of the basic body plan in *Isoëtes*:

1) Relationship between number of leaves per rosette (x) and corm width (y):

$$y = 0,66 x + 1,79$$

2) Relationship between number of leaves per rosette (x) and total root length (y):

$$y = 0,28 x + (-1,12)$$

3) Relationship between number of leaves per rosette (x) and number of macrospores per plant (y):

$$y = 17,72 x + (-120,84)$$

4) Relationship between number of microsporophylls (x) and number of macrosporophylls per rosette (y):

$$y = 0,79 x + (-0,86)$$

5) Relationship between rosette surface area (x) and number of spores per macrosporangium (y):

$$y = 0,40 x + 37,80$$

All regressions are highly significant ($P < 0,001$) and proved valid too, in European *Isoëtes echinospora*.

Results and discussion

The mean values determined on 10 *Isoëtes* species and hybrids are presented in Tab. 2. Fossil *Isoëtes beestonii* is the most ancient known species of the genus, originating in earliest Triassic (Retallack 1997); the data were given by Retallack (pers. comm.).

Sometimes the total root length could not be obtained, if the roots within a sample were recognized incomplete. As was observed in European *Isoëtes lacustris* and *Isoëtes echinospora*, the mean number of leaves per rosette was at least 10 within a sample of sporogenous plants, accounting for all species and hybrids examined, except for *I. riparia*. The lowest mean number of leaves per rosette (9,3) has been obtained in a subarctic lake of Norway. The high number of leaves per rosette and the spore number per macrosporangium in *I. beestonii* are nearly the same as was established in *I. lacustris* inhabiting the German lake Garrensee, where the species experiences very clear water in a temperate climate.

All results which were gained on the species and hybrids studied support the regressions which were established on European *Isoëtes lacustris*. It is emphasized that even the terrestrial

species support the quantitative description in *Isoëtes*, though their leaves are ephemeral and a new rosette is developed every year. It is stressed that not only the leaf number is not diagnostic (Kott and Britton, 1985), but the relationships between leaf number and further morphology or fertility features are not diagnostic either.

According to Taylor & Hickey (1992) *Isoëtes* species were evergreen aquatics initially. The evolution of novel character states occurred as members of the genus radiated into terrestrial habitats following the Cretaceous, when adaptation to more xeric environment evolved. Subsequently many of these novel states were lost, as plants reverted to aquatic habitats, perhaps during wetter periods. These serial environmental shifts resulted in character state reversals, parallelisms and convergences as character or character states were gained, lost or modified (Taylor & Hickey, 1992). The established validity of the regressions enable the modelling of plants that belong to ten different species and hybrids in the genus *Isoëtes*; an explanation may be the above- mentioned parallelism and convergence in evolution. However, the mat-forming quillwort *Isoëtes tetraformans*, becoming terrestrial, makes an exception: plantlets develop along an elongating rootstock; the leaves arise distichously, not in spirals, in groups of about 4-8, thus deviating from the relative uniformity of general appearance.

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Tab. 1: The species and hybrids studied and the origin of the specimens

No. of species	Species / hybrid	Collected by	No. of sample	Location	Specimens studied
1	<i>Isoëtes lacustris</i> (macrospora) L.	Brunton	13,660	Buttermilk Falls	10
2	<i>Isoëtes echinospora</i> Durieu	Brunton	13,676	Ottawa River	5
2	<i>Isoëtes echinospora</i> Durieu	Brunton	13,660	Buttermilk Falls	3
3	<i>Isoëtes riparia</i> Engelmann ex A. Braun	Brunton	13,675	Ottawa River	5
4	<i>Isoëtes tuckermanii</i> A. Braun ex Engelmann in A. Gray	Brunton	13,716	Midway Lake	2
5	<i>Isoëtes prototypus</i> D. M. Britton	Brunton	13,684	Pottle Lake	5
5	<i>Isoëtes prototypus</i> D. M. Britton	Brunton	13,711	Sandy Lake	4
6	<i>Isoëtes X harveyi</i> A. A. Eaton	Brunton	13,714	Buttermilk Falls	3
7	<i>Isoëtes X dodgei</i> A. A. Eaton	Brunton	13,674	Ottawa River	5
8	<i>Isoëtes X hickeyi</i> Taylor & Luebke	Brunton	13,661	Buttermilk Falls	9
8	<i>Isoëtes X hickeyi</i> Taylor & Luebke	Taylor	6057	Neva Lake	1
9	<i>Isoëtes melanopoda</i> Gay & Durieu	Heafner	990/5	North Carolina	4
10	<i>Isoëtes histrix</i> Bory & Dur.	Troia	-	Western Sicily	3

Tab. 2: Plant features measured on 10 *Isoëtes* species (Mean values)

<i>Morphology and fertility characteristics</i>	<i>No. of species or hybrids</i>										
	1	2	3	4	5	6	7	8	9	10	11*
Number of leaves per rosette	11.5	11.0	7.2	13.5	15.5	13.0	11.4	12.2	22.0	17.0	36 G 5
Number of macrosporophylls per rosette	1.9	2.8	2.2	2.0	2.0	3.0	2.8	2.9	4.8	6.0	8 G 6
Number of microsporophylls per rosette	3.3	5.9	3.4	4.0	4.0	4.5	5.4	5.0	6.0	7.0	16 G 10
Number of spores per macrosporangium	31.1	47.1	47.7	47.0	63.0	53.0	53.9	50.2	72.0	30.0	128 G 40
Total root length (m)	2.4	1.8	1.9	-	-	-	1.8	2.9	-	-	-
Cormus width (mm)	8.2	7.3	6.3	8.5	18.3	11.6	10.1	9.4	14.6	8.0	28 G 2
Rosette surface area (cm ²)	20.7	13.4	9.4	9.1	26.8	11.0	15.0	25.8	89.1	19.0	274

*) Fossil *Isoëtes beestonii* (Retallack, pers. comm.)

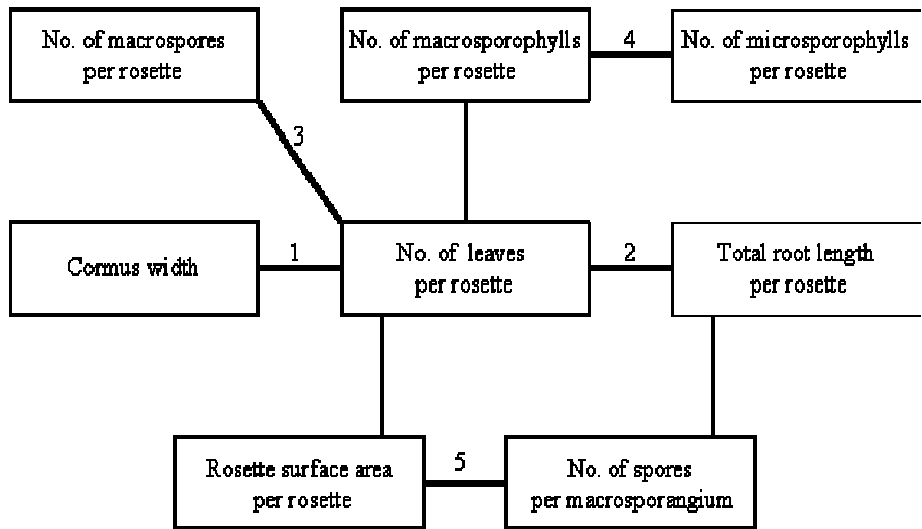


Fig. 1: Correlations established between plant features in *Isoetes lacustris*

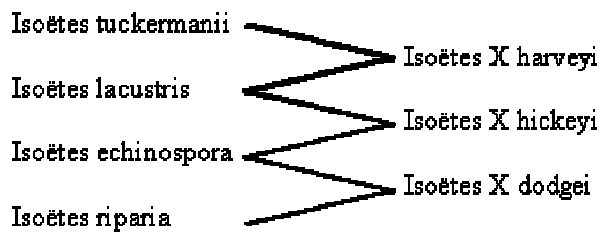


Fig. 2: Relationships between species and hybrids studied