ARTÍCULOS

Botanica Complutensis
ISSN-e 1988-2874

EDICIONES COMPLUTENSE

https://dx.doi.org/10.5209/bocm.75525

Habitat differentiation and geographic separation of *Isoetes velata* populations in central Iberian Peninsula

José Antonio Molina[1]

Abstract. Populations of *Isoetes velata* were studied in order to provide more information on their habitat and distribution in the Western and Northwestern Iberian Peninsula. Habitat together with morphology of megaspores were used as diagnostic features. The form *I. velata* subsp. *velata* f. *lereschii* is considered here as a synonym of *I. velata* subsp. *asturicense* and therefore only two taxa remain within the species: *I. velata* subsp. *velata* and *I. velata* subsp. *asturicense*. Intermediate individuals have been found in the Western Central System. The differentiation within the *I. velata* group appears to be the result of gradual genetic divergence after isolation. Palaeobotanical data confirm the presence of *I. velata* subsp. *asturicense* in Late Glacial lake sediments in northwestern Spain. Cluster classification of the soft-water vegetation with *Isoetes velata* subsp. *asturicense* revealed two main groups in the Spanish Central System. A single association, the *Sparganio angustifolii-Callitrichetum fontqueri* which includes Iberian Atlantic stands of *Sparganium angustifolium* and *Isoetes velata* subsp. *asturicense*, is here recognized. Besides, a variant of the association with *Eleocharis acicularis* is identified in shallow temporary waters in the Western Sierra de Gredos.
Keywords: glacial lakes, Iberian Peninsula, Isoetaceae, soft-water vegetation, spore morphology.

[es] Diferenciación de hábitat y separación geográfica de poblaciones de *Isoetes velata* en la Península Ibérica central

Resumen. Se han estudiado poblaciones de *Isoetes velata* con el fin de aportar información sobre su hábitat y distribución en el oeste y noroeste de la Península Ibérica. El hábitat junto con la morfología de las megasporas se utilizaron como caracteres diagnósticos. La forma *I. velata* subsp. *velata* f. *lereschii* se considera aquí como sinónimo de *I. velata* subsp. *asturicense* y, por lo tanto, solo quedan dos taxones dentro de la especie: *I. velata* subsp. *velata* e *I. velata* subsp. *asturicense*. Se han encontrado individuos intermedios en el Sistema Central occidental. La diferenciación dentro del grupo *I. velata* parece ser el resultado de una divergencia genética gradual después del aislamiento. Los datos paleobotánicos confirman la presencia de *I. velata* subsp. *asturicense* en sedimentos de lagos del Tardiglaciar en el noroeste de España. La clasificación numérica de la vegetación con *Isoetes velata* subsp. *asturicense* reveló dos grupos principales en el Sistema Central español. Se reconoce aquí una única asociación, *Sparganio angustifolii-Callitrichetum fontqueri*, que incluye comunidades atlánticas ibéricas de *Sparganium angustifolium* e *Isoetes velata* subsp. *asturicense*. Además, se identifica una variante de la asociación con *Eleocharis acicularis* en aguas temporales poco profundas de la Sierra de Gredos Occidental.
Palabras clave: lagos glaciares, Península Ibérica, Isoetaceae, vegetación de aguas oligotróficas, morfología de esporas.

Introduction

Isoetes velata/*longissima* group is a species complex in which genetic investigations could probably clarify the taxonomy of the including taxa (Troia & Rouhan 2018). In this work, the taxonomic criterion of Flora iberica (Prada 1986) is followed. *Isoetes velata* A. Braun in Bory & Durieu has the highest infra-specific diversity in Europe (Derrick et al. 1987). Within this taxon two subspecies have been described in the Iberian Peninsula (Prada 1986): *I. velata* subsp. *velata* and *I. velata* subsp. *asturicense* (Laínz) Rivas-Martínez & Prada, both of them with the lowest chromosome number found in the genus (2n=22). The two subspecies have been distinguished by size and sculpture of megaspores. According to Prada (1986), *I. velata* subsp. *velata* has megaspores of diameter 380-470 μm with a tuberculate perisporium. By contrast, *I. velata* subsp. *asturicense* has megaspores 325-410 μm in diameter with a smooth or slightly tuberculate proximal side. Additionally, *Isoetes velata* subsp. *velata* f. *lereschii* (Reichb. fil.) Prada has been described. This taxon has been characterized by small leaves (from 5 to 15 cm) with few fibrous subepidermic fascicles, thin cell walls and few stomata. Their megaspores are ornamented with sharp tubercles (Rivas-Martínez et al. 1982).

Infraspecific taxa of *Isoetes velata* have been also supported by both habitat and distribution features. *I. velata* group forms part of two different communities within the phytosociological classes *Isoeto-Littorelletea* and *Isoeto-Nanjuncetea*. The former includes the Holartic perennial amphibious vegetation from fresh meso-oligotrophic water. Species of Boreal and Atlantic distribution are included in this class (Schaminée et al. 1992). Soft-water vegetation in the Iberian mountains (*Littorellion*) encompasses isoetid vegetation growing in clear, permanent, oligotroph-

[1] Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, c/ José Antonio Novais 12, 28040-Madrid (Spain)
E-mail: jmabril@ucm.es
ORCID: http://orcid.org/0000-0003-4348-6015

ic, carbon-deficient and low-alkalinity waters, within which *Isoetes velata* subsp. *asturicense* has been cited as characteristic species in the NW ranges of the Iberian Hesperic Massif (Molina et al. 1999, Molina 2017) usually at glacial lake shores (Prada 1986). On the other hand, *Isoetes velata* subsp. *velata* occurs in Mediterranean Ibero-Atlantic temporary waters (*Isoetion*, *Isoeto-Nanojuncetea*) forming part of ephemeral amphibious vegetation consisting of therophytes and geophytes (Molina 2005; Molina 2017). The type form lives in shallow fresh water ponds and lakes. The habitat for the *lereschii* form has been related to oligotrophic ponds and lakes from Central Sierra de Gredos (Prada 1983) where it was considered to be endemic (Rivas-Martínez et al. 1982). It is worth noting that amphibious communities are the most important vegetation target for conservation in Iberia related to oligotrophic environments with a bioclimatic Atlantic distribution (Benavent et al. 2014).

Based on morphometric differences together with other distinguishing characteristics as habitat, Romero & Real (2005) have suggested that *I. asturicense* (Laínz) Laínz should be considered as separate species of *I. velata*. In this work, megaspore characteristics and habitat attributes in *Isoetes* populations from the western Iberian Peninsula, where both *I. velata* susbp. *velata* and *I. velata* subsp. *asturicense* have been cited (Rivas-Martínez et al. 1982; Castroviejo et al. 1983; Casaseca et al. 1988), are examined. Results will provide more information about *Isoetes velata* variability with possible taxonomical implications. Palaeobotanical information is also discussed (Maldonado 1994).

Methods

Populations of *Isoetes* at ten locations were studied (Table 1, Fig. 1). Four of them corresponded to glacial lakes either from the northern slope of western Sierra de Gredos (location 2, 3, 4 and 6) or from Montes de León (location 7). Two other sites (1 and 5) were high mountain wetlands. The remaining three localities were temporary ponds located at Sierra de Guadarrama piedmont (8, 9) or in central-western lowlands (10). Nine megaspores of each of three different individuals from each population were measured with a Nikon SMZ-2T stereomicroscope. The ornamentation of the megaspores was observed under the scanning electron microscope (ISI-SX25). *Isoetes* megaspores from Late Glacial sediments of the Sierra de Queixa-Manzaneda (Orense, NW Spain) were also studied.

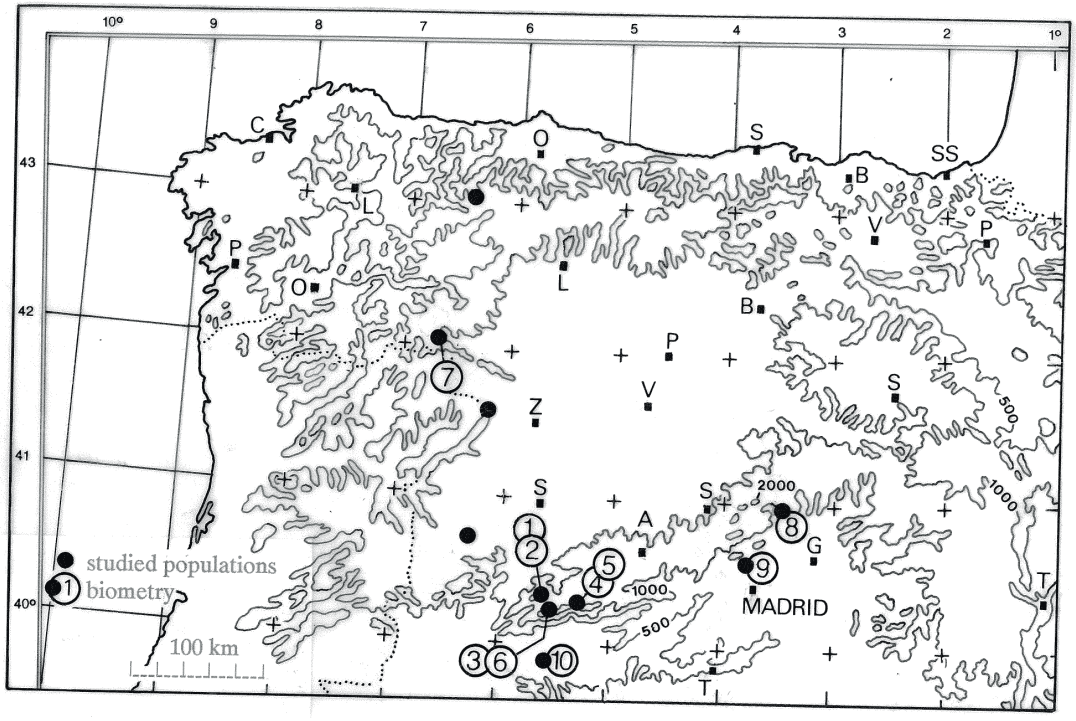

Fig. 1. Geographical location of the study populations. For sites description see Table 1.

A total of 27 published and unpublished phytosociological relevés collected in the Spanish Central System, were gathered (Appendix 1). An agglomerative classification method was applied using the b-flexible linkage method (b = 0.25) with Sørensen distance performing with the program JUICE 7.0 (Tichý 2002). Percentage cover values were square-root transformed in order to reduce the importance of dominant species. The crispness of classification was checked using the method in Botta-Dukát et al. (2005).

Results

Table 1 shows the results obtained in the morphological study of the megaspores. Populations above 1790 m had megaspores of 280-460 µm size. The sculpture varied from homogenous populations with megaspores slightly tuberculate (Fig. 2, a-b) to mixed populations with individuals with slightly tuberculate megaspores and individuals with megaspores clearly tuberculate (Fig. 2, c-d). The Late Glacial megaspores from Sierra de Queixa-Manzaneda (1360 m) appeared smooth and were 300-360 µm in diameter. All these populations are assigned to *Isoetes velata* subsp. *asturicense*, and consequently this taxon shows higher megaspore variability than hitherto known. The individuals from Laguna Grande de Gredos (1950 m) are a clear example. The range of their megaspore size (360-460 µm) matches the overlap of both subspecies (380-410 µm) as indicated by Prada (1986), though it is closer to the high-mountain subspecies. The populations below 1300 m always had strongly tuberculate megaspores between (340-) 360-480 µm (Fig. 2, e-f). Thus, we consider *I. velata* subsp. *velata* f. *lereschii*, described from Sierra de Gredos ("*in aquis puris lacunae inferior*"), as a synonym of *I. velata* subsp. *asturicense*.

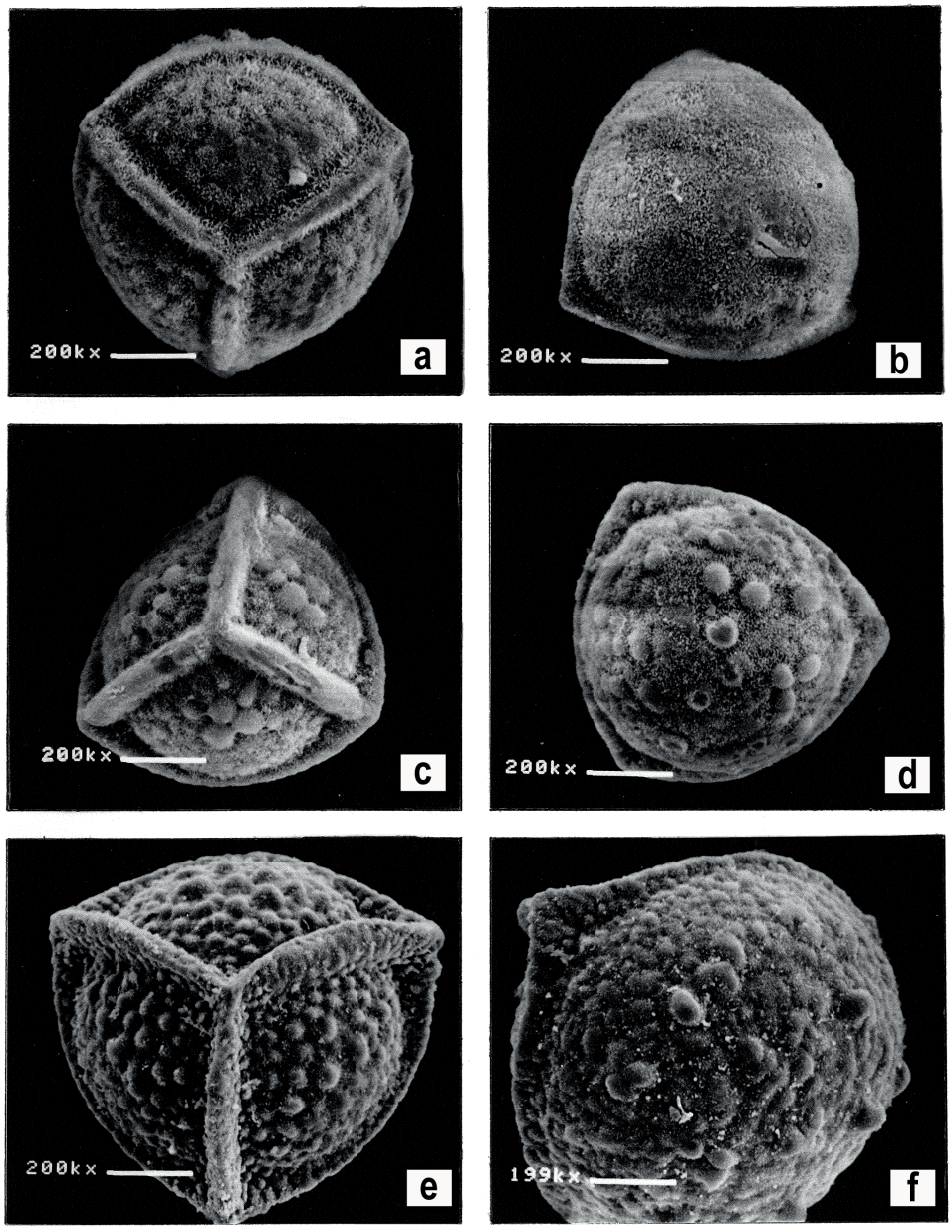

Fig. 2. *Isoetes velata* subsp. *asturicense*. Ávila, Sierra de Béjar, Solana de Ávila, lagunas del Trampal (MAF 145958): a) megaspore in proximal view; b) megaspore in distal view. Ávila, Sierra de Béjar, Solana de Ávila, charcas de Trochagosta (MAF 145956): c) megaspore in proximal view; d) megaspore in distal view. *Isoetes velata* subsp. *velata*: Madrid, Embalse de Santillana (MAF 792243): e) megaspore in proximal view; f) megaspore in distal view. Scale bar = 100 µm.

The clusters resulting from the hierarchical classification of the soft-water vegetation with *I. velata* subsp. *asturicense* in the Spanish Central System can be interpreted floristically and ecologically. They were arranged in two groups (A, B) according to the crispness of the classification (Table 2). Group A included 22 relevés and was characterized by a high frequency of *Sparganium angustifolium* Michx. It occurred mainly in slightly fluctuating shores of oligotrophic glacial lakes on acidic gley soils (Fig. 3a). Group B encompassed 5 relevés and was characterized by a high frequency of *Eleocharis acicularis* (L.) Roem. & Schult. and moss layer. It was found in shallow hollows temporarily flooded in the western Sierra de Gredos (Fig. 3b).

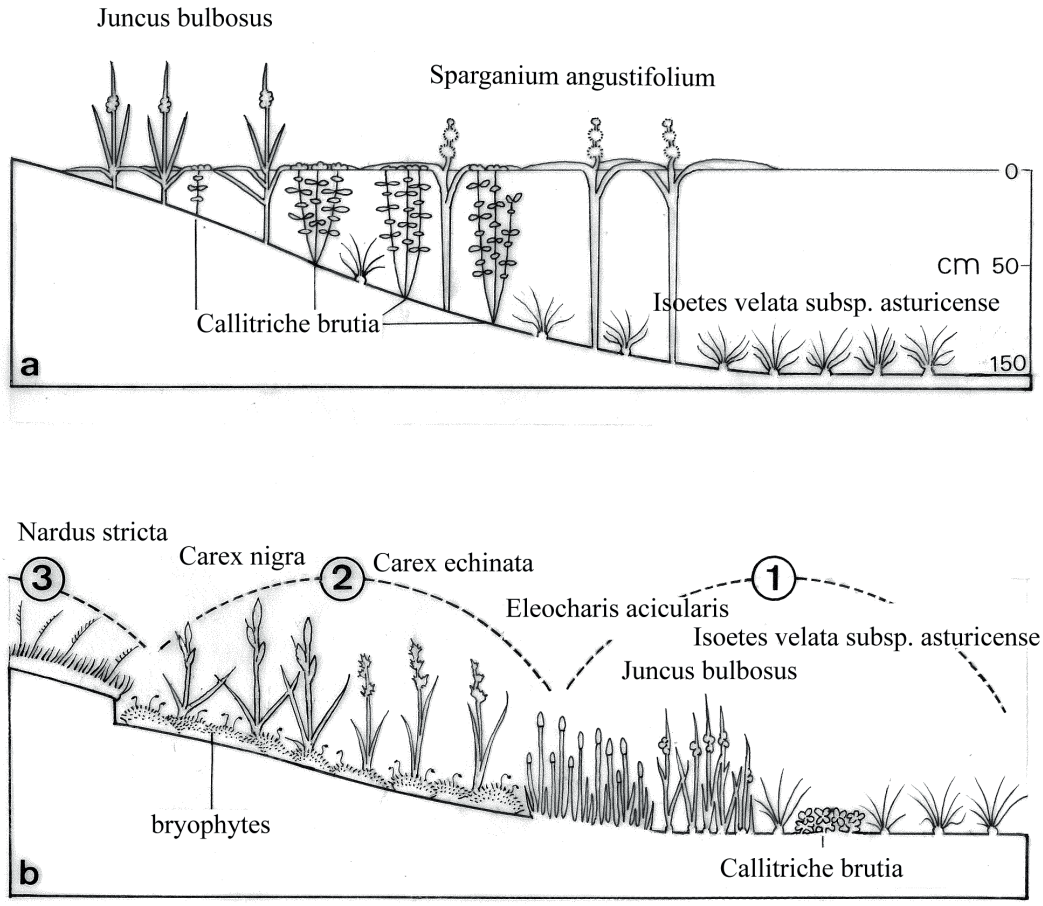

Fig. 3 Sectional views of the amphibious vegetation with *Isoetes velata* subsp. *asturicense* in the Spanish Central System: a) laguna de los Caballeros, a permanent glacial lake, *Sparganio angustifolii-Callitrichetum fontqueri* var. with *Isoetes velata* subsp. *asturicense*; b) lagunas del Trampal, a seasonal infilled pond, 1: *Sparganio angustifolii-Callitrichetum fontqueri* var. with *Eleocharis acicularis*, 2: *Caricetum carpetanae*, 3: *Poo legionensis-Nardetum strictae*.

Discussion

Clinal variation is one of the major patterns in the specific variation observed in *Isoetes* megaspore ornamentation (Hickey 1986). The variability in the megasporal sculpture of *Isoetes velata* in northwestern Iberia can be related to the altitudinal gradient. The lower elevation populations always have strongly tuberculate megaspores whereas those populations with slightly tuberculate megaspores only occur in the high mountain. Mixed populations including individuals of both phenotypes have also been observed at high altitudes (Table 1). The strong tuberculation of some individuals from these populations might be explained by the variability that *Isoetes velata* subsp. *asturicense* shows in the Central System. There is a wide variability not only in the sculpturing but also in the size of the megaspores, even at nearby sites. This explains why different authors identified two different high mountain taxa in the Central System (*I. velata* subsp *asturicense* and *I. velata* subsp. *velata* f. *lereschii*). It is noteworthy that *Isoetes velata* subsp. *velata* f. *velata* has not been found at any western high mountain site.

Other diagnostic characters such as the presence of stomata and fibrous subepidermic fascicles are related to exposure to air during leaf development (Kott & Britton 1985). *Isoetes velata* subsp. *velata*, with its abundant stomata and numerous fibrous subepidermic fascicles, is better adapted to amphibious

conditions, while *I. velata* subsp. *asturicense*, with few stomata and less abundant and poorly developed fascicles (Prada 1986) is more restricted to submerged habitats. These features as well as the ecological affinity suggest the form *lereschii* is closer to the subspecies *asturicense*.

Hickey et al. (1989) suggest that the genus *Isoetes* is presently undergoing a quick and continuous speciation in two ways, one gradual and other sharp. Most of the terrestrial species appearing in isolated populations of basic diploids seem to be the result of a gradual speciation via isolation and genetic divergence, while some of the aquatic species, frequently in mixed populations with different ploidy levels, seem to have evolved abruptly via interspecific hybridization and chromosome duplication (Taylor & Hickey 1992). Both subspecies within the *Isoetes velata* group have a basic diploid chromosome number, which suggest a gradual separation by isolation of common ancestral populations. The different ecology of both taxa points out an important role of habitat in the process of divergence.

The diversification of *I. velata* in northwestern Iberia might be explained by the isolation of some populations as a result of climatic changes. During the several Quaternary glacial ages this taxon retreated to the southwestern lowlands, though some populations might have found refuge in lakes and ponds in the northern Plateau (Fig. 4). Megaspores of *Isoetes* type *asturicense* have been identified from Late Glacial sediments (13,000-10,000 years BP) from a glacial lake in northwestern Spain (Maldonado 1994), which implies the presence of a taxon already adapted to permanent and oligotrophic waters that during the Lateglacial Interstadial (13,000-11,000 years BP) and Holocene climatic amelioration (last 10,000 years) would have reached higher altitudes by colonizing the western glacial lakes. Thermophilous populations might have extended from southwestern lowlands in warm and humid periods, recolonizing its former area. The high mountain taxon seems to be in regression in comparison to earlier, colder periods. The presence of intermediate features in some specimens from the Central System might be the result of the contact between both taxa throughout the Holocene. The isolation of populations in the Cantabrian Range explains the presence of only typical individuals of *I. velata* subsp. *asturicense* in these mountains.

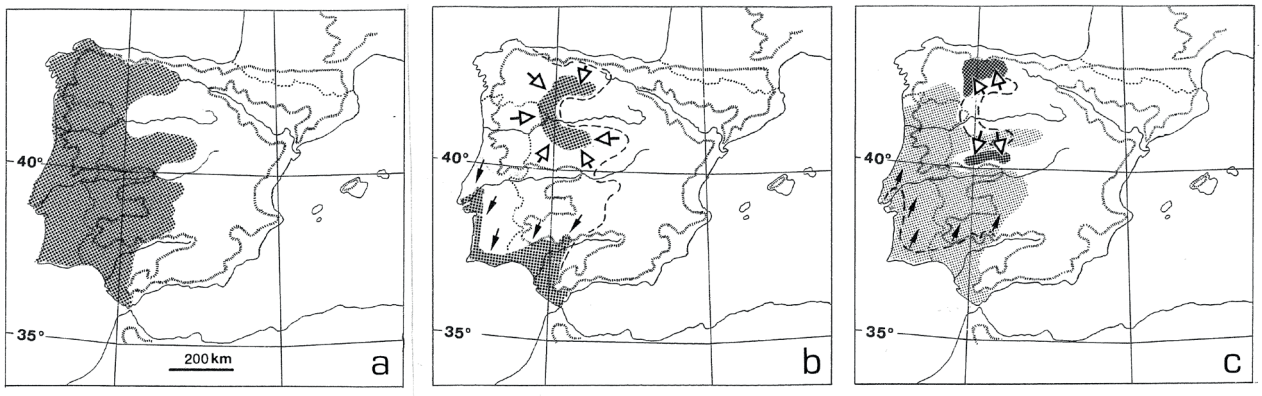

Fig. 4. Hypothetical changes in the distribution range of *Isoetes velata* during the last glacial-interglacial cycle in the Iberian Peninsula: a) warm periods before or during the last glaciation; b) cold periods during the last glaciation; c) present day distribution. Hollow arrows show the altitudinal shift in high mountain populations and filled arrows show the possible migration routes of the lowland populations.

The two identified subspecies within *Isoetes velata* showed the habitat as a diagnostic feature. The high-mountain subspecies (*Isoetes velata* subsp. *asturicense*) occurred typically in submerged and amphibious communities of *Isoeto-Littorelletea* whereas the lowland one (*Isoetes velata* subsp. *velata*) was found in amphibious ephemeral communities of *Isoeto-Nanojuncetea*. Since it is only considered the occurrence of one high-mountain taxon namely *I. velata* subsp. *asturicense* in the present study, all the communities of the Spanish Central System correspond to a single phytosociological association: the *Sparganio angustifolii-Callitrichetum fontqueri*, which was described from Cantabrian Mountains (Molina et al. 1999). This association therefore includes the Ibero-Atlantic stands of *Sparganium angustifolium* and *Isoetes velata* subsp. *asturicense* with other soft-water flora. A variant of the association with *Eleocharis acicularis* is found in shallow temporary waters in the Western Sierra de Gredos.

Nomenclatural summary

Isoetes velata A. Braun in Bory & Durieu, Expl. Sci. Algérie, Atlas, pl. 37 fig. 1(1849)

I. velata subsp. *velata*

I. velata subsp. *asturicense* (Laínz) Rivas-Martínez & Prada

≡ *I. boryana* subsp. *asturicense* Laínz in Bol. Inst. Estud. Asturianos Supl. Ci. 15: 6 (1970)

≡ *I. asturicense* Laínz (Laínz), An. Soc. Brot. 39: 118 (1973)

= *I. boryana* var. *lereschii* Rchb.f. ex Leresche & Levier, Deux Excurs. Bot. 118 (1881)

≡ *I. velata* subsp. *velata* f. *lereschii* (Reichb. fil.) Prada in Rivas-Martínez & col., Lazaroa 3: 33 (1981)

≡ *I. velata* var. *lereschii* (Rchb.f. ex Leresche & Levier) Molina Abril & Sard. Rosc., Guineana 10: 346 (2004)

Specimens examined

I. velata subsp. *asturicense*

Asturias: Arvás-Leitariegos, 30-VII-1976, *Pardo & Prada* (MAF 146920). Ávila: Puerto de Castilla, Laguna del Barco, 1800 m, 30TTK8556, 4-VIII-1991, *Sardinero & Molina Abril* (MAF 145955). Solana de Ávila, Sierra de Béjar, Lagunas del Trampal, 2130 m, 30TTK6865, 5-VIII-1990, *Sardinero* (MAF 145954). Ibídem, 5-VIII-1991, *Sardinero & Molina Abril* (MAF 145958). Sierra de Gredos, Prado de las Pozas, 30TUK0960, 25-VII-1958, *Rivas Goday & Rivas-Martínez* (MAF 66583). Sierra de Béjar, Solana de Ávila, charcas de Trochagosta, 2210 m, 30TTK6965, 5-VIII-1990, *Sardinero* (MAF 145956). Navalperal de Tormes, Laguna Grande de Gredos, 30TUK0658, 18-IX-1976, *Prada* (MAF 146396). Ibídem, 8-VII-1993, *Sardinero* (MAF 146918). Solana de Ávila, Laguna Negra, 2070 m, 30TTK6964, 5-VIII-1994, *González Canalejo & Sardinero* (MAF 145957). Navalguijo, Laguna de los Caballeros, 2080 m, 30TTK7955, Herb. S. Sardinero.

I. velata subsp. *velata*

Cáceres: Navalmoral de la Mata, 30STK81, 28-V-1983, *Rico* (MAF 123534). Madrid: Estación de Gargantilla de Lozoya, charcas temporales, 1100 m, 30TVL3935, 13-VI-1985, *Molina, Pangua & Prada* (MAF 124906). Embalse de Santillana, entre Chozas y Manzanares, 30TVL2907, VII-1954, *Rivas & Borja* (MAF 79243). Salamanca: Tenebrón, Laguna Grande, 29TQF20, 12-VI-1990, *Rico & Giráldez* (MAF 143612). Zamora: Ribadelago, en el lago de S. Martín, 1300 m, 29TNG86, 30-VII-1976, *Prada* (MAF 146397). Castro de Alcañices, arroyo de la Ribera, 29TQG3408, 5-VI-1991, *Casaseca, Rico & Giráldez* (MAF 143614).

Acknowledgements

I would like to thank to Salvador Rivas-Martínez and Carmen Prada for their valuable comments on the manuscript.

References

Benavent-González, A., Lumbreras, A., Molina, J.A. 2014. Plant communities as a tool for setting priorities in biodiversity conservation: a novel approach to Iberian aquatic vegetation. Biodivers. Conserv. 23: 2135-2154. DOI 10.1007/s10531-014-0709-3.

Botta-Dukát, Z., Chytrý, M., Hájková, P. & Havlová, M. 2005. Vegetation of lowland wet meadows along a climatic continentality gradient in central Europe. Preslia 77: 89-111.

Casaseca, B., Guráldez, X. & Rico, E. 1988. Precisiones florísticas sobre la alta montaña extremeña. Monogr. Inst. Pirenaico Ecol. 4: 143-147.

Castroviejo, S., Nieto, G. & Rico, E. 1983. Notas y comentarios sobre la flora del Sistema Central español: sierras de Villafranca, El Barco y Béjar. Anales Jard. Bot. Madrid 40: 151-161.

Derrick, L.N., Jermy, A.C. & Paul, A.M. 1987. Checklist of European pteridophytes. Sommerfeltia 6: V-XX; 1-94.

Hickey, R.J. 1986. *Isoëtes* megaspore surface morphology: nomenclature, variation and systemaic importance. Amer. Fern. J. 76: 1-16.

Hickey, R.J., Taylor, W.C. & Luebke, N.T. 1989. The species concept in Pteridophyta with special reference to *Isoëtes*. Amer. Fern. J. 79: 78-89.

Kott, L.S. & Britton, D.M. 1985. Role of morphological characteristics of leaves and the sporangial region in the taxonomy of *Isoetes* in northeaster North America. Amer. Fern J. 75: 44-55.

Maldonado, F.J. 1994. Evolución Tardiglaciar y Holocena de la vegetación en los macizos del noroeste peninsular. Tesis Doctoral E.T.S.I. de Montes. Universidad Politécnica de Madrid, Madrid. 171 pp.

Molina J.A. 2005. The vegetation of temporary ponds with Isoetes in the Iberian Peninsula. Phytocoenologia 35(2-3): 219-230.

Molina, J.A. 2017. Aquatic and Wetland Vegetation of the Iberian Peninsula. In: Loidi, J. (ed.), The Vegetation of the Iberian Peninsula vol 2: 355-396. Springer

Molina, J.A., Sardinero, S. & Pertíñez, C. 1999. Soft-water vegetation (Littorellion) in Spanish mountains. Folia Geobot. 34: 253-260.

Prada, C. 1983. El género *Isoetes* L. en la Península Ibérica. Acta Bot. Malacitana 8: 73-100.

Prada, C. 1986. *Isoetes* L. In: Castroviejo, S. et al (eds.). Flora iberica 1: 15-20. Real Jardín Botánico. CSIC. Madrid

Rivas-Martínez, S., Costa, M., Izco, J. & Sáenz, C. 1982. Flora Matritensis, I (Pteridophyta). Lazaroa 3: 25-61.

Romero, M.I. & Real, C. 2005. A morphometric study of three closely related taxa in the European *Isoetes velata* complex. Bot. J. Linn. Soc. 148: 459–464. https://doi.org/ 10.1111/j.1095-8339.2005.00419.x

Schaminée, J.H.J, Westhoff, V. & Arts, G.H.P. 1992. Die Strandlinggesellschaften (Littorelletea Br.-Bl. & Tüxen 1943) der Niederlande in europäischem Rahmen gefatβt. Phytocoenologia 20: 529-558.

Taylor, W.C. & Hickey, R.J. 1992. Habitat, evolution and speciation in *Isoetes*. Ann. Missouri Bot. Gard. 79: 613-622.

Tichý, L. 2002. JUICE, software for vegetation classification. J. Veg. Sci. 13: 451–453.

Troia, A. & Rouhan, G. 2018. Clarifying the nomenclature of some Euro-Mediterranean quillworts (*Isoetes*, *Isoetaceae*): Indicator species and species of conservation concern. Taxon 67: 996–1004.

Table 1. Size and ornamentation of megaspores of 10 *Isoetes* populations located in the western Iberian Peninsula.

Site		Altitude (m)	Megaspore diameter (µm)	Tuberculation (#)	Taxon
1	Charcas de Trochagosta	2210	300-350	*/**	*Isoetes velata* subsp. *asturicense*
2	Lagunas del Trampal	2130	280-340	*	*Isoetes velata* subsp. *asturicense*
3	Laguna de los Caballeros	2080	320-390	*	*Isoetes velata* subsp. *asturicense*
4	Laguna Grande de Gredos	1950	360-460	*/**	*Isoetes velata* subsp. *asturicense*
5	Prado de las Pozas	1910	320-380	*	*Isoetes velata* subsp. *asturicense*
6	Laguna del Barco	1790	340-380	*/**	*Isoetes velata* subsp. *asturicense*
7	Lago de S. Martín	1300	400-480	**	*Isoetes velata* subsp. *velata*
8	Gargantilla de Lozoya	1140	380-460	**	*Isoetes velata* subsp. *velata*
9	Embalse de Santillana	900	360-420	**	*Isoetes velata* subsp. *velata*
10	Navalmoral de la Mata	280	360-400	**	*Isoetes velata* subsp. *velata*

(#) * = slightly tuberculate; ** = strongly tuberculate

Table 2. Synoptic table of the soft-water vegetation with *Isoetes velata* subsp. *asturicense* in the Spanish Central System, showing the frequency values of species in each of the 2 vegetation groups (columns) obtained in the classification analysis (full table in Appendix 1). Only species with a frequency ≥ 20% in at least one group are included. Dark-grey and light-grey shaded values indicate diagnostic species with high (Φ > 0.5) and moderate fidelity (Φ > 0.25), respectively.

Group	A	B
Nº relevés	22	5
Isoetes velata subsp. asturicense	100	100
Sparganium angustifolium	95	0
Juncus bulbosus	23	60
Eleocharis acicularis	0	100
Antinoria agrostidea subsp. natans	27	0
Subularia aquatica	27	0
Callitriche brutia	68	20
moss layer	9	80
Carex nigra	0	20

Appendix 1. Soft-water vegetation with *Isoetes velata* subsp. *asturicense* in the Spanish Central System. *Sparganio angustifolii-Callitrichetum fontqueri*: typical variant (Group A, rel. 1-22); variant with *Eleocharis acicularis* (Group B, rel. 23-27).

No. order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Altitude (m x 10)	206	206	206	206	207	190	206	198	198	206	207	193	193	198	193	203	210	214	214	214	214	210	214	214	214	214	214
Area (m^2)	2	4	4	4	4	4	4	2	2	2	0.5	1	1	2	1	4	2	2	2	2	2	2	1	1	1	1	1
Group (see Table 2)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B
Characteristic and differential species:																											
Isoetes velata subsp. asturicense	5	5	5	3	4	3	4	2	4	5	3	3	5	3	2	2	4	1	2	2	1	+	4	3	3	3	3
Sparganium angustifolium	.	3	2	3	4	3	+	2	3	1	3	2	+	3	4	3	3	2	2	2	2	1	.	.	.	.	.
Juncus bulbosus	.	.	.	.	+	+	2	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	2	1	3	.	.
Eleocharis acicularis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	3	4	4
Antinoria agrostidea subsp. natans	.	.	.	.	.	.	.	.	.	.	2	3	3	1	1	2	.	.	.	.	.	.	.	.	.	.	.
Subularia aquatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	3	2	1	4	.	.	.	.	.
Accompanying:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Callitriche brutia	.	.	.	.	+	2	2	2	2	2	2	+	1	2	.	.	3	2	1	2	2	.	1	.	.	.	.
moss layer	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	2	1	.	3	3
Alopecurus aequalis	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Drepanocladus exannulatus	.	.	.	.	2	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Philonotis fontana	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum inundatum	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fontinalis antipyretica	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus peltatus	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.

Data sources: Ávila: 1-4, 7, 10, Navalguijo, Laguna de los Caballeros (Sardinero, S. 2004. Flora y vegetación del macizo occidental de la Sierra de Gredos. Guineana 10:1-474); 5, 11, Navalperal de Tormes, Laguna Grande de Gredos (Rivas-Martínez, S. 1964. Estudio de la vegetación y flora de las Sierras de Guadarrama y Gredos. Anales Inst. Bot. Cavanilles 21: 5-325); 6, Navalperal de Tormes, arroyo de las Pozas (Rivas-Martínez 1964); 8-9, 14, Navalperal de Tormes, Laguna Grande de Gredos (Sardinero 2004); 12-13, 15, Navalperal de Tormes, arroyo de las Pozas (Sardinero 2004); 16, Solana de Ávila, Laguna Negra (Sardinero 2004). 17, 22, Solana de Ávila, lagunas del Trampal (Navarro, F., Sánchez, J.A. & Valle, C.J. 1979. Comentarios florísticos y ecológicos sobre *Subularia aquatica* L. Publ. Dep. Bot. Fac. Farm. Salamanca 1: 37-44); 23-27, Solana de Ávila, lagunas del Trampal.