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SYSTEMATICS, BIOGEOGRAPHY AND DIVERSIFICATION OF INDIAN QUILLWORTS (*ISOETES* L.)*

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A brief review of the Indian quillworts (*Isoetes* L.) including its systematics, diversification, evolution, biodiversity and conservation are presented.

Key words: *Isoetes*, biodiverstiy, systematics, megaspore.

The genus *Isoetes* L., a heterosporous lycopsid, consists of an underground rhizomorph bearing a rosette of simple, upright linear sporophylls. The genus is the sole living representative of the Isoetalean clade and occupies a unique position in land plant evolution. In recent years, the genus has been investigated on several counts including its physiology-CAM cycle (Keeley, 1998), DNA nucleotide sequences (Hoot & Taylor, 2001; Rydin & Wikstrom, 2002; Taylor, Lekschas, Wang, Liu, Napier & Hoot, 2004 and Hoot & Taylor (2004), its evolution (Pigg, 1992, 2001; Retallack, 1997; Srivastava, 2000; Srivastava & Srivastava, 2001) and the study of inter-specific hybrids (Britton & Brunton, 1995), in addition to several other aspects (Taylor & Hickey, 1992).

The genus needs further investigation in the remote areas for understanding its biodiversity and genome study including molecular analysis for evolving conservation strategies.

An attempt to provide a brief account of the main findings on the Indian quillworts has been made.

SYSTEMATICS

To date 16 species of the genus *Isoetes* have been reported from different parts of the Indian subcontinent. *I. coromandelina* was described by C.A. Linn (fil) in 1781 as the first report from the Coromandel coast, Tamil Nadu. After 150 years, *I. sahyadariensis*, the second species was described by Mahabale in 1938 from Panchgani in Maharashtra and Kalahattigiri, Bababudhangiri and other peaks of Sahyadris hills in Karnataka. This was followed by the discovery of two new species, *viz.*, *I. sampathkumaranii* and *I. dixitei* by Rao (1944) and

Fig.1 *I. divyadarshanii* Shukla, Srivastava & Shukla Lonawala, Pune, Maharashtra

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Fig.2 Plants of *Isoetes* L. growing in natural localities, A, *I. reticulata* Bharadwaj & Jena Atru, Kota, Rajasthan: B, C, *I. mahadevensis* Srivastava, Pant & Shukla, Chhota Mahadev, Pachmarhi, M.P.; D, *I. coromandelina* L. Raipur, M.P.; E, *I. dixitei* Shende Panchgani, Table-land, Maharashtra; F, *I. panchganiesis* Srivastava, Pant & Shukla Panchgani, Table-land, Maharashtra

Shende (1945) from the Lalbagh Botanical Garden, Bangalore in Karnataka and Panchgani, in Maharastra respectively. After a gap of 17 years, Pant & Srivastava (1962) published a comprehensive review on the genus *Isoetes* and described two new species, e.g., *I. indica* and *I. panchananii* from Ram Nai, Rewa, Madhya Pradesh. Subsequently, in a span of 50 years, 10 more new species have been added to the existing 6 raising the total number of species to sixteen. At present, the state-wise distribution of *Isoetes* species are as follows: three species from Madhya Pradesh: *I. pantii* Goswami & Arya (1970), *I. bilaspurensis* Panigrahi (1981), *I. mahadevensis* Srivastava, Pant & Shukla (1993), from Narsinghgarh, Bilaspur and Pachmarhi respectively; three species from Rajasthan: *I. tuberculata* Gena & Bhardwaja, *I. reticulata* Gena & Bhardwaja, *I. rajasthanensis* Gena & Bhardwaja (1984), the first two species from Atru, Kota and the last one from Mount Abu; two species from Maharashtra: *I. panchaganiensis* Srivastava, Pant & Shukla (1993) from Panchgani and I. *divyadarshanii* Shukla, Srivastava & Shukla (2005) from Lonawala respectively : I. *udupiensis* Shukla, Srivastava, Shukla & Rajagopal (2005) from Udupi (Dakshina Kannada), Alevoon, Karnataka and one from Manipur: *I. debii* Sinha (1992) from Manyang, Imphal.

Isoetes species are distinguished on the basis of a number of characters, but the following characters need special mention because of their prime importance in the delineation of species.

KEY CHARACTERS

(I) Main characters:

(i) Megaspores (ii) Microspores (iii) Velum coverage (iv) Peripheral strands (v) Rhizomorphs (corms)

(II) Subsidiary characters:

(i) Chromosome numbers (ii) Ligules, labia, scales and phyllopodia (iii) Length of plants (iv) Number of leaves (v) Size of sporangia (vi) Habit and habitat

(III) Recent studies: rbcL sequence

I- Main characters

(i) Megaspores

The megaspore is the most important parameter which can be used to distinguish different species. Most Indian species have been mainly "created" on the basis of the ornamentation of the megaspore. The main ornamentation pattern of the megaspores in Indian species is either tuberculate or reticulate (Srivastava *et al.* 1995). All species from India fall in these two categories with some variations. Further investigation of different populations of a species has revealed that the ornamentation of megaspores and size of megaspores varies within the same population (Srivastava *et al.* 1992). As such, it has put a question mark on the reliability of this character. Of late scientists have started questioning the single character taxonomy (Hickey, 1986).

While the megaspores of some species, e.g., *I. coromandelina* exhibit perceptible variation within the same population (see, Srivastava *et al.* 1993) on the other hand the megaspores of *I. panchganiensis I. udupiensis* and *I. divyadarshanii* exhibit least variation.

This has not lowered the importance of the megaspore but has given signals to scientists that this character should not be used arbitrarily but with caution. It is still one of the most important characters, which gives the first hand distinction between different species. The size and variation in the ornamentation of megaspores provide important clues about its genetic constitution and purity. However, it needs to be supplemented with other characters.

A species should not be based on a single character as the practice has been. The full range of the variation of the primary and secondary characters of megaspores, including TEM and SEM studies, should be taken into consideration before determining the status of a species (Tryon & Lugardon 1991). Though these studies are utmost important, yet they are not very decisive in the delineation of different species. This has necessitated the reassessment of all Indian species to determine their genuineness especially these which are based only on the megaspore character.

(ii) Microspores

Out of 16 species of *Isoetes*, the microspores of only eleven species are known. The microspores of all the investigated species are echinate. But they differ in size and arrangement of spines. SEM studies of the microspores are very essential to have a complete picture of their ornamentation. The size, arrangement and density of spines of the microspores of each species present somewhat different patterns of arrangement of spines but the distinction is not sharp enough to use it for the delineation of different species. But *I. mahadevensis* and *I. udupiensis* can be distinguished from the rest of Indian species on the basis of their microspore ornamentation alone (Srivastava, 1995; Shukla *et al.* 2005).

The microspores of different populations of *I. coromandelina* are echinate but they exhibit a wide range of variation in the shape and size of the spines. These variations are the characteristic of the microspores of each population (Srivastava *et al.* 1996).

The microspore is an important taxonomic character but it has not been given due importance and has not been utilized to its maximum, despite its great taxonomic importance. One of the reasons, for the neglect of this character may have been its rarity and complete absence in some of the populations. In most of the populations, the plants are megasporangiate rarely a few plants are found with both micro-and megasporangia. However, there are few species with dominant microspory, e.g., *I. udupiensis*. But in every species both kinds of sporangia are present, one has only to scan a large number of plants of a population to spot out bisporangiate plants.

(iii, iv) Velum coverage and peripheral strands

In all the species belonging to the Section Palustres (Tuberculatae), the velum is absent except *I. dixitei* (in which the velum is rudimentary) and the peripheral strands are present. On the contrary, the species belonging to the section Terrestres (Reticulatae), the velum is present and peripheral strands are absent.

The velum may cover the entire sporangium leaving only a small opening at the base-fenestra (*I. panchganiensis, I. sahyadarinsis*) or varies from 1/4 to 3/4 (*I. panchananii, I. mahadevensis, I. reticulata, I. rajasthanensis, I. sampathkumaranii*). The number of peripheral fibrous strands varies in different species. They are of two types-primary and secondary. The peripheral fibrous strands are not strongly developed in *I. udupiensis* and *I. divyadarshanii*. The presence of peripheral strands in leaves appear to be closely linked to the habitat conditions depending upon whehter the plant is aquatic terrestrial or amphibious (Pfeiffer, 1922). Their absence in aquatic leaves perhaps reflects their reduced need of physical support.

(v) Rhizomorphs (Corms)

The number of lobes in a rhizomorph (corms) usually two lobed (in majority of species of the Section: Terrestres) or 3-4 lobed occasionally more lobed (in Section: Palustres), are important taxonomic characters.

(II) SUPPORTING CHARACTERS:

(i) Chromosome number:

The chromosome number is not very helpful in the distinction of different species, but the karyotype analysis may be decisive in some cases.

(ii) Ligules and Labia:

Ligules and labia are characteristic of species and they are strong supporting characters (Goswami, 1976; Sharma & Singh 1984, Bhu, 1992; Pant *et al.*, 2000).

Scales and Phyllopodia:

Scales are present in almost all species except *I. udupiensis* but phyllopodia are known so far only in *I. dixitei*. The scales of different species of *Isoetes* are distinguished from one another on the basis of their size and shape (Srivastava & Wagai, 1996).

(iii) Length of plants:

The size of plants varies within the same

species. But the average length of plants is characteristic and helpful in categorizing different species. For example, the plants of *I. coromandelina* may reach up to 80cm, while the maximum height of the plants of *I. sampathkumaranii, I. reticulata, I. rajasthanensis, I. panchganiensis* is never beyond 13cm.

(iv and v) Number of leaves and size of sporangia:

Helpful to some extent.

(vi) The habit and habitat:

Very important in order to determine the relationship between plants and environment.

Thus, in the final assessment of the species, the subsidiary characters play a vital decisive role.

(III) Recent Studies: rbcL Sequences

Amongst Indian quillworts, the knowledge of *I. coromandelina* is very crucial for understanding the evolution and diversification of the genus. It is one of the basic species of the genus. In recent years, Hoot & Taylor (2001) selected *I. coromandelina* as the root of their molecular trees based on three lines of evidences : "(1) preliminary rbcL data for selected species of *Isoetes* and lycopods, (2) previous morphological work suggesting that the more plesiomorphic character states and geographic distributions are found in section Coromandelina (Taylor & Hickey, 1992) molecular evolution in *Isoetes* appears to evolve in clock-like fashion."

REPRODUCTIVE BIOLOGY AND CHROMOSOME NUMBER

Ekambaram & Venkatanathan (1933) have described normal sexual reproduction, as well as, the regular formation of bivalents during meiosis in *I. coromandelina*. However, this observation needs confirmation. No report of sexual reproduction in any Indian species exits. Ninan (1958) has questioned the reliability of the observation of Ekambaran & Venkatanathan (1933). This is further corroborated by the cytological analysis made by Abraham & Ninan (1958), Ninan (1958), Verma (1960, 1961), Pant & Srivastava (1965). All of them have reported that meiosis is irregular in *Isoetes* and there is no reduction division. Both divisions are mitotic resulting in the formation of dimorphic megaspores. This may be one of the reasons for the absence of sexual reproduction in most of the Indian populations of *Isoetes*. In order to overcome sexual reproduction, the genus has evolved another strategy to compensate it by vegetative and apogamous reproduction. Pant & Srivastava (1965) and Goswami (1975a) have reported apogamous reproduction in *I. indica* and *I. pantii* respectively. Srivastava *et al.* (1996) have reported *in situ* germination in *I. panchganiensis* var *panchganiensis*, *I. mahadevensis*, and *I. coromandelina*. Goswami & Bhu (1998) and Goswami and Sharma (1995) have reported *in situ* germination of megaspores with archegonia inside microsporangia of *I. pantii* and Gena (1998, 2002) described *in situ* germination in Rajasthan material of *I. tuberculata*.From these accounts, it seems that the main mode of reproduction in the Indian quillworts is vegetative, by means of corms (rhizomorphs) or megaspores without fertilization (apogamous). Sexual reproduction could be occurring in some species of *Isoetes*.

Out of 16 species, the chromosome number of only 13 species are known.

The chromosomal data available show the presence of a polyploid series from 2x 2n=22+1f to 10x2n=110+1f. The presence of a fragment of chromosome in each population, so far investigated, seems to be the characteristic feature of Indian species of *Isoetes* except *I. udupiensis* and *I. divyadarshanii*, and *I. sampathkumaranii*.

I. coromandelina	2x(2n=22+1f) to 6x(2n=66+1f)
	2n=22+1, Abraham & Ninan (1958), Ninan (1958);
	2n=33+1, Abraham & Ninan (1958), Ninan (1958); Verma (1960, 1961); Pant & Srivastava (1965); Srivastava *et al.* (2002)
	2n=44+1 Pant & Srivastava (1965); Srivastava et al. (2002).
	2n=66+1 Srivastava *et al.*

	(2002)
I. dixitei	2x=(2n=22+1) to 6x (2n=66+1) Srivastava *et al.* (unpublished)
I. tuberculata	2x=(2n=33) Bhardwaj & Gena (1992) 2x=(2n=22+1) Tripathi & Yadav (2004)
I. sampathkumaranii	2x=(2n=66) Abraham & Ninan (1958)
I. indica	2x=(2n=44+1) Pant & Srivastava (1965)
I. panchananii	2x=(2n=44+1) Pant & Srivastava (1965) 2x=(2n=110+1) Vasudeva & Bir (1983)
I. reticulata	2x=(2n=55) Bhardwaj & Gena (1992) 2x=(2n=44+1) Tripathi & Yadav (2004)
I. rajathnensis	2x=(2n=44) Bhardwaj & Gena (1992) 2x=(2n=55+1) Tripathi & Yadav (2004)
I. pantii	2x(2n=36,39,46,48+2 or 3 extra chromosomes) Goswami (1975, 2001); Bhu & Goswami (1990)
I. panchganiensis	2x=(2n=33+1) Srivastava *et al.* (unpublished)
I. mahadevensis	2x=(2n=44+1) Srivastava *et al.* (1997)
I. divyadarshanii	2x= (2n=22) Shukla *et al.* (2005)
I udupiensis	2x= (2n=22) Shukla *et al.* (2005)

Out of 13 taxa investigated, 4 are diploids, 8 are tetraploids and 3 are hexaploids (based on published and unpublished data).

I. coromandelina is the most dynamic and stable species. It exhibits a wide range of variation in the chromosome number within the species. There are many factors which have made this species most viable and stable. But the chromosomal diversity appears to be the prime cause of its success. It has provided strength to survive in varied environmental conditions. Its triploid populations are the most robust, common and widespread. Tetraploids are restricted and hexaploids are very rare. Its diploid population is confined only to the Coromandel coast. The *I. dixitei* is diploid, teraploid and hexaploid, like *I. coromandelina* but confined only to its specific regions. The remaining species are tetraploids except *I. panchganiensis, I. reticulata* and *I. sampathkumaranii* which are triploid, pentaploid and hexaploid respectively. *I. pantii* is tetraploid with varying chromosome number (Goswami 1975b).

Thus, the chromosomal diversity of Indian quillworts is no less significant than the world quillworts. All the chromosomal data available throughout the world show the presence of a polyploid series from 2x (2n=22) to 12 x (2n=132) and 8 species to have intraspecific polyploidies. Out of 81 taxa whose chromosome numbers are reported, 27 are diploids, 30 are tetraploids and 13 natural hybrids (Takamiya, 1999).

Srivastava (1998) has grouped the Indian species into following three species complexes on the basis of general morphology of the plants and their megaspores.

I. *Isoetes coromandelina* complex

Section: Palustres (= Tuberculatae)

Species: *I. coromandelina, I. indica, I. pantii, I. tuberculata, I. debii*

I. udupiensis and *I. divyadarshanii* newly described species, also belong to this category.

II. *Isoetes dixitei* complex

Section: Palustres (= Tuberculata

Species: *I. dixitei, I sahyadriensis, I bilaspurensis*

III. *Isoetes panchananii* complex

Section: Terrestres (= Reticulatae)

Species *I. panchananii, I. sampathkumaranii, rajathanensis, I. reticulata, I. panchganiensis, I. mahadevensis*

Fraser-Jenkins (1997) has however, merged all the Indian species into a single species, i.e., *I. coromandelina* without making any detailed comparison of the key characters, like megaspore ornamentation, velum coverage, peripheral fibrous strands etc. of different species. It is unfortunate that he has simply done without giving any reason. This type of work infact should be done only by those workers who have developed a life-long expertise of the taxon. Pant & Srivastava (2000) have strongly criticized this merger. They have stated that "Fraser-Jenkins can hardly claim any expertise on the genus *Isoetes* except his view on the merger of different Indian species of *Isoetes* with *I. coromandelina* almost invariably suffixed with question mark indicate not only lack of confidence but also caution which he himself advocates". This stand of merging Indian species into one is un-natural, arbitrary and untenable.

BIODIVERSITY AND CONSERVATION

On the basis of floristic diversity, concentration of endemism climate and topography of the country, Nayar (1996) divided India into 20 phytogeographical divisions.

A few species of *Isoetes* have been listed in IUCN Red Data Book (Belousova & Denisova, 1992). But not even a single Indian species of *Isoetes* has been incorporated in the Red Data Book of Indian plants (Nayar & Sastry, 1987).

Despite its evolutionary importance, the genus has not been given due importance with reference to its conservation in India. Bir (1987), Dixit & Krishna (1990), Madhusoodan (1991) and Ghosh & Ghosh (1997) have discussed the conservation status of Indian species and expressed concern about their survival. Shukla *et al.* (2002) for the first time discussed in detail, the various aspects of conservation of Indian species of *Isoetes*.

Out of 20 phytogeographical divisions (PGDS) Indian species are known only from 11 PGDs. Out of 16 species 10 are local endemic, *I. sahyadriensis, I. dixitei, I. panchganiensis, I. pantii I. bilaspurensis, I. reticulata, I. tuberculata, I. debii I. udupiensis* and *I. divyadarshanii* and remaining 6 are of wider endemism. Excepting, *I. coromandelina* the all Indian species are under the "Threatened" or critically endangered category. There is not one, but many regions of diversification and radiation of *Isoetes* in the Indian subcontinent. The main centres of radiation are, the Coromandel coast, Tamil Nadu, Pachmarhi, M.P.; Panchgani, Maharashtra, and Atru, Rajasthan (see Shukla *et al.* 2002).

Since the quillworts are of no economic and medicinal value, they have not received due importance in terms of conservation despite their evolutionary significance. Plants are mercilessly uprooted to clean up the ponds for agriculture purposes. Even the type localities of a number of species are completely or partially destroyed. Table-land of Panchgani, which is the type locality of three species, viz, *I. sahyadriensis, I. dixitei* and *I. panchganiensis,* is no more a safe place for *Isoetes*. In the name of beautification it is completely renovated to attract tourists.

The same is the condition of *I. sampathkumaranii, I. bilaspurensis* and others. Immediate steps are needed not only to conserve the type localities but to protect all the places of their occurrence. Both *in situ* and *ex situ* conservation are necessary for their conservation in addition to implementation of National Plant Collection Scheme and creation of captivity centres for threatened species of all the groups. The diploid plants are very important to understand the evolution and diversification of the Indian quillworts. Diploid populations are very few and are on the decline. Special steps should be taken to conserve both the species and its diploid populations.

FOSSIL RECORD

Only 17 fossil species have so for been described from the Triassic to the Eocene in addition to some Isoetalean like plants (see Srivastava *et al.* 2004). The identity of some of these is doubtful (see Gvauvogel-Stamm & Lugardon, 2001). The first species of the genus, *Isoetes beestonii* Retallack was described by Retallack (1997) from the early Triassic

of Queensland, Australia. The diversification of the genus started from the Triassic but reached to its maximum during the Cretaceous. From India, only two fossil species namely, *Isoetites serratifolius* Bose & Roy (1964) and *Isoetites janaianus* Banerjee (1989) are described from the early Cretaceous, from Bhuj Formation, Gujarat.

The recent discovery of a number of heterosporous lycopods, e.g., *Clevelandodendron ohioensis* Chitaley & Pigg (1996) from the late Devonian of Ohio and *Longostachys latisporophyllus* Zhu, Hu & Feng emend Cai & Chen (1996) from the late Middle Devonian (Givetian) of China, *Sublepidodendron songziense* Chen emend (Sublepidodendraceae Krausel et Weyland) Wang *et al* (2002) from the Late Devonian of Hubei, China and *Lepidostrobus xinjiangensis* Wang, Li, Geng & Chitaley (2003) from the Upper Devonian of Xinjiang China has not only stretched the evolutionary thread of the isoetalean clade to the Middle Devonian but throws fresh light on the evolution, origin and diversification of the clade.

The knowledge of the Indian quillworts is still far from being complete. Its full knowledge is very essential to have a complete picture of the diversification and evolution of this unique genus.

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